Landscapes of the apes:

Modelling landscape use of chimpanzees and early hominins across an environmental gradient

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To Ruben and my mother

For their unconditional love, support, and belief in me

ABSTRACT

As primate habitat is declining rapidly, studying the flexibility of primates to adapt to changing landscapes is important. Landscape-scale studies of primate habitat use are, however, scant. Predictive models can provide important tools in investigating primate landscape use. Chimpanzees (*Pan troglodytes*) face habitat loss throughout their range, but their susceptibility to change remains unclear. Changing landscapes also played a vital role in human evolution, but evidence on early hominin behaviour remains limited. Chimpanzee responses to changing landscapes may provide new insights into early hominin landscape use due to chimpanzees' close relatedness to humans. This thesis used individual-based and referential modelling to explore hominid (i.e. chimpanzee, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) landscape use along an environmental gradient from forests to savannahs to determine their adaptability to change. Based on literature review, this thesis first quantitatively defined chimpanzee landscapes as dense forests, forest mosaics and savannahs using vegetation and climate data. Relationships between chimpanzee behaviour and habitat were identified based on literature and expert reviews. Data were used to set out rules for a NetLogo individual-based model on chimpanzee landscape use. Model output highlighted differences in activity budgets, internal states and daily path lengths for chimpanzees in forests, mosaics and savannahs due to the availability of resources. Maintaining homeostasis was increasingly more difficult in more open landscapes. A savannah chimpanzee case study model based on field data for Issa, Tanzania, verified these findings and showed that savannah chimpanzees faced particular survival challenges; additional adaptations were necessary for survival. Using a referential modelling approach and adapting the chimpanzee models to suit early hominin diet and morphology, early hominin landscape use models highlighted that, similar to chimpanzees, early hominins struggled more in savannahs than in forests. Early hominins were, however, more successful in maintaining homeostasis and more optimally used open vegetation as compared to chimpanzees, due to their morphological adaptations to a wider dietary breadth and bipedality, providing greater locomotor efficiency and better thermoregulatory abilities. *Australopithecus* was more successful than *Ardipithecus*. This research thus quantitatively characterised the selective pressures that shape hominid landscape use, and thereby provided a unique contribution to primatology and human origin studies. Models have important applications for conservation and further research, such as exploring the environmental context of hominid evolution and predicting the impacts of various landscape changes on hominid survival.

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I declare that while registered as a candidate for the University's research award, I have not been a registered candidate or enrolled as a student for an award of any other academic or professional institution.

I furthermore declare that no material contained in the thesis has been used in any other submission for an academic award.

I confirm that the work presented in this thesis is my own work. All materials, data sources, findings and ideas used in this thesis other than my own are fully and appropriately acknowledged throughout the document. Data and findings from Chapter 3 of this thesis were used in the following publication:

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LIST OF ABBREVIATIONS AND NOTATIONS

#	Number
#ftrees	Number of food trees (DBH $\geq$ 10cm)
#trees	Number of trees (DBH $\geq$ 10cm)
#strees	Number of small trees (DBH $<$ 10cm)
#vines	Number of vines (DBH $\geq$ 10cm)
%	Percentage
%ftrees	Percentage of feeding trees (DBH $\geq$ 10cm)
%frtrees	Percentage of feeding trees (DBH $\geq$ 10cm) in fruit
α	Significance level
°C	Degrees Celsius
am	Ante meridiem, before noon
Alt	Altitude
Apr	April
arch.	Architecture
avail.	Availability
Ar. ramidus	*Ardipithecus ramidus*
Ardipithecus model	*Ardipithecus ramidus* landscape use model
Au. anamensis	*Australopithecus anamensis*
Au. Afarensis	*Australopithecus afarensis*
Aug	August
Australopithecus model	*Australopithecus anamensis*/ *afarensis* landscape use model
C_3	Plants using the Calvin cycle/ C_3 photosynthetic pathway to fix carbon, e.g. trees. Food sources such as fruit.
C_4	Plant species using the Hatch-Slack/ C_4 photosynthetic pathway to fix carbon, e.g. grasses. Food sources such as nuts and tubers.
ca.	Circa
CanCov	Canopy cover
CanCon	Canopy connectivity
CAR	Central African Republic
CH	Crown height
Ch	Chapter

chimpanzee model	Generic chimpanzee landscape use model
cm	centimetres
COSTECH	Commission for Science and Technology (Tanzania)
conn.	Connectivity
Crown Width E	Crown width East
Crown Width N	Crown width North
Crown Width S	Crown width South
Crown Width W	Crown width West
CWE	Crown width East
CWN	Crown width North
CWS	Crown width South
CWW	Crown width West
DBH	Diameter at Breast Height
Dec	December
dens.	Density
DRC	Democratic Republic of Congo
Dry_{all}	Total number of dry months per year
Dry_{long}	Length of the longest consecutive dry season per year
Early hominin model	*Ardipithecus* and/or *Australopithecus* landscape use models
e.g.	for example
etc.	Etcetera
F	Forest (landscape) or Forest (vegetation type)
FAI	Fruit Availability Index
Feb	February
FR	Forest Reserve
G	Grassland (vegetation type)
Generic model	Generic chimpanzee landscape use model
GIS	Global Information System
GMERC	Greater Mahale Ecosystem Research and Conservation
GPS	Global Positioning System
ha	hectares
i.e.	that is
IPS	International Primatological Society
Issa	Issa Valley field study site, Tanzania

Issa model	Issa chimpanzee landscape use model
ISLHE	Institute for Studies on Landscape and Human Evolution
IUCN	International Union for Conservation of Nature
Jan	January
Jun	June
Jul	July
ka	Thousand years ago
kCal	kilocalories
kg	kilograms
km	kilometres
km^2	square kilometres
L_{day}	Luminosity at daytime
L_{night}	Luminosity at nighttime
LBH	Lowest Branch Height
LEAP	Landscape Ecology and Primatology
Lux	Luminous flux
M	Forest Mosaic (landscape)
m	metres
Mar	March
Ma	Million years ago
mm	millimetres
n/a	Not applicable
NGO	Non-governmental organisation
Nov	November
NP	National Park
Oct	October
ODD	Overview, Design Concepts and Details
P_{ann}	Annual precipitation
P. t .eliotti	*Pan troglodytes eliotti*
P. t. schweinfurthii	*Pan troglodytes schweinfurthii*
P. t. troglodytes	*Pan troglodytes troglodytes*
P. t. verus	*Pan troglodytes verus*
pm	Post meridiem, after noon
PSGB	Primate Society of Great Britain
Q_1	Lower quartile (25%)

Q_3	Upper quartile (75%)
R	Rocky outcrops (vegetation type)
S	Savannah (landscape), Savannah (vegetation type), or Swamp (vegetation type)
S^+	Sensitivity when increasing target (or base) value
S^-	Sensitivity when decreasing target (or base) value
Sep	September
spp.	Species (several)
T_{ann}	Annual temperature
T_{day}	Temperature at daytime
T_{night}	Temperature at nighttime
TAWIRI	Tanzania Wildlife Research Institute (Tanzania)
TH	Tree Height
THV	Terrestrial Herbaceous Vegetation
tree cover	Hansen global tree cover (Hansen et al. 2013)
UAV	Unmanned Aerial Vehicle
USO	Underground Storage Organ
vs.	versus
W	Woodland (vegetation type)
WR	Wildlife Reserve
WWF	World Wildlife Fund

CHAPTER 1

General introduction

Nonhuman primates play a vital role in tropical ecosystem processes and are of key importance to tropical biodiversity (e.g. Lwanga 2006, Estrada et al. 2017). As nonhuman primates (hereafter "primates") are closely related to modern humans, studies on primate behavioural ecology can provide important insights into human behaviour, ecology and evolution (e.g. Estrada et al. 2017). Primate populations worldwide are declining, and approximately 60% of primate species are currently threatened with extinction (Estrada et al. 2017). Globally, primate habitat is changing rapidly, and continued deforestation, habitat fragmentation, habitat degradation and climate change, mainly caused by unsustainable anthropogenic pressures, are the main threats to primate survival (e.g. Arroyo-Rodriguez and Fahrig 2014, Estrada et al. 2017). How a primate uses its overall environment to forage most efficiently for food and water, and to find safe sleeping sites, determines how likely it is to survive at any particular location and how susceptible it is to change (e.g. Deppe and Rotenberry 2008, Dunbar et al. 2009). It is therefore of immense importance to study primate habitat use at large spatial scales across multiple landscapes (i.e. primate "landscape use"), in order to determine primate responses to habitat alterations (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014).

The landscape use of a species is a hierarchical process where behaviour is guided by internal physiological states; suitable habitats at a landscape scale are located accordingly for each behaviour based on required and preferred micro-habitat characteristics (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Micro-habitat characteristics include a location's micro-climate (e.g. temperature, humidity, luminosity) and vegetation features (e.g. tree height, tree density, food tree density, canopy cover, canopy connectivity, availability of food and water) (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Landscape use is therefore primarily determined by the abundance, density and spatial arrangement of preferred and required resources (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Generally, a landscape is composed of different types of habitat (i.e. vegetation types), such as forest, woodland, grassland, bamboo and swamp (e.g. White 1983). Each of these vegetation types is expected to possess a distinct set of micro-habitat characteristics (e.g. White 1983).

A species may be able to adapt to a wide range of different landscapes, especially if it is relatively generalised in its behavioural requirements for vegetation features and micro-climate characteristics (e.g. Venier and Fahrig 1996). Theoretical understanding of a species' habitat use at a landscape scale is essential to predict how that species will cope with future changes in its environment. However, few studies use a landscape-wide approach to determine how small-scale variations in micro-climate and vegetation structure affect the overall survival chances, abundance and distribution patterns of species across a wider range of environments (e.g. McGarigal and Cushman 2002, Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014). It remains to be understood which vegetation features and micro-climates are most critical for species' survival and how flexibly animals may be able to adapt to various landscape conditions and environmental change scenarios. Only through detailed studies will it be possible to determine which vegetation types are especially important for animals, enabling the establishment of appropriate mitigation strategies for species conservation.

Habitat loss, fragmentation, and degradation have landscape-scale and local-scale effects (e.g. Fahrig 2003, Arroyo-Rodriguez and Mandujano 2009). As a consequence of changing landscapes, species constantly have to adapt to new environmental conditions. Numerous studies have shown that animals are generally negatively affected by environmental change, and various effects are highlighted. For example, Sharma et al. (2013) concluded that for six primate species in the Upper Brahmaputra Valley, India, species richness declined severely as a consequence of habitat loss. Lynch and Whigham (1984) showed that patch isolation, patch area and patch floristic diversity had a significant effect on bird abundance in Maryland, USA. Additionally, Wahungu et al. (2005) showed that forest patch size was significantly correlated with the number of primate groups around the Tana River Primate National Reserve, Kenya, with smaller forest patches containing fewer groups. Eastern chipmunks (*Tamias striatus*) in Pennsylvania, USA, had to alter their behaviour as a result of habitat fragmentation due to the increased risk of predation and decreased availability of resources (Mahan and Yahner 1999). Arroyo-Rodriguez and Mandujano (2006) furthermore found that fragmentation reduced the habitat quality for howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico, by changing the plant composition and vegetation structure in the fragments. Badger (*Meles meles*) presence and numbers in Spain decreased with increasing patch isolation and decreasing patch quality (Virgos 2001). However, these and many other studies are done at a local scale (or "patch-scale") only, making it difficult to infer landscape-wide effects of environmental change on animal landscape use, distribution and survival (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a).

Landscape-scale studies investigate the effect of habitat alterations across a broader range of environments (e.g. Fahrig 2003, Arroyo-Rodriguez and Fahrig 2014). In fact, habitat loss and fragmentation are landscape-scale processes, which are thus best measured and correctly interpreted with a landscape-wide approach (e.g. Fahrig 2003, Arroyo-Rodriguez and Mandujano 2009). Patch-scale studies of habitat fragmentation often include measures such as patch size and patch isolation, although these measures are not independent of total habitat amount at the landscape scale, and ignoring these potential relationships may lead to misinterpretation of the results (e.g. Fahrig 2003). The habitat configuration of a landscape (e.g. the total habitat cover and connectivity, the number and size of patches) should therefore be taken into account when interpreting primate responses to habitat alterations, as these may vary in landscapes with different habitat configurations (e.g. Arroyo-Rodriguez and Mandujano 2009, Arroyo-Rodriguez et al. 2013a). The difference between patch-scale and landscape-scale studies is therefore that patch-scale studies take single patches as independent observational units, whereas landscape-scale studies take whole landscapes as independent units of observation (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014; Figure 1.1). Landscape-scale studies of animals are few, but examples include the effects of habitat loss and fragmentation on genetic diversity (e.g. Gibbs 2001), migration (e.g. Collingham and Huntley 2000), species richness (e.g. Gurd et al. 2001), extinction thresholds (e.g. Fahrig 2002), and species abundance and distribution (e.g. Venier and Fahrig 1996), see Fahrig (2003) for a review.

Individual-based modelling

Because studying animal habitat use in a variety of landscapes at large (i.e. relevant) spatial scales is a challenging and time-consuming process and it is difficult to observe animal responses to present, past and future landscape changes directly, (predictive) modelling provides an important tool in studying species' landscape use (Dunbar 2002, Arroyo-Rodriguez et al. 2013a). There are various approaches to predictive modelling, including linear programming models, game theory models, systems models, optimality models, stochastic dynamic programming models and agent-based simulation models (see Dunbar 2002 for a review). Agent-based or individual-based models are mathematical representations, or simulations, of the interactions between individuals (or ‘agents’) and specific aspects of their environment (or ‘patches’) (e.g. Grimm et al. 2006; Railsback and Grimm 2012). As such, this approach allows individuals to virtually interact with different environments based on rules of existing species-habitat relationships from field studies (e.g. Dunbar 2002).

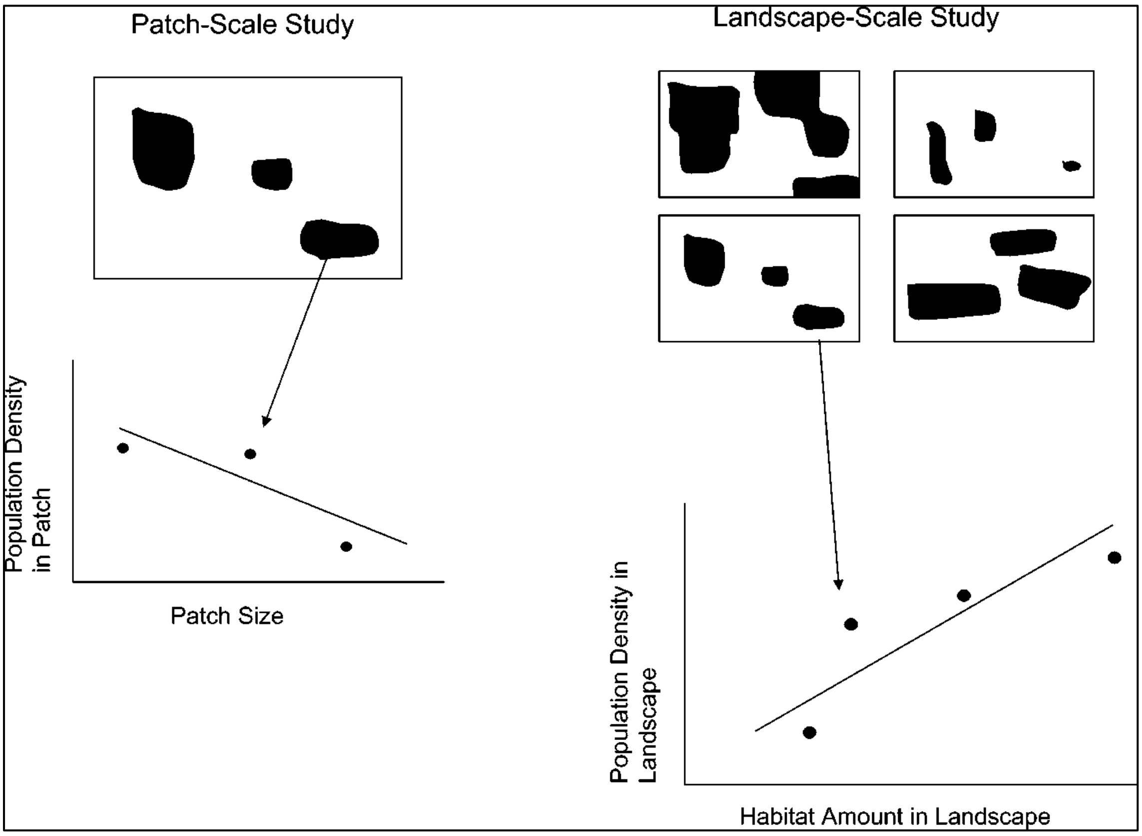

Figure 1.1. Illustrative example of the difference between patch-scale and landscape-scale studies. Where patch-scale studies take single patches as independent observational units, landscape-scale studies take whole landscapes as independent units of observation (e.g. Fahrig 2003, Arroyo-Rodrigues et al. 2013a, Arroyo-Rodriguez and Fahrig 2014). Figure republished with permission of Annual Reviews, from Fahrig (2003, p. 495); permission conveyed through Copyright Clearance Center, Inc.

Individual-based modelling is a rapidly expanding area in ecology (e.g. Grimm et al. 2006). Models have, for example, been used to simulate primate seed dispersal patterns (Bialozyt et al. 2014), species migration (e.g. Collingham and Huntley 2000), primate foraging and movement patterns (e.g. Bonnell et al. 2010, Boyer and Walsh 2010, Hopkins 2016), Eurasian lynx (*Lynx lynx*) dispersal probability (Kramer-Schadt et al. 2004), the life cycle of bumblebee species (Becher et al. 2018), red colobus (*Procolobus rufomitratus*) parasite and disease transmission (Bonnell et al. 2010), bottlenose dolphin (*Tursiops truncatus*) behavioural and physiological responses to disturbance (e.g. Pirotta et al. 2015), primate socio-spatial grouping patterns (e.g. Evers et al. 2011, Evers et al. 2012), coral (*Seriatopora hystrix*) population dynamics (Muko et al. 2014), primate social behaviour (e.g. Evers et al. 2014, Evers et al. 2016), species abundance and distribution (e.g. Venier and Fahrig 1996), primate dominance rank relationships (e.g. Hemelrijk 2002, Hemelrijk et al. 2003), African elephant (*Loxodonta africana*) energetics and population dynamics (Boult et al. 2018), spider monkey (*Ateles* spp.) fission-fusion dynamics (Ramos-Fernandez et al. 2006), oystercatcher (*Haematopus ostralegus*) mortality and population size (e.g. Stillman et al. 2000, Stillman et al. 2001), and the evolution of hominin care-giving (Kessler et al. 2018). Models on species' landscape use, however, remain few (e.g. chacma baboon (*Papio hamadryas ursinus*) time budgets, energy budgets and habitat use: Sellers et al. 2007).

Apart from explaining differences in species' current behavioural patterns, landscape use and identifying priority areas for conservation, individual-based models can also be used to predict the effects of past and future landscape changes, as the modelling approach allows environmental manipulation in scenario testing (e.g. Griffith et al. 2010). Thus, the relative importance of different environmental changes on a species' behaviour, adaptation, evolution and survival can be tested. Habitat loss and fragmentation are major threats to current animal survival, and at a landscape scale, these processes have four major and inter-related effects on habitat patterns (Figure 1.2): ***i)*** a reduction in habitat amount, ***ii)*** an increase in the number of habitat patches, ***iii)*** a decrease in the size of habitat patches, and ***iv)*** an increase in the isolation of habitat patches (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a). Additionally, habitat loss and fragmentation can cause reductions in habitat quality, by increasing the total amount of edge within a landscape and thus increasing the "edge effects" (e.g. Arroyo-Rodriguez and Mandujano 2009, Arroyo-Rodriguez et al. 2013a; Figure 1.2). In conservation biology, edge effects are concerned with the abiotic and biotic changes that occur in previously undisturbed habitat by the creation of distinct edges due to deforestation practices and habitat removal (e.g. Lovejoy et al. 1986, Marsh 2003). Examples of edge effects include modifications in the existing vegetation structure and plant composition of fragments, and changes in local micro-climates (e.g. Saunders et al. 1991, Marsh 2003). Small-scale alterations in the landscapes simulated in the models can assess which of these environmental changes has the greatest effect on species distribution and survival. Furthermore, manipulating the environment will also help to predict at which point behavioural flexibility is insufficient for animals to deal with further landscape changes, thereby identifying their tipping point for coping versus non-coping with environmental change. Additional mitigation strategies can then be developed to address these environmental criteria, avoiding species reaching critically low densities.

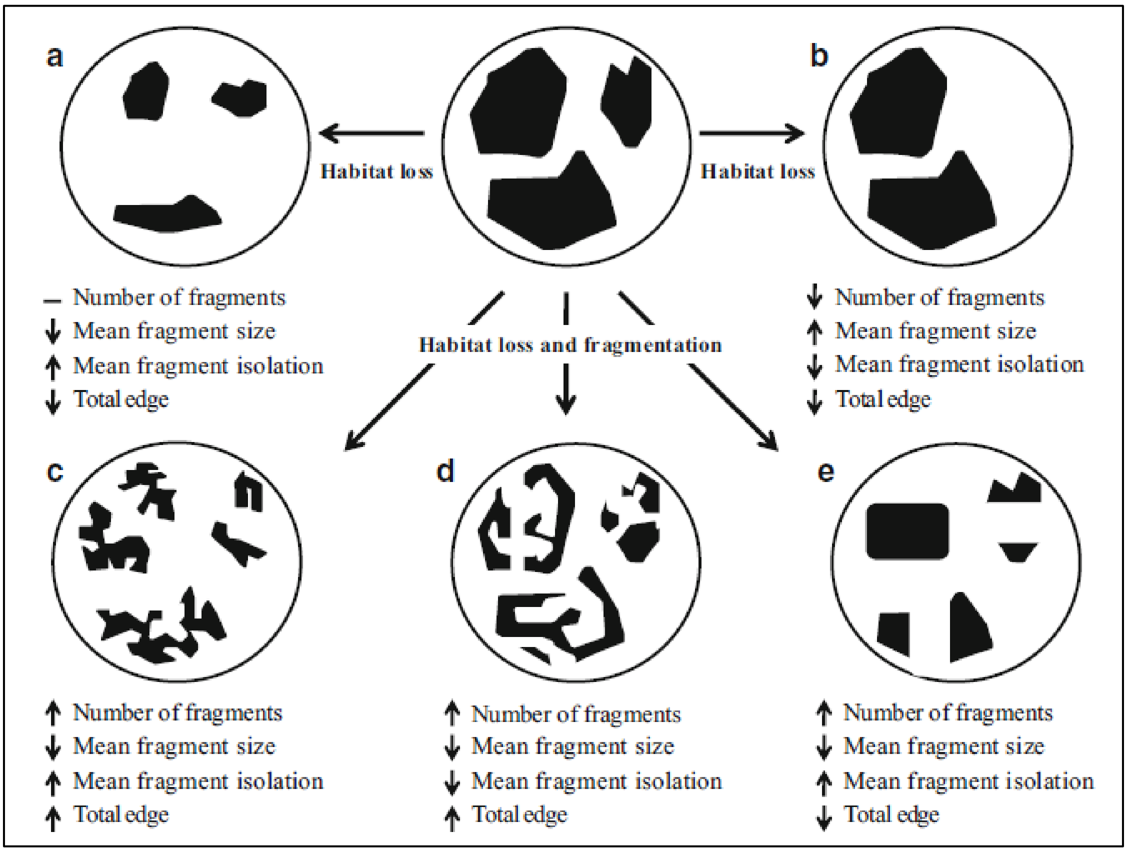

Figure 1.2. Illustrative example of the major effects of habitat loss and fragmentation on a landscape (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a). Figure reprinted with permission of Springer Nature, from Arroyo-Rodriguez et al. (2013a, p. 16); permission conveyed through Copyright Clearance Center, Inc.

Primate landscape use and responses to environmental change

Even though primates can be found across a wide variety of landscapes (for review: Meijaard 2016), primates are among the species most affected by (anthropogenic) habitat loss and landscape change due to their dependence on tropical forests (e.g. de Almeida-Rocha et al. 2017), their slow life histories (e.g. Ross 1989, Charnov and Berrigan 1993), and limited dispersal abilities (e.g. Korstjens and Hillyer 2016). The negative effects of environmental change on primate behaviour, richness and distribution are often discussed (e.g. Wahungu et al. 2005, Arroyo-Rodriguez and Mandujano 2006, Sharma et al. 2013), but landscape-scale studies of primate habitat use across a wide variety of environments are scant and it remains unclear how flexibly primates may be able to adapt to changing landscapes. Few individual-based and predictive models on primate landscape use exist (Sellers et al. 2007). Field studies in degraded habitats have shown that various primate species altered their foraging strategies and time budgets to cope with environmental change (e.g. Clarke et al. 2002, Asensio et al. 2007, Jung et al. 2015, Sha and Hanya 2013). Changes in activity budgets are linked to relationships between (food) resource abundance, frugivory and travel distance (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005, Coward and Grove 2011). As resources in more open landscape are more scarce and widely distributed, increases in travel distance, and thus travel time, are necessary to obtain the required resources (e.g. Palacios and Rodriguez 2001, Clarke et al. 2002, Asensio et al. 2007). In particular, fruit is more scarce and seasonal in more open landscapes (e.g. Ganas and Robbins 2005). Presumably, increased travel time leads to increased feeding and drinking times, either to compensate for the increased amount of travel or due to a shift towards other low-quality dietary items, and this leaves less time available for resting (e.g. Clarke et al. 2002, Asensio et al. 2007, Jung et al. 2015).

One flexible primate species is the chimpanzee (*Pan troglodytes*). Chimpanzees inhabit a wide range of different habitats across equatorial Africa (e.g. Hunt and McGrew 2002, Inskipp 2005), making them an ideal species for studying behavioural adaptability and flexibility to an extensive range of environments. Current chimpanzee individual-based models are limited to simulations of grouping patterns (Te Boekhorst and Hogeweg 1994), and reciprocity and dominance rank relationships (Hemelrijk 1996, Hemelrijk 2002). Chimpanzee landscape use has not yet been studied using the individual-based modelling approach, even though this would provide a powerful tool for exploring chimpanzee landscape-scale habitat use in a variety of environments in a time-efficient way, by incorporating existing data from different chimpanzee study sites. Models on chimpanzee landscape use will show how dependent chimpanzees are on certain vegetation types for their day-to-day activities. Considering the rapid decline and wide-scale change of primate habitat, new information on current chimpanzee-habitat interactions will aid in identifying which vegetation types, vegetation features and micro-climates are most critical for chimpanzee distribution and survival, and will expand current insights into how chimpanzees have adapted to changes in these environmental characteristics in the past, and how they may or may not cope with these changes in the future. This information can then be used to develop effective mitigation strategies (e.g. reforestation) for chimpanzee protection.

An additional advantage of studying chimpanzees is their suitability, as one of humans' closest living relatives, to provide insights into human origins, evolution and behaviour (e.g. Moore 1996, Mitani 2013). Changing landscapes played an important role in human evolution (e.g. Bobe et al. 2002, Potts 2007), and chimpanzees in open, marginal (i.e. scarce in resource abundance and distribution), and mosaic habitats live in similar environments as early hominins once did (e.g. Reed 1997, Hunt and McGrew 2002). As behaviour does not fossilise, exploring the behaviour of early hominins remains one of the great difficulties in the study of human evolution (e.g. Plavcan 2013). Using closely related chimpanzees as a referential model provides a potential solution (e.g. Jolly 2013, Mitani 2013). Findings on chimpanzee landscape use can detail new information on how early hominins would have used their landscape differently or similarly to extant chimpanzees, how they would have responded to environmental changes in their habitats, and how they would have been able to adapt and survive in even more open areas.

Chimpanzees

To date, four chimpanzee subspecies are recognised, and each inhabits a different area of sub-Saharan Africa (e.g. Russak 2013, Figure 1.3): the western chimpanzee (*Pan troglodytes verus* – Schwarz 1934) ranges from southeast Senegal and southwest Mali towards southern Guinea-Bissau, Sierra Leone, Guinea, Liberia, Côte d'Ivoire, and southwest Ghana (e.g. Humle et al. 2016a); the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti* – Gray 1862) inhabits vast areas of southern Nigeria and western Cameroon (e.g. Oates et al. 2016); the central chimpanzee (*Pan troglodytes troglodytes* – Blumenbach 1799) is found in central Africa, extending southwards from southern Cameroon and western Central African Republic (CAR) into Equatorial Guinea, Gabon, northern Congo and the extreme west of the Democratic Republic of Congo (DRC) (e.g. Maisels et al. 2016); and the eastern chimpanzee (*Pan troglodytes schweinfurthii* – Giglioli 1872) is found in the east of the CAR, the extreme southwest of Sudan, the north and east of the DRC, western Uganda, Rwanda, Burundi, and the extreme west of Tanzania (e.g. Plumptre et al. 2016).

Chimpanzees are found in various different habitats, ranging from closed-canopy and wet rainforests to open, dry and mosaic savannahs (e.g. Hunt and McGrew 2002, Inskipp 2005). This variety in habitats is observed across all four subspecies (e.g. Humle et al. 2016b). Chimpanzees living in wet and forested landscapes are sometimes referred to as 'forest chimpanzees' or 'forest-dwellers', whereas chimpanzees living in dry savannah landscapes are often called 'savannah chimpanzees', 'dry-habitat chimpanzees', or 'savannah-dwellers' (e.g. McGrew et al. 1981, Moore 1992, Russak 2013). This is, however, not a taxonomic classification, and clear morphological or genetic differences have yet to be shown. In simple terms, forest chimpanzees are expected to live in forests, whereas savannah chimpanzees are expected to live in more open savannahs. The reality is, however, much more complex, as almost no landscape consists entirely of forest or savannah: a complex, spatially heterogeneous subset of different vegetation types is much more common (Arroyo-Rodríguez and Fahrig 2014). For example, ‘forest’ landscapes may be dominated by forest vegetation, but may additionally contain various other types of habitat, such as swamp, bamboo, bushland, and grassland (e.g. Basabose and Yamagiwa 2002, Watts and Amsler 2013). Similarly, ‘savannah’ environments often include a complex mosaic of vegetation types such as woodland, bamboo, grassland, swamp and/or cultivated fields, and have only a minimal amount of forest cover (e.g. Hunt and McGrew 2002, Stewart and Pruetz 2013). Landscapes differ in their spatial arrangement and proportions of different vegetation types, as well as in their climate (e.g. Ogawa et al. 2007, Bortolamiol et al. 2014). Consequently, landscapes differ in their availability, distribution, and quality of resources, with savannah landscapes generally being more resource scarce and seasonal than forest landscapes (e.g. McGrew et al. 1981, Moore 1996, Hunt and McGrew 2002). As quantitative definitions are lacking, it remains unclear when exactly a chimpanzee can be called a ‘forest chimpanzee’ and its landscape a ‘forest’, and when a ‘savannah chimpanzee’ and its landscape a ‘savannah’.

Figure 1.3. Geographical distribution of the four chimpanzee subspecies across Africa (IUCN SSC A.P.E.S. Database, Drexel University, and the Jane Goodall Institute 2016).

Chimpanzees have been studied in the wild since the 1960s (e.g. Goodall 1986), and chimpanzee behavioural ecology has been investigated intensely over the last few decades. Long-term, ongoing research is, for example, conducted at Bossou, Guinea (e.g. Matsuzawa et al. 2011), Taï, Côte d'Ivoire (e.g. Boesch and Boesch-Achermann 2000), Kibale, Uganda (e.g. Ghiglieri 1984), Budongo, Uganda (e.g. Reynolds 2005), Mahale, Tanzania (e.g. Nakamura et al. 2015), and Gombe, Tanzania (e.g. Goodall 1986), but many more chimpanzee study sites exist today or have existed in the past (e.g. Hunt and McGrew 2002, Morgan et al. 2006, Hernandez-Aguilar 2009). Studies have focused on numerous topics, including chimpanzee feeding ecology and diet (e.g. Bessa et al. 2015), nesting behaviour (e.g. Koops et al. 2012a), travel and ranging patterns (e.g. Nakamura et al. 2013), genetics (e.g. Moore et al. 2015), culture (e.g. Whiten et al. 1999), tool-use (e.g. Goodall 1964), hunting and meat eating (e.g. Watts and Amsler 2013), food sharing (e.g. Pruetz and Lindshield 2012), grouping patterns (e.g. Lehmann and Boesch, 2004), activity budgets (e.g. Murray et al. 2009), sociality (e.g. Riedel et al. 2011), reproduction (e.g. Emery Thompson et al. 2014), self-medication (e.g. Pebsworth et al. 2006), and locomotion (e.g. Munn 2006).

Within their environments, chimpanzees select specific types of vegetation for different behavioural activities and at different times of day based on micro-climate and vegetation characteristics. For example, they prefer specific nest locations based on tree species, tree height and canopy cover (Koops et al. 2012a), they occasionally rest in caves or seek shade to find shelter from heat (Pruetz 2007, Duncan and Pillay 2013), and they will be more likely to find fruit in more densely forested patches (Hernandez-Aguilar 2009, Bryson-Morrison et al. 2016, Potts et al. 2016). Various hypotheses have been proposed to influence which locations chimpanzees prefer for their activities, such as the thermoregulation hypothesis (i.e. the avoidance of overheating and/or undercooling; e.g. Fruth and Hohmann 1996, Koops et al. 2012a), the antivector hypothesis (i.e. the avoidance of disease vectors; e.g. Koops et al. 2012a, Samson et al. 2013), the antipredation hypothesis (i.e. the protection from or avoidance of predators; e.g. Koops et al. 2012a, Stewart and Pruetz 2013), and the optimal foraging theory (i.e. the maximizing of energetic intake; e.g. Pyke et al. 1977, Potts et al. 2016), but actual chimpanzee site selection for particular activities is typically a trade-off between these drivers. To date, details on the required micro-climate and structural characteristics of preferred vegetation types for specific activities remain scarce and often descriptive, and differences exist between different chimpanzee study sites. Considering that vegetation features and micro-climates are likely to be the first things to change due to current habitat alterations (Arroyo-Rodriguez and Mandujano 2006, Riitters et al. 2016), it is important that more information is collected on the role these variables play in chimpanzee-habitat interactions and how this shapes chimpanzees' activity budgets, energy budgets, distribution and survival in various locations. This will help in understanding the extent of behavioural flexibility in chimpanzees, and the effects that future landscape changes will have on chimpanzee landscape use.

Compared to the wealth of information that is known on forest chimpanzees, relatively little is still known on the behavioural ecology of savannah chimpanzees (e.g. Hunt and McGrew 2002, Pruetz et al. 2002, Piel et al. 2017), even though they may form the key to understanding how chimpanzees will cope with increasing habitat fragmentation and climate change throughout their range (e.g. Pruetz 2018). As such, it remains unclear how flexibly chimpanzees are able to adapt to more open landscapes, and how susceptible they are to change. Similar to observed behavioural patterns of other primates in degraded habitats (e.g. Clarke et al. 2002, Asensio et al. 2007, Sha and Hanya 2013), chimpanzees are likely to adapt their activity budgets to suit their environment. Additional changes in the chimpanzee behavioural repertoire may also be expected in more open and/or degraded habitat, including a wider dietary breadth (e.g. human-cultivated crops: Humle 2015; unripe fruit: Wessling et al. 2018a; high-quality meat: Moore et al. 2017), and/or an expansion in material culture (e.g. increased reliance on termite fishing: Bogart and Pruetz 2008; increased reliance on ant-dipping: Sommer et al. 2016; using tools for hunting: Pruetz and Bertolani 2009).

Hominins

Along with the other great apes (i.e. bonobos (*Pan paniscus*), gorillas (*Gorilla* spp.) and orang-utans (*Pongo* spp.)), chimpanzees, humans (*Homo sapiens*) and hominins are members of the family *Hominidae*, and are also referred to as ‘hominids’ (e.g. Coward 2014, Blaxland 2016). Chimpanzees are thus closely related to modern humans, and insights into how flexibly chimpanzees can adapt to changing environments can therefore provide new information on the behaviour and landscape use of early hominins (e.g. Mitani 2013). Early hominins are the earliest members of the human lineage, which includes both modern humans, as well as their fossil relatives (e.g. Coward 2014, Su 2013). Hominins include extinct members of the genera *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Australopithecus*, *Paranthropus* and *Homo*, and within these genera many different species are identified (e.g. Boyd and Silk 2012, Fleagle 2013). *Sahelanthropus*, *Orrorin*, *Ardipithecus*, and early *Australopithecus* species are often considered as primitive ‘early hominins’, living between ca. 7 – 3 million years ago in Eastern Africa (e.g. Simpson 2013, Hammond and Ward 2013).

Fossil remains of early hominins have been found at various sites in southern and eastern Africa, and have been used to investigate the specific environments inhabited by various hominin species (e.g. Reed et al. 1997). Although controversies exist, early hominin environments are broadly reconstructed as mosaic habitats with varying amounts of forest, woodland and grassland cover (e.g. Simpson 2013, Hammond and Ward 2013). Temporal and spatial differences in the specific landscape compositions of different sites are, however, expected (e.g. Simpson 2013, Hammond and Ward 2013), and reconstructions range from dense forests to open savannahs (e.g. Reed 1997, Aronson et al. 2008, Cerling et al. 2011).

Fossil remnants of early hominin species have furthermore been used to study the many aspects of early hominin behavioural ecology (e.g. White et al. 2009, Ungar et al. 2010). Specific attention has been given to early hominin diet, morphology and locomotion (e.g. Boyd and Silk 2012, Fleagle 2013, Sponheimer et al. 2013). For example, many studies have focused on early hominins' morphological adaptations to bipedality, a form of terrestrial locomotion which is expected to be energetically less costly but slower than the more typical quadrupedal locomotion when travelling on the ground (e.g. Rodman and McHenry 1980, Ward 2013, Lieberman 2015, Kinugasa and Usami 2016). Early hominins' bipedal locomotion decreased energy expenditure when moving terrestrially and their bipedal posture reduced exogenous heat gain and thermal stress in open areas, and many interpretations have been drawn from this, including early hominins' higher tolerance to open areas and subsequent wider access to high-quality and isolated food items (e.g. underground storage organs (USOs), or carcasses for scavenging) (e.g. Wheeler 1984, Wheeler 1992, Laden and Wrangham 2005, Lieberman 2015). High-quality food items are often scarce and widely distributed, and may therefore require larger travel ranges (e.g. Coward 2014). Later genera (i.e. *Australopithecus*) are expected to have been morphologically better adapted to bipedalism than 'earlier' hominins (i.e. *Sahelanthropus*, *Orrorin*, and *Ardipithecus*) (e.g. Simpson 2013, Kozma et al. 2018).

As behavioural reconstructions remain a daunting challenge in studies of human origins, interpretations about how early hominins would have behaved in their environments are difficult (e.g. Mitani 2013, Plavcan 2013). As such, questions endure on early hominin landscape use, distribution, adaptability, and survival. It remains to be understood which vegetation features and micro-climates were most important for early hominins in selecting sites for their activities, and how flexibly they were able to adapt to changing environments. This limited amount of knowledge hinders the understanding of early hominin (behavioural) evolution, and other approaches are needed to provide more detailed information.

Chimpanzees as referential models for early hominins

One way of gaining more insights into early hominin behaviour is through using indirect evidence of other primates for behavioural reconstructions (e.g. Mitani 2013, Jolly 2013). This approach is called ‘referential modelling’. There are two kinds of referential models: ‘true analogies’ and ‘best extant models’ (e.g. Jolly 2013). Whereas true analogies focus on comparisons of specific homoplastic traits between unrelated species (Jolly 2013), best extant models aim to reconstruct “the total way of life of the fossil form” (Jolly 2013, p. 449). By definition, a best extant model is “the living species that most closely resembles the fossil in all respects that can be documented, and is therefore presumed […] to resemble it most closely in traits, such as behaviour, that cannot be directly observed” (Jolly 2013, p. 449). Therefore, best extant models are likely to be closely related phylogenetically to the fossil species in question (Jolly 2013).

Due to their close phylogenetic relatedness to humans, chimpanzees are most often used as best extant models in the study of human behavioural evolution (e.g. Mitani 2013). Studies have tried to reconstruct early hominin behaviour based on behavioural similarities and differences between chimpanzees and humans (modern and extinct), focusing, for example, on social organization, tool-use, hunting, and food sharing (see Mitani 2013 for review). Chimpanzees can also be used as a best extant model for understanding the patterns of early hominin landscape use. Especially insights into chimpanzee landscape use in open and marginal environments (e.g. savannahs) could provide a framework for facilitating interpretations of the selective pressures shaping early hominin behaviour, adaptation, and evolution in their landscapes.

Considering the fact that each hominin species has its own physiological and morphological characteristics (e.g. Simpson 2013, Hammond and Ward 2013), it is very likely that for some hominin species, chimpanzees will provide better referential models than for others. Due to similarities in morphological and physiological features, chimpanzees are often assumed to provide best referential models for *earlier* hominins, such as *Sahelanthropus tchadensis, Orrorin tugenensis, Ardipithecus kadabba, Ardipithecus ramidus, Australopithecus anamensis* and *Australopithecus afarensis* (e.g. Moore 1996, Zihlman 1996, Stanford 2012). *Ardipithecus ramidus, Australopithecus* *anamensis*, and *Australopithecus afarensis* are well-documented, while evidence on *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and *Ardipithecus kadabba* remains limited (e.g. Reed 1997, Ungar 2004, Stanford 2012, Simpson 2013). Chimpanzees can therefore be considered as best extant models to study the behavioural ecology of *Ardipithecus ramidus*, *Australopithecus anamensis*, and *Australopithecus afarensis*. Considerable debate exists on whether or not *Australopithecus anamensis* and *Australopithecus afarensis* can be regarded as separate species, and *Australopithecus anamensis*/ *afarensis* is sometimes considered as a single continuous lineage (e.g. Boyd and Silk 2012, Fleagle 2013).

Thesis aim and research questions

The aim of this thesis is to explore the landscape-scale habitat use of three hominid species (i.e. chimpanzees, *Ardipithecus ramidus*, and *Australopithecus anamensis*/ *afarensis*) across a wide range of environments. It investigates the minimal landscape requirements and constraints for chimpanzees and early hominins to determine how flexibly these hominids can adapt to changing landscapes. Specifically, the following research questions are addressed:

I) How will chimpanzee (*Pan troglodytes*) landscape use vary when environments differ from forests to more open habitats, and how is this linked to the presence of specific vegetation features and micro-climate characteristics?

II) How would the landscape use of the early hominins *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* have differed when environments varied from forests to more open habitats, how would this have differed between the early hominin species, and among early hominins and extant chimpanzees?

Because it is difficult to observe hominids’ direct responses to present, past and future landscape changes, this thesis uses an individual-based modelling approach based on hominid-habitat relationships from field studies. This approach allows individuals to virtually interact with different environments and different landscape change scenarios based on rules from published literature. As detailed data on early hominins remain scarce, this study furthermore uses a referential modelling approach based on findings from chimpanzees to explore early hominin behaviour and landscape use. Exact hypotheses are outlined per chapter in the section below.

Thesis outline

The review and empirical data chapters of this thesis are subdivided into two parts: **I)** Chimpanzee landscape use (Chapter 2 – Chapter 5), and **II)** Early hominin landscape use (Chapter 6). The thesis is completed by a general overview and conclusion in **Chapter 7**.

Part I: Chimpanzee landscape use

Part I of this thesis investigates the influence of specific vegetation features and micro-climate characteristics on the landscape-scale patterns of chimpanzee habitat use. As essential background research for the thesis, **Chapter 2** investigates the minimal landscape requirements and constraints for chimpanzees in selecting a site for a specific activity based on a review of published chimpanzee-habitat interactions and preferences from field studies. Chapter 2 reviews current knowledge on the hypothesis that chimpanzees select specific sites for specific activities in order to optimise their predator avoidance, thermoregulation and foraging efficiency, where preferred locations are expected to contain:

- ***i)*** For nesting – tall trees, closed canopies, high tree densities, high canopy connectivity, and high amounts of food and water present;
- ***ii)*** For feeding – high amounts of food present, high tree densities, lower mean daily temperatures, lower luminosity, and high food tree densities;
- ***iii)*** For resting – lower mean daily temperatures, lower luminosity, tall trees, closed canopies, high tree densities, high canopy connectivity, and high amounts of food and water present;
- ***iv)*** For drinking – high amounts of water present, lower mean daily temperatures, and lower luminosity;
- ***v)*** For travel – tall trees, closed canopies, high tree densities, high canopy connectivity, lower mean daily temperatures, lower luminosity, and low understory densities.

Findings form the basis for the individual-based model rules on chimpanzee behaviour used in Chapter 4 and Chapter 5.

Chapter 3 of this thesis provides a first quantitatively measurable definition and review of the various landscapes used by chimpanzees, and compares the vegetation and climate characteristics of the main landscape categories used in chimpanzee literature: forest and savannah. It investigates how the landscape classifications used by chimpanzee researchers in presenting their study sites map onto traditional biome, vegetation and climate classification schemes, and identifies which vegetation and climate characteristics best separate the classifications provided by chimpanzee researchers. Chapter 3 tests the hypothesis that observed differences in vegetation composition and climatic conditions of chimpanzee study sites can be used to quantitatively characterise chimpanzee landscapes:

i) Based on differences in vegetation cover and climate, a first distinction can be presented between chimpanzee forest and savannah landscapes;

ii) Within chimpanzee forest landscapes, differences in climate and vegetation allow a further distinction between chimpanzee dense forest and forest mosaic habitats.

This information forms the basis for the rules on creating virtual environments for the individual-based models on chimpanzee landscape use in Chapter 4 and Chapter 5.

Chapter 4 of this thesis examines how activity budgets, energy budgets, and daily path lengths for chimpanzees change when their habitats differ along an environmental gradient from dense forests to forest mosaics and open savannahs. This is investigated using an individual-based modelling approach based on the findings of Chapter 2 and Chapter 3. Chapter 4 tests the hypothesis that chimpanzees in different environments behave differently due to the availability of resources:

i) The presence of preferred vegetation features and micro-climate characteristics makes forest vegetation types most ideal for chimpanzees across landscapes. Other vegetation types, such as woodland, swamp, bamboo, and grassland are increasingly less ideal;

ii) Chimpanzees in dense forest habitats use only optimal forest vegetation types for their daily activities, as these are readily available to them. Consequently, forest chimpanzees can be very specific in their site selection for particular activities. In forest mosaic and savannah landscapes, optimal forest vegetation types are used as much as possible, but forests are generally not widely available. Compared to forest, other vegetation types such as woodland and grassland have a wider range of vegetation features and micro-climates. Mosaic and savannah chimpanzees will limit their use of suboptimal vegetation types in such a way that they do not experience environmental conditions beyond those encountered in forest, e.g. using grassland areas only in the cooler times of day, and/or using locations with the tallest trees and highest tree densities when in woodland;

iii) Daily travel distance for chimpanzees is longest in savannah environments, shortest in dense forests and intermediate in forest mosaics due to the differences in overall resource availability and distribution within the different landscapes;

iv) Time spent nesting is similar for chimpanzees in all landscapes, due to the inability of performing other activities at night (i.e. chimpanzees are a diurnal species). Time spent travelling, feeding, and drinking is greatest in savannahs, shortest in dense forests, and intermediate in forest mosaics, due to the quality, availability and distribution of resources within the different landscapes. Time spent resting is greatest in dense forests, shortest in savannahs and intermediate in forest mosaics, due to the differences in amount of ‘spare’ time available after performing their other daily activities.

This information can be used to predict the impacts of future landscape change scenarios on chimpanzee behaviour and survival, to present a framework for understanding the underlying reasons of behavioural innovation and adaptation to specific landscapes in hominid evolution, and to provide a referential model for the landscape use of early hominins.

Chapter 5 of this thesis establishes how accurately the individual-based model of Chapter 4 based on generic chimpanzee literature alone is able to predict chimpanzee landscape use at a specific chimpanzee study site, and evaluates how the inclusion of site-specific details of a particular study site influences model output on chimpanzee landscape use. Specifically, it explores the activity budgets, energy budgets and survival of savannah chimpanzees at Issa Valley, Tanzania using an individual-based modelling approach based on field-collected data. Here, the generic chimpanzee landscape use model of Chapter 4 is adapted to suit the behaviour, habitat and characteristics of Issa chimpanzees. As knowledge on savannah chimpanzee behaviour and ecology remains limited, the findings of the Issa model are compared with the savannah chimpanzee findings of the generic chimpanzee landscape use model. Chapter 5 hypothesises that both models will differ in their output:

i) The inclusion of site-specific data for the Issa model, i.e. data on the behaviour, habitat and characteristics of Issa chimpanzees, makes Issa model output more realistic, and only the Issa model encloses a sufficient amount of detail to present a realistic picture of chimpanzee landscape use at this site.

Observed differences and similarities between the two models can be used to verify the model output of the generic chimpanzee landscape use model of Chapter 4, which was based on chimpanzee literature only. This information can be used to support future conservation efforts by measuring chimpanzee behaviour and landscapes in the most effective and time-efficient way when developing realistic predictive models of chimpanzee landscape use at specific study sites.

Part II: Early hominin landscape use

Part II of this thesis explores the landscape use of early hominins. **Chapter 6** investigates how activity budgets, energy budgets and daily path lengths would have varied for two early hominin species (i.e. *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) when their landscapes differed along an environmental gradient from forests to more open landscapes, and how this differed among the early hominin species and between early hominins and chimpanzees. This is achieved by first presenting a review on hominin paleoenvironments and hominin-habitat relationships. Based on findings from Chapter 2 – Chapter 5, the generic chimpanzee landscape use model of Chapter 4 is then adapted to suit the behaviour, characteristics and habitats of early hominins wherever feasible, and is combined with findings from chimpanzees (i.e. referential modelling). Chapter 6 tests the hypothesis that behavioural strategies would have differed across landscapes and between the three hominid species (i.e. chimpanzees, *Ardipithecus* and *Australopithecus*):

i) As was the case with chimpanzees, differences in vegetation composition and climatic conditions at fossil hominin localities can be used to provide a quantitatively measurable definition of the various environments used by early hominins, characterising dense forests, forest mosaics and savannahs;

ii) Just like chimpanzees, early hominins would have preferred specific sites for specific activities based on optimising their thermoregulation, predator avoidance, and foraging efficiency, and preferred locations for feeding, drinking, nesting, resting, and travel would therefore have contained comparable vegetation features and micro-climate characteristics as those preferred by chimpanzees;

iii) Similar to predictions for chimpanzees, when hominin environments changed from forests to marginal savannahs, early hominins would have increased their daily travel distance, as well as feeding, travelling and drinking time, and would have decreased their resting time when the environment became more open and scarce. Time spent nesting would have been similar across environments, due to the inability of performing other activities at night before the invention of using fire;

iv) Even though most preferences in site selection for specific activities would have been similar for early hominins and modern chimpanzees, early hominins would have been able to more optimally use open vegetation types (e.g. woodland, savannah grassland), because of their locomotor patterns (i.e. bipedality) being energetically less costly and providing thermoregulatory advantages in open habitat over the quadrupedal gait of chimpanzees, leading to greater access to high-quality and isolated resources (i.e. food, water). Consequently, early hominins would, just like chimpanzees, have preferentially used forest vegetation types for nesting, drinking and resting, but in contrast to chimpanzees, would have used both forest and more open vegetation types for travelling and feeding;

v) As another consequence of early hominins' reduced thermoregulatory stress and wider access to open area resources, early hominins would have spent less time feeding, more time travelling, and would have travelled longer daily distances than chimpanzees in order to access high-quality and isolated food items. Due to assumed morphological, physiological and behavioural similarities, time spend drinking, resting and nesting would have been similar to those observed for chimpanzees.

vi) Within the early hominin species, *Ardipithecus ramidus* would have been more restricted to closed vegetation types (i.e. forest, woodland) and would have used more open vegetation types less optimally than *Australopithecus anamensis*/ *afarensis* due to the latter's greater morphological commitment to terrestrial bipedal locomotion, and vegetation type usage would have differed between the two early hominin species;

vii) As a result of the 'gradient' in bipedal locomotion efficiency, *Ardipithecus ramidus* would have spent more time feeding, less time travelling, and would have travelled shorter daily distances than *Australopithecus anamensis*/ *afarensis*.

This information can be used to predict the impacts of landscape changes on early hominin behaviour, to evaluate the outcomes of different behavioural strategies on early hominin survival, and to provide a framework for understanding the underlying role of landscapes in early hominin adaptation and evolution.

PART I

CHIMPANZEE LANDSCAPE USE

CHAPTER 2

Chimpanzee behaviour and habitat relationships: A review of preferences and requirements in site selection for specific vegetation and micro-climate characteristics

Abstract

Chimpanzees select specific types of vegetation for different activities and at different times of day based on micro-climate and vegetation characteristics. Detailed insights into the environmental aspects preferred by chimpanzees for their daily activities can help focus conservation efforts to enable more efficient chimpanzee habitat protection. Exact details on the vegetation and micro-climate characteristics required for specific activities, however, remain scarce and often descriptive. This study aimed to investigate the minimal landscape requirements and constraints for chimpanzees in selecting a site for an activity based on a review of chimpanzee-habitat interactions and preferences from field studies. It reviewed current knowledge on the hypothesis that chimpanzees would select specific sites for specific activities to optimise their predator avoidance, thermoregulation, and foraging efficiency, and that specific vegetation features and micro-climates (e.g. closed canopies, low temperatures, high food availability) would be selected accordingly. Whilst the environmental context of chimpanzee nest building is relatively well-studied, details on the used and preferred micro-habitat characteristics in chimpanzee site selection for feeding, drinking, resting and travel remain limited. This made it difficult to review the outlined hypotheses, and more research is necessary to further the understanding of the ecological determinants and underlying reasons of chimpanzee site selection. In a first attempt to characterise chimpanzee-habitat relationships for modelling purposes, this study presented an overview on the importance of various vegetation and micro-climate characteristics in chimpanzee site selection based on informed-opinion, expert-based reviews and landscape-scale studies. Findings of this study provide new insights into the extent of chimpanzee behavioural flexibility, patterns of landscape use and chimpanzee-habitat interactions, which may aid in the development of more appropriate mitigation strategies (e.g. reforestation) to protect chimpanzee habitat and their required resources. Future research may facilitate behaviour-habitat comparisons between sites, species, and extinct early hominins.

Keywords: habitat selection, feeding, drinking, nesting, resting, travel.

Introduction

One of the key issues in conservation biology is an in-depth understanding of the ecological determinants of animal abundance and distribution, and consequently animal behaviour and range use (e.g. Rendings et al. 2003, Rovero and Struhsaker 2007, Deppe and Rotenberry 2008). Animals have been shown to preferentially select specific habitats for their behaviours, and habitat preferences have been linked to various drivers, including the availability of resources such as food and water, and/or a reduction in the risk of predation (e.g. Enstam and Isbell 2004). As a consequence, conservation efforts to date often include a specific focus on conserving an animal's overall environment (e.g. IUCN Red List of Threatened Species 2016). Across various study sites, it has been shown that chimpanzees (*Pan troglodytes*) select specific types of vegetation (e.g. forest, woodland, swamp, savannah grassland) for different behavioural activities and at different times of day based on micro-climate (e.g. temperature, luminosity) and vegetation characteristics (e.g. tree height, (food) tree density, canopy cover and connectivity, presence of water and food; e.g. Pruetz 2007, Koops et al. 2012a, Duncan and Pillay 2013). This information is important for chimpanzee conservation, as it enables a deeper understanding of chimpanzee-habitat interactions in deciding where and when chimpanzees perform their daily activities. Especially since micro-climate and vegetation characteristics are likely to be the first things to change due to current habitat alterations and climate change (e.g. Arroyo-Rodriguez and Mandujano 2006, Riitters et al. 2016), it is important that more information is collected to further the understanding of chimpanzee habitat requirements, preferences and flexibility. Many current chimpanzee conservation actions and management plans focus on avoiding the large-scale clearance of chimpanzee habitat to promote chimpanzee survival (e.g. Humle et al. 2016b), but exact details on the vegetation features and micro-climate characteristics preferred and required by chimpanzees for specific activities remain scarce and often descriptive. No generalised overview across chimpanzee study sites has been presented. Detailed information on the micro-climates and structural characteristics of vegetation types required by chimpanzees will highlight which parts of the landscape are especially important for their activities. This may lead to more appropriate efforts and mitigation strategies for chimpanzee habitat protection.

Throughout the chimpanzee's geographical range in equatorial Africa, many chimpanzee study sites can be identified (e.g. Goodall 1986, Reynolds 2005, Matsuzawa et al. 2011). Consequently, much information is available on chimpanzee behavioural ecology across a wide range of environments. Many studies have focused primarily on specific aspects of chimpanzee behaviour (e.g. Bates and Byrne 2009, Murray et al. 2009), although other studies have also investigated the environmental context in which these behaviours are observed (e.g. Pruetz and Bertolani 2009, Koops et al. 2012a). For example, for nest building, chimpanzees prefer nesting locations that contain tall trees with low first branches, dense canopies and particular tree species (e.g. Koops et al. 2012a). Chimpanzee resting activities occur in caves at some study sites to find shelter from heat (Pruetz 2007). Chimpanzee feeding and grouping behaviour has been studied in relation to the presence and distribution of food (e.g. Chapman et al. 1995, Furuichi et al. 2001, Janmaat et al. 2013a), as well as to tree and food tree density (Furuichi et al. 2001, Hernandez-Aguilar 2009, Potts et al. 2016), and studies suggested that chimpanzees are generally more likely to find food in more densely forested patches (e.g. Furuichi et al. 2001, Hernandez-Aguilar 2009, Potts et al. 2016). Chimpanzees, furthermore, seem to adapt their arboreal and terrestrial activities to forest micro-climate and, to some extent, food availability (Takemoto 2004). Detailed information on the preferred vegetation structures and climatic characteristics for other behaviours are not often reported.

Various drivers have been suggested to explain why chimpanzees prefer specific locations for their behaviours, and many of these drivers have been studied in regards to chimpanzee nest building (e.g. Koops et al. 2012a). Proposed hypotheses in driving chimpanzee site selection include the thermoregulation hypothesis (e.g. Fruth and Hohmann 1996, Koops et al. 2012a), the antivector hypothesis (e.g. Koops et al. 2012a, Samson et al. 2013), the antipredation hypothesis (e.g. Koops et al. 2012a, Stewart and Pruetz 2013), and the optimal foraging theory (e.g. Pyke et al. 1977, Potts et al. 2016). The thermoregulation hypothesis theorises that many animal behaviours are attributable to behavioural thermoregulation, i.e. the process of maintaining an optimal body temperature and avoiding overheating and/or undercooling (e.g. Kosheleff and Anderson 2009, Koops et al. 2012a). The antivector hypothesis suggests that location selectivity for particular behaviours is driven by the avoidance of disease vectors such as parasitic arthropods (e.g. Koops et al. 2012a, Samson et al. 2013). The antipredation hypothesis explains that the protection from, or the avoidance of, predators is the most important factor in deciding where to perform an activity (e.g. Anderson 2000, Koops et al. 2012a, Stewart and Pruetz 2013). Last, the optimal foraging theory outlines that individuals are limited by energetic constraints and should consequently prefer to use (and forage) in areas where their net energy intake will be highest (e.g. Pyke et al. 1977, Potts et al. 2016). All these hypotheses could, in theory, explain why chimpanzees would prefer certain types of vegetation (and thus certain vegetation features and micro-climate characteristics) for their behaviours more than others. To date, however, no consensus has been reached as to which, if any, of these drivers is most important in explaining chimpanzee site selection for specific activities, and contrasts between study sites exist. Actual chimpanzee site selection is likely a trade-off between these different drivers. Studies in other primate species have argued the importance of dense tree cover, low understory density, tall trees, large trunk diameter at breast height (DBH), high food tree density, lower temperature at daytime, and higher temperature at night in habitat selection for daily activities, mostly with regards to antipredation, optimal foraging, and thermoregulation (e.g. Rovero and Struhsaker 2007, Bettridge and Dunbar 2012, Cheyne et al. 2012, Thompson et al. 2016). For example, Rovero and Struhsaker (2007) highlighted the importance of tree basal area, tree height, and food plant species richness in determining the abundance of Udzungwa red colobus (*Procolobus gordonorum*). Bettridge and Dunbar (2012b) highlight that decreased bush level vegetation cover and increased tree cover may reduce predation risk. Agile gibbons (*Hylobates albibarbis*) selected tall trees as sleeping sites, and Cheyne et al. (2012) argue that this is a predator avoidance strategy. Thompson et al. (2016) showed that mantled howler monkeys (*Alouatta palliata*) chose relatively warmer locations when nighttime temperatures were low, and relatively cooler sites during daytime.

The aim of this study is therefore to present a literature-based review of the preferred and required vegetation features and micro-climate characteristics in chimpanzee site selection for specific activities across study sites in order to develop a more detailed understanding of chimpanzee-habitat relationships and patterns of landscape use. This study will focus on feeding, drinking, nesting, resting, and travelling. Within published literature, chimpanzees' daily activity budgets are often assessed in relation to feeding, travel and resting activities over the 12-hour active day range, in which resting behaviour often also includes social time (e.g. Doran 1997, Potts et al. 2011). Nesting behaviour is additionally important when investigating chimpanzees' behavioural patterns over a 24-hour period. Even though drinking behaviour is not often included in published studies of chimpanzees' daily activity budgets because of its rare occurrence, the inclusion of this behaviour is important, as it is paramount for chimpanzee hydration (e.g. Nishida 1980, Popkin et al. 2010), and may be an important driver of chimpanzee ranging behaviour where water is scare (e.g.

McGrew et al. 1981). With regards to behavioural preferences and requirements, this study reviews current knowledge on the hypothesis that chimpanzees select specific sites for specific activities in order to optimise their predator avoidance, thermoregulation, and foraging efficiency, where preferred locations are predicted to contain: ***i)*** for nesting – tall trees, large DBHs, high lowest branch heights (LBH), closed canopies, high tree densities, high canopy connectivity, and high food and water availability; ***ii)*** for feeding – high amounts of food present, high tree densities, lower mean daily temperatures, lower luminosity, and high food tree densities; ***iii)*** for resting – lower mean daily temperatures, lower luminosity, high trees, large DBHs, high LBHs, closed canopies, high tree densities, high canopy connectivity, and high food and water availability; ***iv)*** for drinking – high amounts of water present, lower mean daily temperatures, and lower luminosity; and ***v)*** for travel – tall trees, large DBHs, closed canopies, high tree densities, high canopy connectivity, lower mean daily temperatures, lower luminosity, and low understory densities.

Methods

Study species

This study focused on chimpanzees (*Pan troglodytes*) in their natural environments across equatorial Africa. As it aimed to provide a literature-based review of chimpanzee preferences and requirements for specific vegetation and micro-climate characteristics in behavioural site selection across study sites, all four chimpanzee subspecies (i.e. *P. t. verus*, *P. t. ellioti*, *P. t. troglodytes*, and *P. t. schweinfurthii*) were analysed equally.

Data collection and analyses

Data on chimpanzee activities, vegetation features and micro-climates were collected during a thorough literature review of publications on chimpanzee behavioural ecology in their natural landscapes. Both peer-reviewed (e.g. journal papers, books, book chapters) and grey literature (e.g. university theses, NGO reports, state agency reports) were included. The Web of Science platform was used to search for relevant literature. Key search terms included ‘chimpanzee’, ‘feed’, ‘drink’, ‘nest’, ‘rest’, ‘travel’, ‘landscape’, ‘environment’, ‘habitat’, ‘climate’, and ‘vegetation’. Additionally, relevant literature was searched for using the name of specific chimpanzee study sites.

For each relevant publication encountered, this study noted the name and location (GPS referenced) of the chimpanzee study site, along with details on the specific behaviour studied (i.e. feeding, drinking, nesting, resting, and travel), and where and when this behaviour was observed in relation to specific vegetation features and micro-climate characteristics. With regards to *where* specific behaviours were observed, this study outlined for each publication whether the behaviours were studied with regards to the following vegetation and micro-climate characteristics: tree species, tree height, tree DBH, tree LBH, tree crown width, tree crown height, tree crown connectivity, tree leaf cover, tree branch architecture, canopy cover, canopy connectivity, understory density, tree density, food tree density, food availability, water availability, local temperature and local luminosity. Also some more general environmental variables were included: slope, altitude, woody cover, and vegetation type. Whenever a certain vegetation feature, micro-climate characteristic, or general environmental variable was studied in relation to chimpanzee feeding, drinking, nesting, resting, or travelling, details were noted on the preferred average and range of values used. Furthermore, the importance of the various characteristics in chimpanzee site selection was assessed. With regards to *when* specific behaviours were observed, this study outlined for each publication whether the behaviours were studied with regards to the following internal states and environmental circumstances: energy, hydration, fatigue, temperature, precipitation, time of day, sun rise, and sun set. Where specified, details were noted on the preferred average and range of variables used. If absolute values for micro-climates, vegetation features, general environmental variables, internal states and environmental circumstances preferred for specific activities remained unknown, then relative information was searched for. The resulting database outlined site-specific information on chimpanzee site selection for each reviewed publication. To present a detailed overview on chimpanzee preferences and requirements across sites and studies, data for all studies were taken together and summarised. The resulting tables introduce the mean and range of the vegetation features, micro-climate characteristics, general environmental variables, internal states, and environmental circumstances used and preferred for the various chimpanzee behaviours across sites, studies, seasons, sexes and vegetation types.

To support the literature-based data collection on chimpanzee preferences and requirements in behavioural site selection, this study created a questionnaire on the environmental determinants of chimpanzee site selection for chimpanzee experts. This questionnaire reviewed the importance of various vegetation features, micro-climate characteristics and general environmental variables for chimpanzees at specific field study sites (Appendix 2.1). The importance of each vegetation feature, micro-climate characteristic and general environmental variable was scored on a 1 – 4 scale for each activity, with 1 = very important, 2 = important, 3 = not very important, and 4 = not important. Questionnaires were sent out to the JISCMAIL mailing list of the Primate Society of Great Britain (PSGB), and were shared through the social media channels of the PSGB and the International Primatological Society (IPS). Three questionnaires were returned. Together with the informed opinion of the author, data from the expert-based reviews were taken together and summarised to present a detailed overview of the vegetation and micro-climate characteristics responsible for chimpanzee site selection. In case of disagreement or equal ties between reviews, the author's informed opinion based on extensive literature review and experience from observing chimpanzees in the wild was decisive, and literature data provided by the author were used.

Results

Chimpanzee site selection: Where to perform a behaviour

Many vegetation features, micro-climate characteristics and general environmental variables remain to be studied or lack detail with regards to *where* chimpanzees perform their daily feeding, drinking, nesting, resting and travel activities (Table 2.1). Chimpanzees' drinking locations, for example, have only sparsely been attributed to water availability, tree density, local temperature, local luminosity and vegetation type (Table 2.1). Intuitively, chimpanzees drink where there is water, and it has been specified that chimpanzees collect water from both standing and free-flowing water sources, and drink water either directly or with the use of tools. Water availability is furthermore likely a strong selective pressure in guiding chimpanzee daily activities. Following geographical literature (e.g. Ellison et al. 2017), it is moreover assumed that most water sources occur within forest vegetation types, where tree density is high, daytime temperatures are low, nighttime temperatures are high, and overall luminosity is lower than in surrounding vegetation. Forest along rivers and/or seasonal water courses in mosaic settings are often referred to as gallery forests. Partially, the lack of knowledge on the environmental context of chimpanzee drinking locations can be attributed to the fact that many of the vegetation features investigated in this study are not applicable with regards to drinking. On the other hand, however, it also coincides with the finding that not much research is done overall on chimpanzee drinking behaviour (Table 2.1).

The environmental context surrounding chimpanzees' feeding locations has been studied in relation to tree species, tree DBH, food availability, water availability, local temperature and vegetation type (Table 2.1). Overall, chimpanzees prefer specific tree and plant species for feeding, although feeding preferences are site-specific and preferred species-lists only partly overlap between sites depending on availability. Across study sites, between 43 and 223 plant species are consumed. Chimpanzees feed on fruit, leaves, bark, flowers, seeds, pith, and gum, but ripe fruit is preferred overall. Both forest and woodland vegetation types are used for feeding across sites. Whereas forest is the most important vegetation type for feeding at some field study sites, woodland is equally important, or even more important, at other sites. It remains to be studied, however, whether these preferences are due to the presence of food, or a consequence of specific preferences for certain vegetation types per se. In Bossou, for example, forest use reflects the spatial and temporal availability of food (Bryson-Morrison et al. 2017), but a location's micro-climate may also be important in selecting a feeding location (Takemoto 2004). DBH is not directly linked to chimpanzee feeding activities, although trees with larger DBHs produce more fruit. As surface water was an important drinking source for Fongoli chimpanzees, food intake decreased with increasing distance to water in savannah landscapes, which indicates that chimpanzees prefer to feed close to water sources (as measured during the baobab (*Adansonia digitata*) fruiting season: Lindshield et al. 2017; Table 2.1).

Chimpanzee nest building behaviour is by far the best studied in relation to its environmental context. Location selectivity for nesting has been associated to tree species, tree height, tree DBH, tree LBH, tree crown width, tree crown height, tree crown connectivity, tree leaf cover, tree branch architecture, canopy cover, canopy connectivity, food tree density, food availability, water availability, local temperature, slope, altitude, and vegetation type (Table 2.1). Even though site-specific preferences for particular locations exist across study sites, it was shown that, in general, chimpanzees prefer to nest in trees of a particular species (e.g. *Cynometra alexandri*, *Elaeis guineensis, Uvariopsis congensis*; Samson and Hunt 2014) with an average height of 14.9m, a mean DBH of 29.9cm, an average LBH of 5.6m, a mean crown width of 9.4m, a mean crown height of 9.8m, a mean leaf cover of 68.3%, an average crown connectivity of 48.4%, and within trees that have vertically inclined, alternate branches, one stem and one canopy. Preferred nesting locations furthermore have an average canopy cover of 61.4%, a mean canopy connectivity of 48.4%, a low density of understory, a high density of feeding trees, are in close proximity to food and water, are on intermediate slopes, and at a particular altitude (i.e. > 1,000m altitude at Nimba, Guinea, and 1,770 – 2,380m at Bwindi, Uganda). Nests have been observed in both forest and woodland vegetation types, but forest is preferred when checked against availability. Across studies, the preferred ranges of particular vegetation features and general environmental variables are large. For example, reported heights of trees used for nesting cover the range 1 – 53m, DBHs range 2.0 – 354.8cm, and canopy cover and connectivity range 0 – 100% across sites and seasons (e.g. Stewart 2011; Table 2.1).

Chimpanzee resting behaviour has been studied with regards to tree species, tree DBH, understory density, food availability, local temperature and vegetation type (Table 2.1). When resting in tree nests, chimpanzees show a preference for specific tree species (e.g. *Cynometra alexandri, Celtis durandii, Ficus sur*; Brownlow et al. 2001) with an average DBH of 43cm. Chimpanzees have also been observed resting in ground nests, in which specific understory plant species are used for ground nest construction based on availability. Daytime nests are structurally much simpler than night nests (e.g. Brownlow et al. 2001). As daytime resting is often done in between feeding episodes, it is assumed that resting locations are in close proximity to food sources. Resting locations are often selected in cooler micro-climates. Resting is observed in both woodland and forest. Chimpanzees also rest in the absence of nests, i.e. on bare ground or tree branches (e.g. Hernandez-Aguilar 2006). The environmental context surrounding a resting location where no nest is used, has not been studied to date (Table 2.1).

Chimpanzee travel is least studied in relation to its environmental context, and has only been linked to food availability, food tree density, local temperature and vegetation type (Table 2.1). With regards to vegetation types, it has been documented that travel occurs in forest, woodland, and savannah grassland, but details on specific preferences remain absent. It is furthermore indicated that travel may occur preferably in cooler micro-climates and may be food-directed, with chimpanzees mostly travelling towards areas with increased food tree densities and/or food availability (Table 2.1).

Table 2.1. Documented effects of the vegetation features, micro-climates, and general environmental aspects studied in relation to chimpanzee feeding, drinking, nesting, resting and travel based on published literature. Table results outline *where* to perform these activities for chimpanzees. 'n/a' stands for 'not applicable', i.e. this environmental variable is not relevant for this behaviour. 'unknown' stands for 'the effect of the environmental variable on where to perform an activity is not known for this behaviour'.

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
Vegetation Feature					
Tree Species	n/a	Site-specific preferences for specific tree and plant species. Food species preference partly overlaps between sites and studies,	Site-specific preferences for specific tree species. Tree preference partly overlaps between sites and studies,	Site-specific preferences for specific tree and plant species in building daytime nests.[29, 46]	Unknown

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
		depending on availability; 43 to 223 food species are recorded per site.[12-19, 57]	depending on tree species availability.[8, 12, 28-37]		
Tree Height	n/a	Unknown	Mean tree height used for nesting (across Issa, Assirik, Kahuzi-Biega, Semliki, Fongoli, Ngel-Nyaki and Nimba): 14.9m. Range of tree heights used for nesting (across Issa, Assirik, Ngel-Nyaki and Fongoli): 1 – 53m.[4, 30, 33, 36-39]	Unknown	Unknown
Tree DBH	n/a	Trees with larger DBHs produce more fruit; positive correlation between DBH and fruit availability.[20]	Mean DBH of trees used for nesting (across Kahuzi-Biega, Budongo, Issa, Nimba, Ugalla, Ngel-Nyaki and Fongoli): 29.9cm. Overall range of nesting tree DBHs (across Semliki, Ngel-Nyaki, Issa, Ugalla, Fongoli): 2.0 – 354.8cm.[4, 29, 30, 33, 36, 37, 39, 40]	Mean DBH of daytime nesting trees (at Budongo): 43cm. The range of DBHs of trees used for resting remains unknown. DBHs used for nesting at daytime are larger than DBHs of trees used for nighttime nesting.[29]	Unknown
Tree LBH	n/a	Unknown	Mean LBH of nesting trees (across Nimba, Fongoli and Issa): 5.6m. Overall range of lowest branch heights (across Issa and Fongoli): 0 – 20m.[33, 36, 37]	Unknown	Unknown
Tree Crown Width	n/a	Unknown	Mean crown width of trees used for nesting (across Issa and Fongoli): 9.4m. Overall range of crown widths (across Issa and Fongoli): 2.0 – 30m.[37]	Unknown	Unknown
Tree Crown Height	n/a	Unknown	Mean crown height of nesting trees (across Issa, Fongoli, and	Unknown	Unknown

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
			Nimba): 9.8m. Overall range of crown heights (across Issa and Fongoli): 0 – 37m.[33, 36, 37]		
Tree Leaf Cover	n/a	Unknown	Mean leaf cover of nesting trees (across Fongoli and Issa): 68.3%. Overall range of nesting tree leaf cover (across Fongoli and Issa): 0 – 95%.[37]	Unknown	Unknown
Tree Branch Architecture	n/a	Unknown	The majority of nests (at Nimba) are found in trees with vertical inclined branches as opposed to horizontal branches, in trees with alternate branches as opposed to opposite branches, and in trees with one main stem and one canopy.[36]	Unknown	Unknown
Canopy Cover	Unknown	Unknown	Mean canopy cover of nesting trees (across Fongoli and Issa): 61.4%. Overall range of nesting tree canopy cover (across Fongoli and Issa): 0 – 100%.[37]	Unknown	Unknown
Canopy Connectivity/ Tree Crown Connectivity	Unknown	Unknown	Mean canopy/ crown connectivity of the nesting tree with neighbouring trees (across Fongoli and Issa): 48.4%. Overall range of canopy connectivity between the nesting tree and surrounding trees (across	Unknown	Unknown

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
			Fongoli and Issa): 0 – 100%. It is stated that a sleeping tree mostly provides at least one ‘escape route’ to a neighbouring tree.[37, 41]		
Understory Density	Unknown	Unknown	Chimpanzees preferably nest in open understory habitats.[42]	Understory plant species are used for building daytime ground nests based on availability.[46]	Unknown
Tree Density	Most (permanent) water sources are found in forest vegetation types, where tree density is higher than in other vegetation types.[1-3]	Unknown	Unknown	Unknown	Unknown
Food Tree Density	Unknown	Unknown	A positive relationship between food tree density and nest density exists (at Kibale) This implies that nests are built where food tree density is high. It remains to be studied, however, whether this is due to food tree density per se, or solely the presence of ripe fruit.[43]	Unknown	Dependent on the subsequent activity of an individual (e.g. feeding), travel may be directed towards a location with a higher food tree density.[15]
Food Availability	Unknown	Chimpanzees feed on fruit, leaves, bark, flowers, seeds, pith and gum, although ripe fruit is preferred. Foods vary in nutritional content and quality.[12-19, 57]	Chimpanzees often nest in close proximity to food resources, although nesting in trees bearing ripe fruit is uncommon.[23, 30, 31, 36, 37, 41, 44]	It is generally assumed that chimpanzees rest in between feeding episodes, and therefore resting locations are expected to be in close proximity to food resources.[29]	Depending on the subsequent activity of an individual, travel may be directed towards a location with food present.[15, 53]
Water Availability	Chimpanzees collect water from both	Chimpanzee food intake decreases with increasing	Chimpanzees often nest in close proximity	Water availability and scarcity had a	Water availability and scarcity had a

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
	standing and free-flowing water sources, such as ponds, pools, puddles, rivers, springs, streams, tree holes and/or self-made wells. Collecting water is either done directly using their mouths or hands, or indirectly using tools (e.g. leaf sponges). Water availability and scarcity had a strong influence in guiding chimpanzee behaviour in open and dry landscapes.[4-9,54,56]	distance to water sources (at Fongoli). Water availability and scarcity had a strong influence in guiding chimpanzee behaviour in open and dry landscapes.[16, 56]	to water (at Ugalla and Assirik). Water availability and scarcity had a strong influence in guiding chimpanzee behaviour in open and dry landscapes.[41, 45, 56]	strong influence in guiding chimpanzee behaviour in open and dry landscapes.[56]	strong influence in guiding chimpanzee behaviour in open and dry landscapes.[56]
Micro-Climate Characteristic					
Local Temperature	Most (permanent) water sources are found in forest vegetation types, where temperatures are cooler during the day and hotter during the night as compared to more open vegetation types.[10,11]	Chimpanzees seem to select cooler micro-climates for their daily activities (at Bossou).[55]	Ambient temperature within a tree does not significantly seem to affect nest height (at Nimba). Differences in local temperature between nest sites and non-nest sites remain to be investigated.[46]	Chimpanzees select cooler micro-climates for their daily resting activities (at Bossou).[55]	Chimpanzees select cooler micro-climates for their daily travel behaviours (at Bossou).[55]
Local Luminosity	Most (permanent) water sources are found in forest vegetation types, where luminosity levels are lower than in surrounding vegetation.[10,11]	Unknown	Unknown	Unknown	Unknown
General Variable					
Slope	Unknown	Unknown	The majority of	Unknown	Unknown

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
			nests are found on slopes, as opposed to flat terrain. At Nimba, most nests are found on slopes with intermediate steepness (between 21 – 40 degrees), and least nests could be found on mild slopes (between 0 – 20 degrees).[26, 36]		
Altitude	Unknown	Unknown	Site-specific influences of altitude on nest site selection exist; e.g. in Nimba nests are found between 681m and 1,169m above sea level, but nest locations above 1000m are preferred. In Bwindi, nest are found between 1,770m and 2,380m.[32, 46]	Unknown	Unknown
Woody Cover	Unknown	Unknown	Unknown	Unknown	Unknown
Vegetation Type	Most water sources occur in forest vegetation types. Forests in mosaic settings along seasonal and/or permanent water sources are often referred to as gallery forests.[1-4]	Forest and woodland are used for feeding. At some sites, forest is most important (or preferred) for feeding (e.g. Bafing, Kalinzu, Loango, Assirik, Bossou), whereas at other sites, woodland is just as important, or even more important than forest (e.g. Issa, Ugalla, Assirik). Vegetation types used for feeding are expected to vary based on food availability, which indicates that it might be the presence of food that is important, and not the	Forest is preferred for nesting at most study sites (e.g. Budongo, Gashaka, Semliki, Issa, Ugalla, Fongoli, LCNP, Assirik, Ishasha, Kalinzu, Lac Tumba Landscape, Goualougo, and La Belgique). In more open landscapes, woodland is also often used, but when checking nesting frequency against vegetation type availability, it is found that forest is	Forest, woodland, and other vegetation types are used for resting at most study sites (e.g. Issa, Semliki, Bossou and Assirik). It is assumed, though, that forest is the preferred vegetation type for daily activities, including resting.[3, 4, 21, 52]	Chimpanzees travel mostly within forest (e.g. Issa, Assirik, and Semliki), although travel in other vegetation types, such as woodland and savannah grassland is also documented (e.g. Issa, Bossou and Assirik).[3, 4, 8, 21, 52]

Environmental Variable	Drinking	Feeding	Nesting	Resting	Travel
		vegetation type per se.[21-27,52]	preferred, and woodland is used randomly or even avoided (e.g. Fongoli, and Issa).[4, 16, 26, 28, 31, 35, 38, 40, 47-51]		

References used: [1]Pruetz and Bertolani 2009, [2]Ogawa et al. 2014, [3]Russak 2014, [4]Hunt and McGrew 2002, [5]Nishida 1980, [6]Sugiyama 1995, [7]Tonooka 2001, [8]Inskipp 2005, [9]Sharma et al. 2016, [10]Grimmond et al. 2000, [11]Thompson et al. 2016, [12]Reynolds 2005, [13]Pruetz 2006, [14]Russak 2013, [15]Ban et al. 2016, [16]Lindshield et al. 2017, [17]Foerster et al. 2016, [18]Basabose 2002, [19]McLennan and Ganzhorn 2017, [20]Chapman et al. 1992, [21]Tutin et al. 1983, [22]Schoeninger et al. 1999, [23]Furuichi et al. 2001, [24]Duvall 2008, [25]Russak and McGrew 2008, [26]Hernandez-Aguilar 2009, [27]Head et al. 2012, [28]Sept 1992, [29]Brownlow et al. 2001, [30]Basabose and Yamagiwa 2002, [31]Furuichi and Hashimoto 2004, [32]Stanford and O'Malley 2008, [33]Hernandez-Aguilar et al. 2013, [34]Samson and Hunt 2014, [35]Carvalho et al. 2015a, [36]Koops 2011, [37]Stewart 2011, [38]Pruetz et al. 2008, [39]Dutton et al. 2016, [40]Ogawa et al. 2007, [41]Anderson 1984, [42]Sanz et al. 2007, [43]Balcomb et al. 2000, [44]Fruth and Hohmann 1996, [45]Ogawa et al. 2014, [46]Koops et al. 2012a, [47]Morgan et al. 2006, [48]Inogwabini et al. 2012, [49]Stewart and Pruetz 2013, [50]Tagg et al. 2013, [51]Pascual-Garrido et al. 2013, [52]Bryson-Morrison et al. 2017, [53]Janmaat et al. 2013b, [54]Sousa 2011, [55]Takemoto 2004, [56]Wessling et al. 2018a, [57]Matsumoto-Oda 2002.

Relative importance of vegetation and micro-climate characteristics

The lack of data on the importance of various vegetation features, micro-climate characteristics and general environmental variables makes it difficult to determine exact locations *where* chimpanzees perform their daily activities. Also the relative importance of various environmental characteristics often remains to be understood, which hinders the assessment of whether some features are more important than others. Koops (2011), for example, showed that among various other features, DBH, LBH, leaf cover, and leaf size were the most important variables in selecting a nest site location for chimpanzees at Nimba, Guinea. Based on informed-opinion and expert-based reviews from questionnaires, Table 2.2 presents an overview of the relative importance of the vegetation features, micro-climate characteristics and general environmental variables. With regards to optimising thermoregulation, predator avoidance and foraging efficiency, the following vegetation features, micro-climate characteristics and general environmental variables are considered important for each behaviour: 1) for drinking – water availability, followed by local temperature, local luminosity and vegetation type; 2) for feeding – food availability, food tree density and tree species, followed by tree height, DBH, crown width, and crown height, and by tree density, local temperature, local luminosity, woody cover, and vegetation type; 3) for nesting – tree species, DBH, LBH and leaf cover, followed by tree height, crown width, crown height, crown connectivity, branch architecture, canopy cover, canopy connectivity, tree density, food availability, altitude and woody cover, and by understory density, food tree density, water availability, local temperature, local luminosity, slope and vegetation type; 4) for resting – local temperature and local luminosity, followed by tree height, LBH, crown connectivity, leaf cover, branch architecture, canopy cover, canopy connectivity, understory density, tree density, altitude and woody cover, and by crown width, crown height, food tree density, food availability, water availability, slope and vegetation type; and 5) for travel – crown connectivity, canopy cover, canopy connectivity, local temperature and local luminosity, followed by understory density, tree density, food tree density, food availability, water availability, slope, altitude and woody cover, and by vegetation type (Table 2.2).

Table 2.2. Relative importance of the vegetation features, micro-climates, and general environmental aspects reviewed in this study with regards to chimpanzee feeding, drinking, nesting, resting and travel, based on informed-opinion and expert-based review*. Table results indicate important variables in deciding *where* to feed, drink, nest, rest and travel for chimpanzees. Within the table 'n/a' stands for 'not applicable' meaning that this environmental variable is not relevant for this specific behaviour. In the column 'importance', '1' stands for very important, '2' stands for important, '3' stands for not very important, and '4' stands for not important.

Environmental Variable	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travelling**
	Importance	*Importance*	*Importance*	*Importance*	*Importance*
Vegetation Feature					
Tree Species	n/a	1	1	4	4
Tree Height	n/a	2	2	2	4
Tree DBH	n/a	2	1	3	4
Tree LBH	n/a	4	1	2	4
Tree Crown Width	n/a	2	2	3	4
Tree Crown Height	n/a	2	2	3	4
Tree Crown Connectivity	n/a	4	2	2	1
Tree Leaf Cover	n/a	4	1	2	4
Tree Branch Architecture	n/a	4	2	2	4
Canopy Cover	4	4	2	2	1
Canopy Connectivity	4	4	2	2	1
Understory Density	4	4	3	2	2
Tree Density	4	3	2	2	2
Food Tree Density	4	1	3	3	2
Food Availability	4	1	2	3	2
Water Availability	1	4	3	3	2
Micro-Climate					
Local Temperature	3	3	3	1	1
Local Luminosity	3	3	3	1	1
General Variable					
Slope	4	4	3	3	2
Altitude	4	4	2	2	2
Woody Cover	4	3	2	2	2
Vegetation Type	3	3	3	3	3

*Findings based on the author's informed opinion and expert knowledge from questionnaires on the environmental determinants of chimpanzee site selection for activities. Questionnaires completed by Dr. K. Koops, Dr. A. Pascual-Garrido, and Prof. V. Reynolds.

Importance of vegetation and micro-climate characteristics in landscape-scale studies

Not all vegetation features, micro-climate characteristics and general environmental variables outlined above are equally important when exploring behaviour at a landscape scale. Reviews of primate responses to habitat alterations only include a subset of these characteristics: tree species, tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, food availability, water availability, local temperature, local luminosity, slope, altitude, woody cover, and vegetation type are discussed in landscape-scale studies (Table 2.3). For this thesis, these characteristics are therefore termed 'landscape-scale micro-climate and vegetation characteristics'. Even though this does not deny the importance of tree DBH, LBH, crown width, crown height, crown connectivity, leaf cover and branch architecture, it indicates that these features may operate on small, local scales and/or may be correlated with features that are incorporated at landscape scales.

Table 2.3. The vegetation features, micro-climate characteristics and general environmental aspects discussed in landscape-scale studies. Within the table, 'Yes' means that a variable is incorporated in landscape-scale reviews of primate habitat use. 'No' means that a variable is not included in landscape-scale reviews. The latter does not indicate that a feature is not important, it implies, however, that this feature is too small-scale (and/or significantly correlated with any of the other variables) for landscape-scale inclusion.

Environmental Variable	**Incorporated in landscape-scale reviews?**	**References (major)**
Vegetation Feature		
Tree Species	Yes	Isabirye-Basuta and Lwanga 2008 Arroyo-Rodríguez and Mandujano 2009 Barelli et al. 2015 Estrada et al. 2017
Tree Height	Yes	Arroyo-Rodríguez and Mandujano 2009 Pyritz et al. 2010
Tree DBH	No	-
Tree LBH	No	-
Tree Crown Width	No	-
Tree Crown Height	No	-
Tree Crown Connectivity	No	-
Tree Leaf Cover	No	-
Tree Branch Architecture	No	-
Canopy Cover	Yes	Isabirye-Basuta and Lwanga 2008 Arroyo-Rodríguez and Mandujano 2009 Barelli et al. 2015 Estrada et al. 2017
Canopy Connectivity	Yes	Arroyo-Rodríguez and Mandujano 2009 Arroyo-Rodríguez and Fahrig 2014
Understory Density	Yes	Isabirye-Basuta and Lwanga 2008 Pyritz et al. 2010 Estrada et al. 2017

Environmental Variable	**Incorporated in landscape-scale reviews?**	**References (major)**
Tree Density	Yes	Isabirye-Basuta and Lwanga 2008
Food Tree Density	Yes	Isabirye-Basuta and Lwanga 2008
Food Availability	Yes	Sanderson et al. 2002 Isabirye-Basuta and Lwanga 2008 Arroyo-Rodríguez and Mandujano 2009 Arroyo-Rodríguez and Fahrig 2014 Barelli et al. 2015 Estrada et al. 2017
Water Availability	Yes	Sanderson et al. 2002 Arroyo-Rodríguez and Mandujano 2009 Arroyo-Rodríguez and Fahrig 2014 Luo et al. 2016
Micro-Climate		
Local Temperature	Yes	Isabirye-Basuta and Lwanga 2008 Arroyo-Rodríguez and Mandujano 2009
Local Luminosity	Yes	Arroyo-Rodríguez and Mandujano 2009
General Variable		
Slope	Yes	Luo et al. 2016
Altitude	Yes	Da Silva et al. 2015 Luo et al. 2016
Woody Cover	Yes	Hansen et al. 2013
Vegetation Type	Yes	Isabirye-Basuta and Lwanga 2008 Arroyo-Rodríguez and Mandujano 2009 Luo et al. 2016

Chimpanzee site selection: When to perform a behaviour

With regards to *when* chimpanzees perform their daily activities, knowledge on the role of various internal states and environmental circumstances remains limited. Some general trends are, however, observed (Table 2.4). For precipitation, for example, heavy rains impede chimpanzees' daily activities, forcing them to rest more during daytime or nest longer at night (i.e. delay nest departure in the morning, or build nests earlier in the evening). Similarly for temperature, high temperatures at daytime are expected to increase resting time and decrease the time spent on other daily activities such as feeding. The effect of temperature on when to travel is inconsistent across studies. Chimpanzees are expected to drink more when temperatures are high, and are observed to delay nest departure after low nighttime temperatures. Chimpanzees are furthermore expected to perform their activities preferably within their thermo-neutral zone between 20-29°C. Within this range of temperatures, chimpanzees do not have to increase their metabolic rate or energy expenditure for heating and/or cooling. For time of day, chimpanzees nest from sunset to sunrise, resulting in an active day of ~12 hours. Even though most daily behaviours are observed throughout the active day, resting peaks around midday, feeding peaks in early morning and late afternoons, drinking tends to peak in late afternoons, and travel peaks halfway through the morning and at the end of the afternoon. Sometimes, travel and feeding activities are observed during nighttime. With regards to internal states, it is assumed that chimpanzees strive to maintain homeostasis, which would require neutral to positive energy and water (i.e. hydration) balances, and a neutral to negative fatigue balance. Water is gained through drinking and fatigue is lost through resting and nesting. Hydration stress has been observed for chimpanzees during dry seasons. Energy is gained and lost through various processes, most notably energy gain through feeding, and energy loss through travel. Energy balance is observed to vary with food availability. Eating highly fibrous foods may increase resting time due to digestion. Positive energy balances delay nest departure in the morning (Table 2.4).

Table 2.4. Documented effects of the internal states and general environmental circumstances studied in relation to chimpanzee feeding, drinking, nesting, resting and travel activities based on published literature. Table results outline *when* to feed, drink, nest, rest and travel for chimpanzees. Within the table ‘‘Unknown’ stands for ‘effect of the environmental variable/ internal state on when to perform an activity is not known for this behaviour’.

Environmental Variable and/or Internal State	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
Global Variable					
Time of day	Drinking occurs throughout the active day, peaking in late afternoons.[1]	Chimpanzees feed throughout the active day, although feeding peaks in early morning and late afternoons. Feeding occurs sometimes during nighttime.[3, 5-7, 35-37]	Chimpanzees leave their nest on average between 6am – 7am, and build their night nests between 6pm – 7pm, i.e. an active day of ~12 hours.[24-27]	Chimpanzees rest throughout their active day, peaking around noon, when temperatures are highest.[3, 7]	Travel occurs throughout the active day, although travelling peaks mid-morning and late afternoon. Travel sometimes occurs at nighttime.[3, 7, 35-37]
Sunrise	Unknown	Feeding is generally the first thing chimpanzees do after departing their nest at sunrise.[3]	Sunrise in equatorial regions is mostly around 6am. Chimpanzees generally leave their nests after sunrise.[8, 28]	Unknown	Unknown
Sunset	Unknown	Feeding is generally the last activity chimpanzees perform before nesting at sunset.[3]	Sunset in equatorial regions is around 6pm. Chimpanzees generally start building their nests around sunset.[8, 28]	Unknown	Unknown
Precipitation	Chimpanzees likely drink less when precipitation is high, i.e. drinking is assumed inversely related to precipitation	Heavy rains inhibit chimpanzees’ daily activities, e.g. feeding less when rainfall is high.[1, 8]	High amounts of rainfall at night delay nest departure the next morning. Heavy rains at the end of the day causes chimpanzees to nest earlier than	Heavy rains inhibit chimpanzees’ daily activities, e.g. resting more when rainfall is high.[1, 8]	Heavy rains inhibit chimpanzees’ daily activities, e.g. travel less when rainfall is high.[1, 8]

Environmental Variable and/or Internal State	**Drinking**	**Feeding**	**Nesting**	**Resting**	**Travel**
	trends.[1]		usual.[8, 11]		
Temperature	A positive correlation is expected between drinking and temperature. At Mahale, chimpanzees indeed drink more in the warm months at the end of the dry season. Preferably, chimpanzees perform their behaviours within their thermo-neutral zone (i.e. the range of temperatures where they do not have to increase their metabolic rate and energy expenditure for heating or cooling), between 20-29°C.[1-4]	When temperatures increased, feeding decreased for chimpanzees (at Budongo), i.e. less feeding when temperatures are high. Chimpanzee thermo-neutral zone: 20-29°C.[3, 4]	Low temperatures at nighttime delay nest departure the next morning. Chimpanzee thermo-neutral zone: 20-29°C.[3, 4, 8, 11, 29]	A positive relationship exists between temperature and percentage of time spent resting. Resting also often occurs in the shade, where temperatures are lower. Chimpanzee thermo-neutral zone: 20-29°C.[3, 4, 7, 26, 30]	The effect of temperature on when to travel is inconsistent: e.g. in Budongo travel is positively correlated with temperature in the sun, whereas in Fongoli, chimpanzees travel less when temperature is high. Chimpanzee thermo-neutral zone: 20-29°C [3, 7]
Internal State					
Energy	Unknown	Chimpanzees are expected to aim to maintain a neutral to positive balance between energy intake and expenditure. Energy intake can be increased through feeding; Foods vary in net energy gains. At Fongoli, energy balance varies with food availability.[9-23, 38, 39]	A high (positive) energy balance, delays nest departure time the next morning.[11]	It is implied that resting time is longer when highly fibrous foods are eaten, as a result of digestion.[30]	Chimpanzees are expected to aim for a positive energy balance. One way to decrease energy expenditure is by reducing travel. Travel costs are positively related with travel speed, and climbing is less costly than walking.[9, 10, 31-34]
Hydration	Chimpanzees are expected to aim to maintain a neutral water (or hydration) balance by drinking to replenish and avoiding dehydration stress. Dehydration stress and water	Unknown	Unknown	Unknown	Unknown

Environmental Variable and/or Internal State	Drinking	Feeding	Nesting	Resting	Travel
	restriction occurs in chimpanzees during dry seasons.[2, 38, 39]				
Fatigue	Unknown	Unknown	It can be predicted that individuals have to nest when their fatigue levels are high, although this is not specified in current literature.	It can be predicted that individuals have to rest when their fatigue levels are high, although this is not specified in current literature.	Unknown

References used: [1]Nishida 1980, [2]Popkin et al. 2010, [3]Kosheleff and Anderson 2009, [4]Takemoto 2004, [5]Goodall 1986, [6]Tweheyo and Obua 2001, [7]Pruetz and Bertolani 2009, [8]Anderson 1984, [9]N'guessan et al. 2009, [10]Amsler 2010, [11]Janmaat et al. 2014, [12]Ban et al. 2016, [13]Conclin-Brittain et al. 2006, [14]McLennan and Ganzhorn 2017, [15]O'Malley and Power 2012, [16]O'Malley and Power 2014, [17]Bryer et al. 2015, [18]Emery Thompson and Wrangham 2008, [19]Emery Thompson 2017, [20]Lesnik 2014, [21]Tennie et al. 2015, [22]Wrangham et al. 1993, [23]Wright et al. 2014, [24]Matsumoto-Oda and Oda 2001, [25]Matsumoto-Oda 2002, [26]Reynolds 2005, [27]Bates and Byrne 2009, [28]Caltech Submillimeter Observatory 2016,[29]Videan 2006, [30]Korstjens et al. 2010, [31]Pontzer and Wrangham 2004, [32]Sockol et al. 2007, [33]Pontzer et al. 2014, [34]Steudel-Numbers 2003, [35]Krief et al. 2014, [36]Tagg et al. 2018, [37]Pruetz 2018, [38]Wessling et al. 2018a, [39]Wessling et al. 2018b.

Insights into maintaining homeostasis

Published literature did not specify exact values for the hydration and fatigue gained and lost through feeding, drinking, nesting, resting and travel, but some information was available on energy loss and gain. Average daily energy expenditure for an adult chimpanzee is 1559 kCal/day (1558 kCal/day for males, 1305 kCal/day for females, and 1814 kCal/day for females with dependent offspring; Pontzer and Wrangham 2004). Chimpanzees spend about 207 kCal/day on travel, which consists of both climbing and walking (243 kCal/day for males, 177 kCal/day for females, and 202 kCal/day for lactating females; Pontzer and Wrangham 2004). Fruits vary in energetic content, but on average, chimpanzees gain about 3.1 kCal/gram dry weight while feeding on fruit (Emery Thompson and Wrangham 2008, McLennan and Ganzhorn 2017). Energy gains or losses through resting, drinking, and nesting have not been specified to date.

Discussion

This study reviewed the minimal landscape requirements and constraints for chimpanzees in selecting a site for a specific activity based on current knowledge of chimpanzee-habitat interactions and known preferences from field studies. This was carried out in order to explore chimpanzee behavioural flexibility and landscape use, and to provide a deeper understanding of the underlying reasons of why chimpanzees would choose certain locations over others. Overall, this study aimed to review current knowledge on the hypothesis that chimpanzees would select specific sites for specific activities to optimise their predator avoidance, thermoregulation, and foraging efficiency, and that specific vegetation features and micro-climate characteristics would be selected accordingly. Although the environmental determinants of chimpanzee site selection could be identified for certain activities, the review highlighted that the amount of research published to date remains limited and it remains to be determined which drivers are most important for chimpanzees in deciding *where* and *when* to perform their daily activities.

Chimpanzee site selection

For nest building behaviour, this study reviewed the prediction that chimpanzees would select sites with tall trees, large DBHs, high LBHs, closed canopies, high tree densities, high canopy connectivity, and high amounts of food and water available, following site selection observations in other primate species. The presented review showed that tree height, DBH, LBH, leaf and canopy cover, crown and canopy connectivity, and food and water availability are important for chimpanzees in nest site selection (e.g. Koops 2011, Stewart 2011, Ogawa et al. 2014). In addition, tree species, crown width, crown height, branch architecture, food tree density, slope, altitude, and vegetation type were important in selecting a nest location (e.g. Stanford and O'Malley 2008, Koops 2011, Stewart 2011). Even though this indicates that the preferences and requirements for chimpanzee nest site selection are well-known, the ranges of preferred characteristics are large, research on many environmental features is limited, and the relative importance of different environmental variables remains mostly unknown (e.g. Basabose and Yamagiwa 2002, Koops 2011, Stewart 2011). In some cases, the preferred ranges of vegetation features are so large that a real preference is difficult to identify, and site-specific preferences might be more informative than generalisations across sites.

For chimpanzee feeding, drinking, resting and travel activities, a considerable lack of in-depth details on chimpanzee-habitat interactions hinder the current understanding on *where* chimpanzees perform their daily activities. For example, for feeding behaviour this study aimed to review the prediction that chimpanzees would select sites with high amounts of food present, high tree and food tree densities, lower mean daily temperatures and lower luminosities, but the presented overview showed that only the role of food availability and local temperature have been studied (e.g. Matsumoto-Oda 2002, Takemoto 2004, McLennan and Ganzhorn 2017), making it difficult to assess the importance of other vegetation and micro-climate characteristics. Chimpanzees prefer specific tree species for feeding, trees with larger DBHs produce more fruit, and chimpanzees are more likely to find fruit in more densely forested patches (e.g. Chapman et al. 1992, Hernandez-Aguilar 2009). Chimpanzee food intake decreases with increasing distance to water (Lindshield et al. 2017).

For resting activities, this study reviewed the prediction that chimpanzees would select a location based on low daily temperatures, low luminosities, tall trees, large DBHs, high LBHs, closed canopies, high tree densities, high canopy connectivity and high amounts of food and water present. The presented review showed that resting locations are often in proximity to food sources (Brownlow et al. 2001) and in cooler micro-climates (Takemoto 2004), but the importance of other micro-climate and vegetation features remains to be studied. With regards to daytime nests, studies have highlighted the importance of specific tree species, large DBHs, the presence of understory vegetation and vegetation type (e.g. forest, woodland) in selecting a resting location (e.g. Brownlow et al. 2001, Koops et al. 2012a). Knowledge on the environmental context of resting locations when chimpanzees are not using a daytime nest is unknown. As specified in the introduction, resting time was often not effectively separated from social time in published field studies. For future purposes, however, resting time and social time should be split in order to investigate habitat selection, as well as preferred and required resources, for resting time and social time (e.g. affiliative social time, aggressive social time, grouping; Lehmann et al. 2007) separately.

For chimpanzee drinking, the prediction was reviewed that chimpanzees would select locations with high water availability, lower mean daily temperatures and lower luminosities. The review of this study showed that the presence of water is important in selecting a drinking location (e.g. Nishida 1980, Tonooka 2001), and water can be obtained from free-flowing sources such as ponds and rivers. Additionally, water can also be obtained from tree-holes and hand-dug drinking wells, or can be gained indirectly by consuming certain plant parts (e.g. Sugiyama 1995, Hunt and McGrew 2002, Sharma et al. 2016). The direct influence of other micro-habitat features on chimpanzee drinking behaviour remains to be studied. The presented review highlighted that most water sources can be found within forest vegetation types, where tree density is high and daytime temperatures and luminosities are lower than in surrounding vegetation (e.g. Pruetz and Bertolani 2009, Thompson et al. 2016).

For travel activities, this study reviewed the prediction that chimpanzees would select sites with tall trees, large DBHs, closed canopies, high tree densities, high canopy connectivity, lower mean daily temperatures, lower luminosities, and low understory densities. The presented overview showed that chimpanzees use forest, woodland and grassland (e.g. Tutin et al. 1983, Janmaat et al. 2013b), and that travel may additionally be food-directed (e.g. Janmaat et al. 2013b, Ban et al. 2016) and preferentially occurred in cooler micro-climates (Takemoto 2004). No other vegetation features and micro-climate characteristics were studied in relation to chimpanzee travel activities.

With regards to *when* chimpanzees perform their daily behaviours, the influence of many internal states and environmental circumstances remains unknown. Some general trends were, however, observed with edge of range temperatures and amounts of rainfall impeding chimpanzees' daily activities, with different behaviours peaking at different times of day, and with chimpanzees aiming to maintain homeostasis by keeping their energy, fatigue and hydration budgets neutral (e.g. Nishida 1980, Anderson 1984, Kosheleff and Anderson 2009).

The presented review thus confirms that chimpanzees are highly flexible in their usage of different vegetation features, micro-climate characteristics and general environmental variables, which argues in favour of their adaptability to different environments. Chimpanzees use some vegetation types more than others based on the presence of preferred vegetation structures and micro-climate characteristics (e.g. Hernandez-Aguilar 2009, Russak 2014, Bryson-Morrison et al. 2017). Forest seems to be the preferred vegetation type at most sites (e.g. Hunt and McGrew 2002, Russak 2014), which highlights the importance of forest vegetation in chimpanzee survival. Even though this review brings together the current understanding of chimpanzee behavioural flexibility and patterns of habitat use, and is useful for chimpanzee conservation by identifying a part of chimpanzees' habitat requirements and vegetation type importance, the information remains incomplete. It should furthermore be noted that most reviewed literature focused on chimpanzees in forested environments; data for chimpanzees in savannah landscapes remain limited. The persistent lack of detailed information on the vegetation features, micro-climate characteristics and general environmental circumstances preferred and required for feeding, drinking, nesting, resting and travel across environments renders it difficult to determine the exact locations *where* and *when* chimpanzees would perform their daily activities. It is therefore also difficult to identify at this point *why* chimpanzees select specific sites for specific activities and at different times of day. To date, the thermoregulation hypothesis, the antipredation hypothesis, and the antivector hypothesis have only been studied in relation to chimpanzee nest building and discrepancies between studies exist. For example, whereas some studies have found support for the antipredation hypothesis in nest building (i.e. building nests higher and more peripheral in trees when terrestrial predators were present: Stewart and Pruetz 2013), others have not (Koops et al. 2012a). In addition, some support was found for the antivector hypothesis in nesting (i.e. less arthropods at nest sites compared with non-nest sites: Samson et al. 2013), but mosquito densities did not seem to be a selective pressure in nest site choice in other studies (Koops et al. 2012a). Support has been found so far for the thermoregulation hypothesis in chimpanzee nest building (i.e. avoiding humid conditions in nest site selection: Koops et al. 2012a; and avoiding high wind speeds when selecting a nesting site: Samson and Hunt 2012). The optimal foraging theory has only been studied in relation to travel and feeding, suggesting that chimpanzees optimise their use of high-quality areas (e.g. Potts et al. 2016). The limited amount of knowledge on the minimal landscape requirements, constraints, and underlying motives for chimpanzee behavioural site selection indicates a need for more field-based research to further the current understanding of chimpanzee landscape use. Other primate species have been shown to select specific vegetation features and micro-climate characteristics, potentially as a result of optimising antipredation, foraging efficiency and/or thermoregulation (e.g. Rovero and Struhsaker 2007, Bettridge and Dunbar 2012, Cheyne et al. 2012, Thompson et al. 2016).

Future perspectives and implications

For future purposes, research should focus on collecting more empirical data on the minimal landscape requirements and constraints for chimpanzees to better understand the ecological determinants of their abundance and distribution. With impeding habitat loss, habitat alterations and climate change throughout the primate range (e.g. Arroyo-Rodriguez and Fahrig 2014, Estrada et al. 2017), detailed information on chimpanzee-habitat relationships enable the establishment of more appropriately focused conservation plans and strategies to protect chimpanzee habitat and their required resources (e.g. Cheyne et al. 2012). These efforts may safeguard chimpanzees from reaching critically low densities in their natural habitat. More data on the environmental determinants of chimpanzee site selection would furthermore allow detailed comparisons between sites, studies and species (e.g. Fruth and Hohmann 1996, Rendings et al. 2003, Pruetz 2007, Cheyne et al. 2012, Koops et al. 2012a). These comparisons may provide new insights into the underlying reasons and functions of variability in site selection, and may reveal new information on the selective pressures shaping an animal's landscape use. In this way, knowledge on chimpanzee-habitat relationships may also provide new insights into the behaviour and landscape use of closely related but extinct early hominins. Early hominin behavioural patterns are difficult to explore as behaviour does not fossilise, but detailed, innovative data on chimpanzees can provide a referential model (e.g. Jolly 2013, Mitani 2013, Plavcan 2013). As such, currently presented data and future research efforts on the ecological determinants of chimpanzee site selection have various implications, including determining the extent of chimpanzee behavioural adaptability and flexibility, exploring the consequences of future landscape change scenarios, identifying differences and similarities in chimpanzee site selection across sites and species, and shedding light on the behavioural adaptations and habitat relationships of early hominins.

Modelling purposes

The lack of available data on various vegetation features, micro-climates and general environmental circumstances initially presented some difficulties for the future modelling purposes of this thesis (Chapter 4 – Chapter 6), as the development of individual-based models requires the outline of specific model rules on individual-habitat relationships (e.g. Dunbar 2002). This lack of literature-based data was circumvented by presenting detailed overviews on the importance of various vegetation features, micro-climate characteristics and general environmental variables in chimpanzee site selection based on informed-opinion, expert-based review and landscape-scale studies. Assessments by the author and three chimpanzee experts (K. Koops, A. Pascual-Garrido and V. Reynolds) on the environmental determinants of chimpanzee site selection for feeding, drinking, nesting, resting and travel, resulted in a specific set of vegetation and micro-climate characteristics involved in selecting a site for each behaviour. The importance of these features is assumed to be based upon underlying antipredation, thermoregulation and optimal foraging pressures. Reviews of landscape-scale studies highlighted that only some vegetation features, micro-climates, and general environmental variables, such as tree height, canopy cover, tree density (e.g. Isabirye-Basyta and Lwanga 2008, Arroyo-Rodriguez and Mandujano 2009), needed to be included for landscape-scale analyses of primate habitat use. Furthermore, the quantitative gains and losses of energy, hydration and fatigue through chimpanzees' daily activities were explored. Even though limited information is available for hydration and fatigue, some detailed data were presented on energy gain and expenditure (e.g. Pontzer and Wrangham 2004, Emery Thompson and Wrangham 2008). The resulting overviews equipped this study with the necessary information to outline specific rules on chimpanzee-habitat relationships for the individual-based models on chimpanzee landscape use presented in this thesis. Additional rules that could not be derived from presented chimpanzee landscape and behaviour overviews were based on general theory and knowledge-based considerations (Chapter 4).

Conclusion

Whilst reviewing the vegetation features and micro-climate characteristics preferred and required for chimpanzee daily activities and thereby exploring chimpanzee behavioural flexibility and underlying reasons of chimpanzee landscape use, this study showed that considerable data on this topic are still lacking. Apart from nest building behaviour, not many daily activities have been studied extensively in relation to vegetation features, micro-climates, internal states and general environmental circumstances, making landscape-wide inferences on the minimal landscape requirements and constraints for chimpanzee site selection difficult. Furthermore, where preferred vegetation features for particular activities are specified, the amount of data presented are only limited and the relative importance of many environmental variables remains to be investigated. More research is thus necessary to further the current understanding of the ecological determinants and underlying factors influencing chimpanzee abundance and distribution. As a first attempt to characterise chimpanzee-habitat interactions across sites and studies in more detail, this study presented a detailed overview on the importance of various environmental variables in chimpanzee site selection based on informed-opinion, expert-based review and landscape-scale studies for modelling purposes (Chapter 4 – Chapter 6). Thereby, the presented review identified some specific habitat requirements and important vegetation types for chimpanzees. Appropriate mitigation strategies for chimpanzee habitat protection can be developed accordingly, which will aid in safeguarding chimpanzee survival across their geographical range in equatorial Africa. Findings may furthermore facilitate comparisons in site selection across sites, studies and species, and may shed new light on the behaviour and habitat relationships of early hominins.

CHAPTER 3

Quantifying chimpanzee landscapes: An environmental approach to classifying forest and savannah chimpanzees[1]

Abstract

Although chimpanzees are often referred to as ‘forest chimpanzees’ or ‘savannah chimpanzees’, the exact environmental conditions under which chimpanzee researchers call a chimpanzee landscape a ‘forest’ or ‘savannah’ have yet to be fully defined. It also remains unclear how these categorisations match with traditional biome classifications. This study aimed to provide a first quantitatively measurable definition of chimpanzee landscapes using a qualitative to quantitative process based on existing biome classifications, published field site descriptions, and environmental data. It was hypothesised that differences in temperature, rainfall, seasonality, forest cover, and tree cover at different chimpanzee study sites could be used to quantitatively categorise chimpanzee environments into dense forests, forest mosaics and savannahs. The locations of 43 study sites were matched with three selected biome classifications. Environmental data from study sites were analysed with descriptive statistics, scatterplots and k-means clustering analysis to determine whether environmental conditions support the landscape classifications of chimpanzee researchers. It was shown that the three selected biome classifications were unable to separate chimpanzee forest from savannah sites. Chimpanzee researcher classifications of sites, however, were separable based on environmental data. A clear distinction was found between chimpanzee savannah and forest sites based on forest cover and rainfall, and a further distinction was found within forest landscapes between dense forests and forest mosaics based on relationships between temperature, length of the dry season and forest cover. With detailed definitions, this study is the first to successfully formalise forest and savannah chimpanzee classifications, and to furthermore define a new class of mosaic chimpanzees. The formalised chimpanzee landscape definitions provide a unique contribution to primatology, and have implications for future studies on chimpanzee behavioural variability and hominin adaptations. Chimpanzee study sites can now systematically be classified, bringing consistency and transparency to the literature.

Keywords: Primates, habitat, landscape-based classification, forest cover, mosaic.

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[1] An adapted version of this chapter is submitted to the *International Journal of Primatology*.

Introduction

Nonhuman primates can be found across a wide variety of landscapes (e.g. for review: Meijaard 2016), but primates are often categorised in terms of their main preferred natural habitat and studies traditionally focus on the dominant habitat of the species in question (following e.g. McGrew et al. 1981; McKinney 2015). Many primate species, however, inhabit environments beyond their dominant habitat and show flexibility in the landscapes that they use as a consequence of natural environmental gradients and/or anthropogenic disturbances (e.g. Chapman and Peres 2001; Estrada et al. 2012; McKinney 2015). Such flexibility in habitat selection is considered important for primate survival in response to anthropogenic and naturally-induced changes to their preferred habitats (e.g. Estrada et al. 2017). However, a good understanding of the landscape-scale habitat requirements and preferences of primates is often lacking, and clear classifications of habitat types and landscapes used by various primate species are often scarce. Understanding and classifying the range of habitats used by primate species helps to understand their behavioural variability and ability to adapt to the major changes that their landscapes are currently undergoing.

One primate species that is often categorised in terms of its main habitat is the chimpanzee (*Pan troglodytes*). Chimpanzees are traditionally characterised as being primarily adapted to inhabit forest environments, and as a rainforest-adapted species, chimpanzees are often referred to as ‘forest chimpanzees’ or ‘forest dwellers’ (e.g. McGrew et al. 1981, Hunt and McGrew 2002, Russak 2013). Long-term chimpanzee research has, however, shown that chimpanzees are equally well adapted to inhabit forest mosaics and more open savannah-woodland habitats (e.g. McGrew et al. 1981, Hunt and McGrew 2002, Pruetz et al. 2002). Researchers studying chimpanzees in dry savannah-woodland landscapes currently classify their chimpanzees as ‘savannah chimpanzees’, ‘dry habitat chimpanzees’, or ‘savannah dwellers’ (e.g. McGrew et al. 1981, Russak 2013). At present therefore, chimpanzees are typically regarded as forest chimpanzees, unless otherwise specified. Nevertheless, the exact environmental circumstances under which a chimpanzee should be called a forest chimpanzee and its landscape a ‘forest’, or a savannah chimpanzee and its landscape a ‘savannah’ remain unclear, as quantitative definitions are lacking. It furthermore remains unknown how these categorizations match with traditional biome, vegetation and climate classification schemes.

Quantitatively categorising chimpanzees in terms of their environment produces consistency within chimpanzee literature, and provides important information in determining the exact range of different landscapes that chimpanzees are able to inhabit. This may aid in understanding the sources and functions of chimpanzee behavioural variability across sites (e.g. Moore 1992), which may advance the comprehension of their minimal landscape requirements and constraints. It may also help indicate whether and how chimpanzees will be able to cope with future habitat alterations and climate change throughout their range. Furthermore, understanding what exactly constitutes a forest or savannah landscape for chimpanzees and how this affects their behaviour may also aid in understanding the necessary adaptions for early hominins to function effectively in similar environments (e.g. Copeland 2009; McGrew et al. 1981; Moore 1992).

A first, straightforward solution to classifying chimpanzees according to their landscape would be to use existing climate and vegetation classifications of equatorial Africa. Unfortunately, however, this approach is subject to certain caveats. Though not for a lack of trying, to date no universally accepted climate and vegetation classification scheme has been put forward (Torello-Raventos et al. 2013). Traditionally, ecologists have classified habitats focusing on one or more ‘key variables’, such as climate, vegetation, or by aggregating such primary descriptors into vegetation formations, ecoregions or biomes (reviewed in Torello-Raventos et al. 2013), and each approach has advantages and disadvantages. Many different vegetation and climate maps thus exist, and all show slight variations in environments and distinctions between landscapes (e.g. WWF terrestrial ecoregions: WWF 2018; the Köppen-Geiger system: e.g. Peel et al. 2007; Bioclimatic types: e.g. Blasco et al. 2000). This makes it difficult to decide which climate or vegetation framework to use for chimpanzee landscape classifications. As a consequence, a thorough review of chimpanzees in terms of their habitat is necessary, and alternative approaches to landscape-based classifications may be needed.

The commonly held view that forest chimpanzees occupy dense forests, whereas savannah chimpanzees populate open, marginal savannahs presents an oversimplification, as typically no primate environments are exactly the same (e.g. Arroyo-Rodríguez and Fahrig 2014). Landscapes differ in their vegetation cover or composition (i.e. the presence and relative abundance of different vegetation types, such as forest, woodland, grassland, and swamp), spatial vegetation arrangement (i.e. the spatial layout of different vegetation types), and climate (e.g. rainfall, temperature, length of the dry season), and consequently in their resource quality, abundance and distribution (e.g. Hunt and McGrew 2002, Arroyo-Rodríguez and Fahrig 2014). As compared to chimpanzee forest environments, savannah landscapes are generally considered as being hotter and drier, having only a minimal amount of forest cover, and being scarcer and more seasonal in their resources (e.g. Hunt and McGrew 2002). Quantitative data on these landscape-scale differences provide an alternative approach to categorising chimpanzee environments. McGrew et al. (1981) and Moore (1992) were among the first to attempt to classify chimpanzees according to their habitat based on landscape-scale differences. Combined, they argued that vegetation cover, amount and distribution of rainfall, and temperature are the most important factors for landscape-based classifications, and both studies published a detailed overview of these environmental variables at various chimpanzee study sites. Even though this resulted in informative comparisons of vegetation composition, temperature, precipitation, and rainfall seasonality across chimpanzee sites (McGrew et al. 1981, Moore 1992), no exact definitions of savannah chimpanzees and forest chimpanzees were provided on the basis of these environmental variables. No further attempts to develop clear definitions have been published since then. Consequently, new sites could not easily be classified as forest or savannah, and existing sites remain classified based on chimpanzee researcher descriptions only.

This study therefore aims to present a detailed, landscape-based review and classification of chimpanzees and their environments, defining quantitatively when a chimpanzee can be called a ‘forest chimpanzee’ and its landscape a ‘forest’, and when a ‘savannah chimpanzee’ and its landscape a ‘savannah’, based on existing biome classification schemes in combination with published data on vegetation and climate of different chimpanzee study sites. Additionally, because chimpanzee landscapes ultimately form a natural environmental gradient from forests to savannahs, this study also explores whether meaningful intermediate chimpanzee landscape ‘classes’ can be identified. It is hypothesised that observed differences in vegetation composition (i.e. percentage of forest cover and tree cover) and climatic conditions (i.e. annual temperature, annual precipitation, length of the dry season) of different chimpanzee study sites can be used to quantitatively characterise chimpanzee environments into three typical landscapes: dense forests, forest mosaics, and savannahs. This study therefore uses qualitative data from published chimpanzee study site descriptions together with environmental maps of equatorial Africa to develop quantitative chimpanzee landscape definitions based on numerical data. A first, clear distinction is predicted between forest and savannah landscapes, thereby defining forest and savannah chimpanzees. Compared to forest chimpanzees, savannah chimpanzees are expected to inhabit areas with higher mean annual temperatures, lower amounts of annual precipitation, longer dry seasons, and less tree and forest cover. Within forest landscapes, a further notable distinction is predicted between dense forests and forest mosaics, thereby further defining forest from mosaic chimpanzees. Compared to mosaic chimpanzees, forest chimpanzees are expected to live in areas with lower mean annual temperatures, higher levels of annual rainfall, shorter dry seasons, and more tree and forest cover.

Methods

Study species

Chimpanzees (*Pan troglodytes*) were the study species of this research. In the wild, chimpanzees occupy a wide range of environments, and this variety of habitats is observed across all four chimpanzee subspecies (i.e. the western chimpanzee, *P. t. verus*; the Nigeria-Cameroon chimpanzee, *P. t. ellioti*; the central chimpanzee, *P. t. troglodytes*; and the eastern chimpanzee, *P. t. schweinfurthii*: e.g. Humle et al. 2016b). For analyses, all subspecies were treated equally.

Data collection

A thorough literature review of publications on chimpanzee behavioural ecology in their natural environments was conducted across peer-reviewed and grey literature (e.g. academic journals, articles, books, book chapters, university theses, state agency reports, and NGO reports) to provide insights into the variety of landscapes inhabited by chimpanzees. Specifically, this study searched for publications that outlined information on the spatial vegetation layout, vegetation composition and climate of different chimpanzee study sites using the Web of Science platform. Relevant literature was located using the key words ‘landscape’, ‘habitat’, ‘environment’, ‘vegetation’, and ‘climate’ in combination with ‘chimpanzee’, and by specifically searching for the chimpanzee study sites by name.

Literature data were first explored to determine the terminologies and general descriptions with respect to landscapes and landscape characteristics used in landscape studies. With regards to chimpanzee habitat, for each relevant publication encountered, following McGrew et al. (1981) and Moore (1992), data were collected on the name, location (GPS referenced), current environment, literature-based landscape class and descriptive information of the chimpanzee study site discussed:

Qualitative field site descriptors of chimpanzee study sites. For each study site, it was identified whether published literature classified the chimpanzees at each study site as 'forest chimpanzees' or 'savannah chimpanzees'. This was done either directly if authors had explicitly categorised the chimpanzees at a site as 'forest chimpanzees' or 'savannah chimpanzees', or indirectly based on published environmental field site descriptions of vegetation cover and climate by chimpanzee researchers using set key words (Table 3.1). For sites that were classified as 'forest', a further literature-based distinction was identified between 'dense forests' and 'forest mosaics' based on environmental field site descriptions of chimpanzee researchers using a secondary set of key words (Table 3.1).

Table 3.1. Landscape descriptions and key words as given by chimpanzee researchers used to distinguish between chimpanzee forest and savannah sites, and within forest sites to distinguish between dense forest and forest mosaic sites.

Landscape	**Literature description**
1. Savannah	Landscapes described as hot, dry and open, dominated by woodland and grassland vegetation types, and with only a minimal amount of forest cover. Chimpanzees described as savannah chimpanzees, savannah-dwelling chimpanzees, or dry-habitat chimpanzees.
2. Forest	Landscapes described as cool, humid and wet, mainly characterised by forest vegetation types. Chimpanzees described as forest chimpanzees, forest-dwellers, or forest-dwelling chimpanzees. Within forest environments, a further distinction can be identified between dense forests and forest mosaics.
2a. Forest Mosaic	Forest landscapes dominated by a mosaic of forest and other vegetation types (e.g. woodland, savannah grassland, cultivated fields). Chimpanzees sometimes described as woodland chimpanzees. Mosaic landscapes were often described as originating from dense forest landscapes that have been disturbed, either by anthropogenic influences and/or natural processes and disasters. Consequently, these landscapes were often referred to as forest - agricultural mosaics, forest - farm mosaics, forest - woodland mosaics, and/or forest - savannah mosaics, clearly indicating that forest is not the only dominant type of vegetation.
2b. Dense Forest	Forest landscapes dominated by forest vegetation types, and with only a minimal amount of other vegetation types present (e.g. woodland, savannah grassland, swamp). Chimpanzees often described as forest chimpanzees or forest-dwelling chimpanzees.

Quantitative field site descriptors of chimpanzee study sites: i) Vegetation. For each site, details were recorded on the presence of specific vegetation types (e.g. forest, woodland, bamboo, bushland, swamp, cultivated fields, and grassland), the vegetation cover (i.e. the relative abundance of the different vegetation types), the spatial vegetation layout (i.e. the spatial arrangement of the different vegetation types), and the vegetation features (e.g. tree species, tree height, diameter at breast height (DBH), lowest branch height (LBH), canopy cover, canopy connectivity, crown width, crown height, tree density, food tree density, understory density, food and water availability) of each vegetation type. Landsat derived maps of global tree cover (Hansen et al. 2013) were used to assess the overall percentage of tree cover within a 5km-radius of the GPS-referenced location of chimpanzee study sites (analyses performed in R by A.H. Korstjens). Here, trees were defined as all vegetation taller than 5m in height (Hansen et al. 2013). A 5km-buffer was chosen as this represents an approximate estimate of the maximum chimpanzee home-range size across sites (Chapter 4, p. 96). The GPS-referenced location of the chimpanzee study site is often the location of the research camp, which is presumably not situated in the heart of the chimpanzee territory; with a 5km-buffer, the tree cover of the complete chimpanzee home-range at a site is likely to be included. The closest chimpanzee study sites for the analyses (i.e. Bossou and Nimba, Guinea: Matsuzawa et al. 2011, Koops et al. 2012a) are furthermore about 5km apart, and these are the only sites for which the 5km-buffer overlaps; this further justifies the 5km-buffer. Note that as a more generalised and satellite-based product, values for Hansen tree cover (henceforward called ‘tree cover’) differ from the field-derived values for forest cover, woodland cover, etc., which are vegetation type specific. Therefore, tree cover data outline the coverage of any woody vegetation (including, for example, forest, woodland, swamp) and thus provide an objective measurement of tree cover across a wider range of vegetation types.

Quantitative field site descriptors of chimpanzee study sites: ii) Climate. For each site, details were recorded on mean annual precipitation (mm), mean annual temperature (°C), total number of dry months per year (i.e. months with < 100mm of rainfall: Hunt and McGrew 2002, Matsuzawa et al. 2011, Russak 2013), and length of the longest consecutive dry season, as there is more than one dry season at some study sites. Additional data were recorded on the micro-climate (i.e. local temperature (°C), and luminosity (Lux)) of each vegetation type. In case relevant publications did not include climatic data for a specific site, WorldClim – Global Climate Data were used with a 1km-buffer around the GPS-referenced chimpanzee study site (Hijmans et al. 2005, analysed in R by A.H. Korstjens).

Data analyses

A first comprehensive overview on ‘general’ landscape characteristics was provided, detailing terms to describe what a landscape is composed of, which vegetation types, vegetation features, climates, and micro-climates are commonly present, and how these are typically defined. For each chimpanzee study site encountered, following the environmental descriptions of McGrew et al. (1981) and Moore (1992), data from all reviewed papers were taken together and summarised, resulting in a detailed overview of the specific vegetation, climate and landscape class at each site. If data from different publications appeared contradictory for the same site, the information from the most recent paper with the most up-to-date information was selected.

To provide an illustrative example of the landscape-based classifications of chimpanzees and their environments based on existing biome, vegetation and climate classification schemes, three current environmental maps of equatorial Africa were selected: the WWF terrestrial ecoregions (WWF 2018), the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008) and White's Vegetation Map of Africa (White 1983). The encountered chimpanzee study sites (GPS-referenced) were plotted on these existing biome, vegetation and climate classification schemes either using ArcGIS (ArcMap version 10.2.2) or by visual comparisons. Additionally for the landscape-based classifications of chimpanzees and their habitats, each chimpanzee study site was assigned to its landscape class based on literature descriptions by chimpanzee researchers, and boxplots, scatterplots, data range tables and k-means clustering analysis (IBM SPSS Statistics, version 22) were used to assess whether chimpanzee researchers' landscape classification of study sites naturally grouped into three objectively-formalised landscape classes on the basis of their mean annual temperature (°C), mean annual rainfall (mm), length of the longest consecutive dry season (#), total number of dry months (#), forest cover (%), and tree cover (%). Two measures of rainfall seasonality were included (i.e. the length of the longest consecutive dry season and the total number of dry months), as well as two measures of vegetation cover (i.e. field-assessed forest cover and satellite-mapped tree cover). Only forest cover was used as a measure of vegetation composition due the inherent importance of forested vegetation to chimpanzees (e.g. Kano 1972, Hunt and McGrew 2002), and because it was the most often recorded vegetation cover in chimpanzee literature. Three clusters were used for the k-means clustering analysis, in correspondence with three proposed chimpanzee landscape 'classes', i.e. dense forests, forest mosaics, and savannahs. It was furthermore decided to work with unstandardized data to determine the relative contribution of each environmental variable to the resulting classification. Only study sites with available data for all six vegetation and climate variables were included in the k-means clustering analysis. As a result, 11 out of 43 sites were not included due to lack of data on forest cover. Kruskal-Wallis tests (IBM SPSS Statistics, version 22) were used to assess whether differences in environmental variables between the three proposed chimpanzee landscape classes were significant ($\alpha = 0.05$). In case of a significant difference, *post-hoc* Mann-Whitney U tests (Bonferroni correction: $\alpha = 0.05 / 3 = 0.0167$) were used to identify which pairwise comparison resulted in a significant difference.

Results

General landscape descriptions and definitions

Determining definitions

Frequently used terms in landscape studies include ‘landscape’, ‘landscape composition’, ‘landscape structure’, ‘vegetation types’, ‘vegetation features’, and ‘habitat’. The following definitions were used in this study:

Landscape. Arroyo-Rodriguez and Fahrig’s (2014, p. 902) ecological definition of a landscape was followed in this study, where a landscape is defined as “a heterogeneous land area containing a mosaic of patches or land cover types [here: *vegetation types*]” (see also e.g. Sanderson et al. 2002). Arroyo-Rodriguez and Fahrig (2014, p. 902) additionally explain that a landscape can be described by both its “composition [here: *landscape composition*] and configuration [here: *landscape structure*]”.

Landscape composition. Arroyo-Rodriguez and Fahrig (2014, p. 902) defined the term landscape composition as “the types and proportions of different forms of land cover [here: *vegetation types*] across the landscape”. Landscape composition is often not explicitly defined in published literature.

Landscape structure. As defined by Arroyo-Rodríguez and Fahrig (2014, p. 902), landscape structure emphasises “the spatial arrangement of a given landscape composition”. Landscape structure is also often not explicitly defined in published literature.

Vegetation types. Vegetation types are described as the types of vegetation that cover the landscape (e.g. McGrew et al. 1981, Arroyo-Rodríguez and Fahrig 2014, Russak 2014). Vegetation types include gallery forest, moist evergreen forest, riverine forest, thicket forest, closed woodland, open woodland, bamboo thicket, bushland, savannah grassland, swamp, rocky outcrops, and agricultural fields (e.g. Russak 2013, Arroyo-Rodríguez and Fahrig 2014, Coleman and Hill 2014). Each vegetation type is composed of a specific set of *vegetation features*, which is also called the vegetation architecture (e.g. Manduell et al. 2012).

Vegetation features. Vegetation features are defined as the characteristic structural attributes of a vegetation type (e.g. Seavy et al. 2009, Manduell et al. 2012, Coleman and Hill 2014). Vegetation features include tree and plant species, tree height, crown height, crown width, crown shape, canopy cover, canopy connectivity, DBH, LBH, food availability, water availability, tree density, food tree density, understory density, and branch architecture (e.g. Seavy et al. 2009, Manduell et al. 2012, Coleman and Hill 2014, Slater 2015).

Habitat. The term habitat has been used widely, and many contrasting interpretations exist. Habitat has been used to describe the overall landscape in which a species lives (simply called 'habitat'; e.g. Martinez and Garcia 2015, Voskamp et al. 2014, Terada et al. 2015), the spatial structure and composition of a landscape (referred to as 'habitat structure', 'habitat composition', or 'habitat configuration'; e.g. Hoffman and O'Riain 2011, Arroyo-Rodriguez et al. 2013a), the vegetation types present within a landscape (described as 'habitat' or 'habitat types'; e.g. Hoffman and O'Riain 2011, Coleman and Hill 2014, Russak 2014), and the vegetation features within vegetation types (referred to as 'habitat characteristics' or 'habitat measurements'; e.g. Martinez and Garcia 2014, Voskamp et al. 2014). To avoid confusion, the term habitat was not used in this study.

Following these definitions, a *landscape* is thus described by a specific *composition* and spatial arrangement of different *vegetation types*. Each vegetation type is made up of a particular set of *vegetation features*. The appropriate scale of measurement for a landscape is dependent on the species of interest (Jackson and Fahrig 2012). The above definitions are, however, only based on vegetation. When assessing how a species experiences its overall landscape, other factors should also be considered, most notably topography and climate (e.g. McGrew et al. 1981, Furuichi and Hashimoto 2004). These elements are interrelated, as both topography and climate will influence vegetation, which, in turn, will affect the (local) micro-climates of different vegetation types (e.g. McGrew et al. 1981, Kortland 1983, Blasco et al. 2000, Peel et al. 2006). In its most basic form, a landscape should therefore be regarded on the basis of its vegetation and climate. Climatic characteristics of landscapes include temperature (e.g. mean annual temperature), precipitation amount (e.g. mean annual precipitation), and precipitation seasonality (e.g. the length of the rainy and dry season) (e.g. McGrew et al. 1981, Kortlandt 1983, Blasco et al. 2000).

General landscape characteristics for chimpanzees

Chimpanzee landscapes across equatorial Africa are associated with fourteen main vegetation and land cover types: forest, woodland, bamboo, bushland, shrubland, swamp, terrestrial herbaceous vegetation (THV), cultivated fields, savannah grassland, mangrove, rocky outcrops, bare land, lava flows and beach. Table 3.2 gives the terms used by chimpanzee researchers to describe these vegetation and land cover types.

Each vegetation type is composed of a specific set of vegetation features and micro-climate characteristics. Seventeen vegetation features, two topographic variables, and two micro-climate characteristics are considered in this study across vegetation types: tree species, tree height, tree DBH, tree LBH, tree crown width, tree crown height, tree crown connectivity, tree leaf cover, tree branch architecture, canopy cover, canopy connectivity, understory density, tree density, food tree density, food availability, water availability, woody cover, slope, altitude, local temperature and local luminosity (Table 3.3). Many of these micro-habitat characteristics remain to be studied with respect to specific vegetation types, but those for which clear relationships with specific vegetation types could be identified for chimpanzee field sites are listed in Table 3.4. Specified vegetation features and micro-climate characteristics were used in this study to set out explicit definitions for the fourteen vegetation and land cover types encountered by chimpanzees (Table 3.5).

Table 3.2. Overview of different terms used to describe the main types of land cover used in this study.

Vegetation type	**Terms used***
Forest	Primary Montane Forest, Secondary Montane Forest, Mixed Forest, Gallery Forest, Riverine Forest, Evergreen Forest, Hill Forest, Ecotone Forest, Dense Canopy Forest, Open Canopy Forest, Medium-Altitude Tropical Forest, Primary Subhumid Forest, Secondary Forest, Mature Forest, Colonizing Forest, Moist Evergreen Forest, Coastal Forest, Tropical Rainforest, Primary Forest, Montane Forest, Evergreen Lowland Forest, Dry Forest, Mixed Mature Forest, Regenerating Forest, Lowland Evergreen Forest, Montane Evergreen Forest, Old Growth Forest, Young Forest, Dense Humid Evergreen Forest, Seasonally Inundated Forest, Thicket, Thicket Forest, Riparian Forest, Mixed Species Forest, Vine Tangle, Closed Forest, Secondary Mature Forest.
Woodland	Woodland, Open Woodland, Closed Woodland, Miombo Woodland, Savannah Woodland, Woodland Savannah, Thicket Woodland, Transition Woodland.
Bamboo	Bamboo, Bamboo Thicket, Bamboo Woodland, Bamboo Forest, Thicket.
Bushland	Bushland, Scrub Forest, Thicket, Scrub Woodland, Bush.
Shrubland	Shrubland, Shrubs.
Swamp	Swamp, Swamp Wetland, Swamp Forest, Riparian or Swamp Forest, Wetlands, Lowland Swamp, Papyrus Swamp, Raffia Swamps, Open Marsh, Herbaceous Fresh-Water Swamp and Aquatic Vegetation.
THV	Terrestrial Herbaceous Vegetation, THV, Open Canopy *Marantaceae* Forest, *Marantaceae* Forest, Open Canopy Forest with *Marantaceae* Understory.
Cultivated Fields	Cultivated Land, Cultivated Fields, Settlements, Agricultural Fields, Roads, Abandoned Fields, Anthropogenic Landscapes, Anthropogenic Grassland, Farm Lands, Fallow Areas, Plantations.
Savannah Grassland	Grassland, Plateau, Savannah Grassland, Savannah, Grassland Savannah, Wooded Grassland, Dry Grassland, Herbaceous Savannah, Treeless Grassland, Grassland with some Trees, High-Altitude Grasslands, Anthropogenic Grassland, Grassland with Scattered Trees, Moorland, Subalpine Moorland, Montane Grassland, Afroalpine Vegetation, Bush Savannah, Tree Savannah.
Mangrove	Mangrove, Halophytic Vegetation, Saline and Brackish Swamp.
Non-vegetated	Rocky Outcrops, Rocks, Bare Land, Earth, Sand, Lava Flows, Lava Plains, Beach.

*Based on: McGrew et al. 1981, Anderson et al. 1983, White 1983, Goodall 1986, Collins and McGrew 1988, Sugiyama 1995, Bermejo 1999, Duvall 2000, Brownlow et al. 2001, Basabose and Yamagiwa 2002, Hunt and McGrew 2002, Lanjouw 2002, Watts and Mitani 2002, Huijbregts et al. 2003, Lehmann and Boesch 2003, Furuichi and Hashimoto 2004, Emery Thompson et al. 2006, Hernandez-Aguilar et al. 2007, Hernandez-Aguilar et al. 2013, Pruetz et al. 2008, Bogart and Pruetz 2008, Devos et al. 2008, Bates and Byrne 2009, Hernandez-Aguilar 2009, Stokes et al. 2010, Head et al. 2011, Bertolani and Pruetz 2011, Matsuzawa et al. 2011, Stewart et al. 2011, Hockings et al. 2012, Koops et al. 2012a, McLennan and Hill 2012, Samson 2012, Samson and Hunt 2012, Samson and Hunt 2014, Watts 2012, Pascual-Garrido et al. 2013, Samson et al. 2013, Moore and Vigilant 2014, Oelze et al. 2014, Russak 2014, Sousa et al. 2014, Webster et al. 2014, Bortolamiol et al. 2014, Johnson et al. 2015, Moore et al. 2015, Nakamura et al. 2015, Bessa et al. 2015, Carvalho et al. 2015a, McLester et al. 2016.

Table 3.3. Definitions of the vegetation features, topographic variables, and micro-climate characteristics identified in this study. Descriptions and definitions adapted from Hernandez-Aguilar 2006, Koops 2011, and Slater 2015.

Vegetation Feature	**Definition**
Tree Species	The species of a tree.
Tree Height	Height from the base of the tree to the top of the crown (m).
Tree DBH	Stem diameter/ diameter at breast height (i.e. at ~1.3m) of a tree (cm).
Tree LBH	Height from the base of the tree to underside of the lowest branch (m).
Tree Crown Width	Diameter of the crown (m).
Tree Crown Height	Height of the underside of the lowest branch to the top of the crown (m).
Tree Crown Connectivity	Proportion of overlap of the tree crown in relation to the neighbouring tree crowns (%).
Tree Leaf Cover	Proportion of the tree crown in leaf (%)
Tree Branch Architecture	Branch orientation of a canopy (horizontal/ inclined/ vertical/ opposite/ alternate)
Canopy Cover	Proportion of sky/ground covered by canopy leaves in a given area (%)
Canopy Connectivity	Proportion of overlap in crowns in a given area (%)
Understory Density	Density of understory plant species in a given area (%).
Tree Density	Density of trees in a given area (stems/ha).
Food Tree Density	Density of food trees in a given area (stems/ha).
Food Availability	The presence of edible food in a given area (yes/ no/ quantity).
Water Availability	The presence of drinkable water in a given area (yes/ no/ quantity).
Temperature	Local temperature at a given location at ground level (°C).
Luminosity	Exposure to sunlight at a given location at ground level (Lux).
Slope	Incline of the ground at a given location (flat/ medium/ steep).
Altitude	Elevation of a given location (m above sea level).
Woody Cover	Proportion of a given area covered by trees (%)

Table 3.4. Vegetation features and micro-climate characteristics of the vegetation types identified in this study. ‘Conn.’ stands for connectivity, ‘dens.’ for density, ‘arch.’ for architecture, ‘avail.’ for availability, and ‘n/a’ stands for not applicable. ‘?’ indicates that details on this specific characteristic are missing for this vegetation type. Canopy and crown connectivity measures are based on measures of canopy cover, e.g. closed canopy cover equals high canopy/ crown connectivity. As the exact values of many vegetation features remain to be specified within published literature, this study categorised these variables as either high, medium or low, small, medium or large, closed, medium or open, and/or sparse, medium and dense, based on literature descriptions. High, closed, large and dense refers to values at the upper quartile of the potential range of values. Medium refers to the middle half of the range of potential values. Low, open, small and sparse refers to the lower quartile of the potential range of values.

	Forest	**Woodland**	**Bamboo**	**Bushland**	**Shrubland**	**Swamp**	**THV**	**Cultivated Fields**	**Savannah Grassland**	**Mangrove**	**Rocky Outcrops**	**Bare Land**	**Lava Flows**	**Beach**
Tree species	Various	Various	Various	Various	Various	Various	Various	Various	Various	Various	n/a	n/a	n/a	n/a
Tree height	High *10 – 50m*	Medium *8 – 20m*	Medium	Low *3 – 15m*	Low	?	Medium	?	Low	?	n/a	n/a	n/a	n/a
DBH	Large or small	Small to large	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
LBH	?	< 2m	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
Crown width	?	?	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
Crown height	?	?	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
Leaf cover	Evergreen or semi-deciduous; Dense	(Semi) deciduous; Medium	?	?	?	?	?	?	(Semi) deciduous	?	n/a	n/a	n/a	n/a
Crown conn.	High	Medium	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
Branch arch.	?	?	?	?	?	?	?	?	?	?	n/a	n/a	n/a	n/a
Canopy cover	Closed	Medium	Medium	Open	Open	Open	Open	?	Open	?	n/a	n/a	n/a	n/a
Canopy conn.	High	Medium	Medium	Low	Low	Low	Low	?	Low	?	n/a	n/a	n/a	n/a
Understory	Sparse	Medium	Medium	Medium	Dense	?	Dense	?	Dense	?	n/a	n/a	n/a	n/a
Tree dens.	High	Medium	Medium	Low	Low	Low	Low	?	Low	?	n/a	n/a	n/a	n/a
Food tree dens.	High	Medium	?	?	?	?	?	?	Low	?	n/a	n/a	n/a	n/a
Food avail.	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	Seasonal	No	No	No	No
Water avail.	Permanent	?	?	?	?	Permanent to seasonal	?	?	Scarce and seasonal	Periodically (sea water)	No	No	No	No
Temperature	Cool days, warm nights	Medium hot days, medium cool nights	?	?	?	?	?	?	Hot days, cool nights	?	?	?	?	?
Luminosity	Shaded	Sun and shade	?	?	?	?	?	?	Sunny	?	?	?	?	?
Slope	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Altitude	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Woody cover	> 80%	> 40%	?	> 40%	?	?	?	?	< 40%	?	n/a	n/a	n/a	n/a

*Based on: e.g. McGrew et al. 1981, Tutin et al. 1983, White 1983, Collins and McGrew 1988, Garcia and Mba 1997, Reed 1997, Bermejo 1999, Duvall 2000, Grimmond et al. 2000, Boesch et al. 2002, Hunt and McGrew 2002, Lanjouw 2002, Caldecott and Miles 2005, Reynolds 2005, Gilby et al. 2006, Hernandez-Aguilar 2006, Morgan et al. 2006, Ogawa et al. 2007, Bogart and Pruetz 2008, Devos et al. 2008, Pruetz et al. 2008, Hernandez-Aguilar 2009, Pruetz and Bertolani 2009, Cerling et al. 2011, Matsuzawa et al. 2011, Sousa et al. 2011, Behera et al. 2012, Inogwabini et al. 2012, Hernandez-Aguilar et al. 2013, Russak 2013, Stewart and Pruetz 2013, Ogawa et al. 2014, Russak 2014, Sousa et al. 2014, Carvalho et al. 2015a, Abdallah et al. 2016, Foerster et al. 2016, Kong et al. 2016, Thompson et al. 2016, Ehbrecht et al. 2017, Gaudio et al. 2017, Keppel et al. 2017.

Table 3.5. Final definitions used in this study to describe vegetation types based on Tables 3.2 and 3.4.

Vegetation type	**Definition**
Forest	Vegetation type consisting of a continuous stand of evergreen or semi-deciduous trees which are tall (10m to 50m) and often have large DBHs. Tree density and food tree density is high, crown and canopy cover is closed, and there is high connectivity between canopies. Understory is sparse and there is permanent water available. Temperatures are relatively cool during the day and relatively warm during the night, and there is plenty of shade. Woody cover is mostly > 80%.
Woodland	Vegetation type consisting of a more open stand of (semi-)deciduous trees, in which at least 40% of the land is covered by trees. Trees are of medium height (8m to 20m) and have a wide range of DBHs. (Food) tree density is medium, as is crown/ canopy cover (intermediate between closed and open), crown/ canopy connectivity, and the amount of understory present. Temperatures are intermediate between forest and savannah grassland, and there are both sunny and shaded locations available.
Bamboo	Vegetation type dominated by bamboo species. Trees present have medium heights and there is a medium tree density. Canopies are discontinuous, meaning that the canopy cover and the canopy connectivity are medium. The amount of understory is medium.
Bushland	Vegetation type dominated by bushes. For those trees present, tree density is low, tree height is low (3m – 15m, or lower), woody cover is > 40%, canopy cover is open and there is overall low canopy connectivity. The amount of understory is medium.
Shrubland	Vegetation type dominated by shrubs. Overall tree height for those trees present is low, as is tree density. Canopy cover is open, canopy connectivity is low, and there is a dense layer of understory present.
Swamp	Vegetation type which is permanently inundated by water. Tree density is low, canopy cover is open and canopy connectivity is low. Seasonal to permanent water is available.
THV	Vegetation type characterised by a dense understory of *Marantaceae* species, with sparse, medium-sized trees present, low canopy connectivity and open canopy cover.
Cultivated Fields	Vegetation type altered by human activity, with few natural stands of trees remaining. Lands are being used for cultivation and agriculture.
Savannah Grassland	Vegetation type dominated by understory grasses and other herbs. Woody cover is less than 40%, and present (semi-)deciduous trees are sparsely distributed and low in height. Canopy cover is open, and canopy connectivity is low. There is a low density of food trees. Occasionally, water sources are present, but these are scarce and seasonal. Daytime temperatures are hot and there is little shade available. Nighttime temperatures are relatively cool.
Mangroves	Vegetation type dominated by halophytic vegetation. Areas are subject to tidal flooding by sea-water.
Rocky Outcrops	Land cover type made up of bare rock, with sparse to absent vegetation.
Bare Land	Land cover type consisting of bare pieces of earth, with sparse to absent vegetation.
Lava Flows	Land cover type typified by a solidified flow of once liquid lava, with large boulders and crevasses present, with sparse to absent vegetation.
Beach	Land cover type at the edge of a lake or sea marked by sand and with sparse to absent vegetation.

Qualitative descriptors of chimpanzee study sites

Forty-three chimpanzee study sites were identified across equatorial Africa in this study. Based on qualitative literature statements and descriptions of sites or chimpanzees from chimpanzee researchers (Table 3.1), the 43 study sites could be separated into three landscape classes, i.e. dense forests, forest mosaics, and savannahs

(Table 3.6, Figure 3.1). Of the 43 chimpanzee study sites, nine sites could be classified as savannahs and 34 sites as forests (Table 3.6, Figure 3.1). Within forest environments, 22 sites could be classified as dense forests, and 12 sites as forest mosaics (Table 3.6, Figure 3.1).

Table 3.6. Literature-based landscape classifications of chimpanzees and their environments based on descriptions of chimpanzee researchers (Table 3.1). Site list adapted from Inskipp (2005), and Russak (2013). NP = National Park, FR = Forest Reserve, WR = Wildlife Reserve.

Site	**Literature-based Classification: Chimpanzee Landscape**	**Literature-Based Forest Classification: Forest or Mosaic**	**References used (major)**
Bafing (Mali)	Savannah	n/a	Duvall 2000 Duvall 2008
Bakoun (Guinea)	Forest	Forest Mosaic	Boesch et al. 2017
Bossou (Guinea)	Forest	Forest Mosaic	Sugiyama 1995 Matsuzawa et al. 2011 Hockings et al. 2012
Budongo FR (Uganda)	Forest	Dense Forest	Reynolds 2005 Munn 2006 Hobaiter et al. 2017
Bulindi (Uganda)	Forest	Forest Mosaic	McLennan and Hill 2012 McLennan 2013 McLennan and Ganzhorn 2017
Bwindi-Impenetrable NP (Uganda)	Forest	Dense Forest	Nkurunungi and Stanford 2006 Stanford and O'Malley 2008 Standford 2002
Caiquene-Cadique (Guinea-Bissau)	Forest	Forest Mosaic	Bessa et al. 2015
Comoé (Ivory Coast)	Savannah	n/a	Lapuente et al. 2016
Dzanga-Ndoki NP (CAR)	Forest	Dense Forest	Blom et al. 2001
Fongoli (Senegal)	Savannah	n/a	Pruetz 2007 Pruetz and Bertolani 2009 Bertolani and Pruetz 2011
Gashaka Gumti NP (Nigeria)	Forest	Forest Mosaic[1]	Fowler and Sommer 2007 Sommer et al. 2012 Sommer et al. 2016
Gishwati (Rwanda)	Forest	Dense Forest	Chancellor et al. 2012a Chancellor et al. 2012b Chancellor et al. 2017
Gombe NP (Tanzania)	Forest	Forest Mosaic	Goodall 1986 Rudicell et al. 2010 Foerster et al. 2016
Goualougo Triangle[2] (Republic of Congo)	Forest	Dense Forest	Morgan et al. 2006 Sanz and Morgan 2009 Lesnik et al. 2015
Ishasha River (DRC)	Savannah	n/a	Sept 1992 Schoeninger et al. 1999
Issa Valley (Tanzania)	Savannah	n/a	Hernandez-Aguilar 2009 Stewart and Pruetz 2013 Russak 2014
Ituri FR (DRC)	Forest	Dense Forest	Hart et al. 1986 Thomas, 1991
Kahuzi-Biega NP (DRC)	Forest	Dense Forest	Yamagiwa et al. 1996 Yamagiwa and Basabose 2009 Yamagiwa et al. 2012
Kalinzu FR (Uganda)	Forest	Dense Forest	Hashimoto et al. 1999 Furuichi et al. 2001 Furuichi and Hashimoto 2004

Site	Literature-based Classification: Chimpanzee Landscape	Literature-Based Forest Classification: Forest or Mosaic	References used (major)
Kasakati (Tanzania)	Savannah	n/a	McGrew et al. 1981 Moore 1992
Kibale NP (Uganda)	Forest	Dense Forest	Emery-Thompson et al. 2006 Watts 2012 Watts and Amsler 2013
Kpala (Liberia)	Forest	Forest Mosaic	Ohashi 2015
La Belgique (Cameroon)	Forest	Dense Forest	Tagg et al. 2013 Sanz et al. 2014
Lac Tumba Landscape (DRC)	Forest	Forest Mosaic	Inogwabini et al. 2012
Lagoas de Cufada NP (Guinea-Bissau)	Forest	Forest Mosaic	Carvalho et al. 2013 Carvalho et al. 2015a Carvalho et al. 2015b
Loango (Gabon)	Forest	Dense Forest	Head et al. 2011 Head et al. 2012
Lopé NP (Gabon)	Forest	Dense Forest	Tutin et al. 1997a Tutin et al. 1997b Tutin 1999
Mahale Mountains NP (Tanzania)	Forest	Forest Mosaic[1]	Matsumoto-Oda 2001 Boesch et al. 2002 Nakamura et al. 2015
Minkébé NP (Gabon)	Forest	Dense Forest	Huijbregts et al. 2003
Monte Alén NP (Equatorial Guinea)	Forest	Dense Forest	Garcia and Mba 1997
Moukalaba-Doudou NP (Gabon)	Forest	Dense Forest	Wilfried and Yamagiwa 2014
Mount Assirik (Senegal)	Savannah	n/a	McGrew et al. 1981 Tutin et al. 1983 McGrew et al. 2014
Ndoki-Likouala (Congo)	Forest	Dense Forest	Stokes et al. 2010
Ngel Nyaki FR (Nigeria)	Forest	Dense Forest	Beck and Chapman 2008 Dutton and Chapman 2015 Dutton et al. 2016
Ngotto Forest (CAR)	Forest	Dense Forest	Hicks et al. 2005 Hicks et al. 2009 Freycon et al. 2015
Nimba Mountains (Guinea)	Forest	Dense Forest	Koops et al. 2012a Koops et al. 2012b Koops et al. 2013
Odzala NP (Republic of Congo)	Forest	Dense Forest	Bermejo 1999 Devos et al. 2008
Sapo (Liberia)	Forest	Dense Forest	Anderson et al. 1983 Greengrass 2015
Semliki WR (Uganda)	Savannah	n/a	Hunt and McGrew 2002 Samson and Hunt 2012 Webster et al. 2014
Taï NP (Ivory Coast)	Forest	Dense Forest	Boesch & Boesch-Archerman 2000 Anderson et al. 2002 Eckhardt et al. 2015
Tenkere (Sierra Leone)	Forest	Forest Mosaic	Alp 1993 Alp 1997
Tongo (DRC)	Forest	Forest Mosaic	Lanjouw 2002
Ugalla (Tanzania)	Savannah	n/a	Moore 1992 Ogawa et al. 2014 Moore et al. 2017

[1] Whereas the literature classifies this site as a forest mosaic, the actual percentage of forest cover of the study area/ chimpanzee home-range would imply this site should be classified as a dense forest due to its dominant forest cover (Table 3.1). As this table describes the literature-based classification, however, the mosaic classification specified in literature is used; [2]In early years Goualougo Triangle was referred to as

Nouabalé-Ndoki, due to its location in the Nouabalé-Ndoki National Park, Republic of Congo (Kuroda et al. 1996).

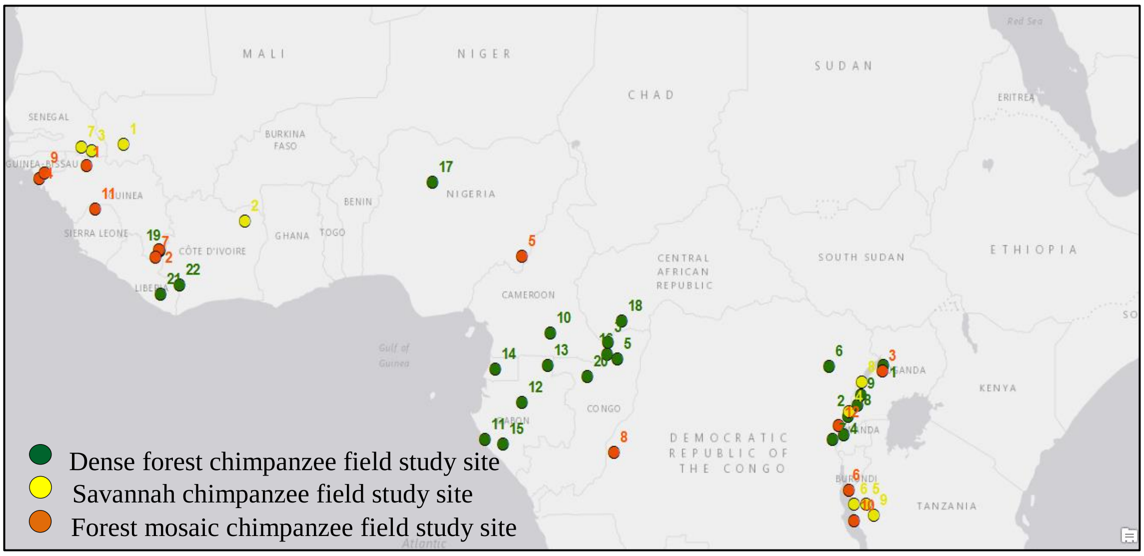


Figure 3.1. Literature-based landscape classification (based on qualitative literature descriptions of sites or chimpanzees from chimpanzee researchers: Table 3.1) of the 43 chimpanzee study sites encountered in this study: dense forest (1 = Budongo, 2 = Bwindi, 3 = Dzanga-Ndoki, 4 = Gishwati, 5 = Goualougo, 6 = Ituri, 7 = Kahuzi-Biega, 8 = Kalinzu, 9 = Kibale, 10 = La Belgique, 11 = Loango, 12 = Lopé, 13 = Minkébé, 14 = Monte Alén, 15 = Moukalaba-Doudou, 16 = Ndoki-Likouala, 17 = Ngel-Nyaki, 18 = Ngotto, 19 = Nimba, 20 = Odzala, 21 = Sapo, 22 = Taï), forest mosaic (1 = Bakoun, 2 = Bossou, 3 = Bulindi, 4 = Caiquene-Cadique, 5 = Gashaka, 6 = Gombe, 7 = Kpala, 8 = Lac Tumba Landscape, 9 = Lagoas de Cufada, 10 = Mahale, 11 = Tenkere, 12 = Tongo) and savannah (1 = Bafing, 2 = Comoé, 3 = Fongoli, 4 = Ishasha, 5 = Issa, 6 = Kasakati, 7 = Mount Assirik, 8 = Semliki, 9 = Ugalla).

Quantitative descriptors of chimpanzee study sites

Vegetation

The 43 identified chimpanzee study sites across equatorial Africa differed widely in their vegetation composition (Table 3.7). The amount of detail presented on the vegetation of each study site varied: Most study sites specified the different vegetation types present within the chimpanzee home-range, and some also quantified the amount of different vegetation types at the site, for example by outlining the specific area (km^2) or relative coverage (% of total area). Sites generally contained between one and five different types of vegetation, the most commonly mentioned ones being forest, woodland, savannah grassland and swamp. Whereas some chimpanzee study sites were characterised by a single dominant type of vegetation, others were composed of many different vegetation types, all with varying proportions and sizes. Many authors primarily focused on quantifying the specific proportion of forest within their study area. Forest was also identified as the only type of vegetation consistently present across all chimpanzee study sites encountered. Across the 43 chimpanzee study sites, forest cover ranged over 1.5 – 100%, and tree cover ranged between 8.5 – 99.9% (Table 3.7).

Table 3.7. Vegetation composition of the chimpanzee study sites encountered in this study. Site list adapted from Inskipp (2005) and Russak (2013). NP = National Park, FR = Forest Reserve, WR = Wildlife Reserve.

Site	**Vegetation types -** *present*	**Vegetation types** *– abundance (%)*[1]	**Vegetation types** *– area (km^2/ ha)*[1]	**Tree cover -** *from Landsat*[6]	**References used (major)**
Bafing (Mali)	Forest Woodland Bamboo Bushland Savannah Grassland	< 5% of forest, other vegetation types not specified.[2]	Not specified.	10.74%	Duvall 2000 Duvall 2008
Bakoun (Guinea)	Forest Woodland Savannah Grassland Rocky Outcrops	Not specified.	Not specified.	27.25%	Boesch et al. 2017
Bossou (Guinea)	Forest THV Cultivated Fields Savannah Grassland	> 7% of forest (only primary forest specified). Other vegetation types (incl. other forest types) not specified.[3]	1km^2 of primary forest (not including other forest types). Area of the other vegetation types not specified.	43.70%	Sugiyama 1995 Humle 2011 Bryson-Morrison et al. 2016 Bryson-Morrison et al. 2017
Budongo FR (Uganda)	Forest	90% forest, and 10% swamp.	-	96.08%	Tweheyo and Lye 2003 Reynolds 2005 V. Reynolds[7]
Bulindi (Uganda)	Forest Swamp Savannah Grassland Cultivated Fields	15% forest, other vegetation types not specified.[4]	2km^2 of riverine forest, other vegetation types (incl. other forest types),not specified.	41.79%	McLennan and Hill 2012 McLennan 2013
Bwindi-Impenetrable NP (Uganda)	Forest Swamp Bamboo	About 98% forest and 1 – 2% bamboo and swamp.	Not specified.	39.52%	Howard 1991 Nkurunungi and Stanford 2006 Stanford and O'Malley 2008
Caiquene-Cadique (Guinea-Bissau)	Forest Mangrove Savannah Grassland Cultivated Fields	85.5% forest, 12.5% cultivated fields, 2% savannah grassland. Other vegetation types not specified.[4]	Not specified.	25.74%	Bessa et al. 2015
Comoé (Ivory Coast)	Forest Savannah Grassland	91% savannah grassland, and 9% of forest.[2]	Not specified.	16.79%	Fisher et al. 2002 Lapuente et al. 2016
Dzanga-Ndoki NP (CAR)	Forest Swamp	Not specified.	Not specified.	99.45%	Blom et al. 2001
Fongoli (Senegal)	Forest Woodland Bamboo Savannah Grassland Cultivated Fields	2% forest, 46% woodland, 36% savannah grassland, 12% bamboo, and 4% cultivated field.	Not specified.	11.81%	Bogart and Pruetz 2008 Pruetz and Bertolani 2009 Stewart and Pruetz 2013
Gashaka Gumti NP (Nigeria)	Forest Woodland	72.3% of forest and 27.7% of woodland.	Not specified.	54.55%	Pascual-Garrido et al. 2013 Sommer et al. 2016
Gishwati (Rwanda)	Forest Cultivated Fields	64.3% forest and 35.7% cultivated fields.[3]	9km^2 of forest, and 5km^2 of cultivated fields.	38.65%	Chancellor et al. 2012b Chancellor et al. 2017
Gombe NP (Tanzania)	Forest Woodland Savannah Grassland Beach Bare Land	25% forest, 58% woodland, and 17% of grassland and beach. Bare land area too small to include.[2]	887 ha of forest, 2040 ha woodland, 599 ha of grassland and beach, and 2.9 ha of bare land.[2]	23.15%	Goodall 1986 Rudicell et al. 2010 Foerster et al. 2016
Goualougo Triangle (Republic of Congo)	Forest Swamp	94.8% forest and 5.2% swamp.	Not specified.	97.72%	Morgan et al. 2006 Devos et al. 2008

Site	**Vegetation types -** *present*	**Vegetation types** – *abundance (%)*[1]	**Vegetation types** – *area (km^2/ ha)*[1]	**Tree cover -** *from Landsat*[6]	**References used (major)**
Ishasha River (DRC)	Forest Woodland Savannah Grassland	Not specified.	Not specified.	21.28%	Sept 1992 Schoeninger et al. 1999
Issa Valley (Tanzania)	Forest Woodland Swamp Savannah Grassland Rocky Outcrops	1.5% forest, 8% savannah grassland and swamp, 90.5% woodland. Coverage of rocky outcrops not specified.	Not specified.	48.28%	Hernandez-Aguilar 2009 Stewart et al. 2011 Russak 2013
Ituri FR (DRC)	Forest Swamp	100% forest.[5]	Not specified.	99.88%	Hart et al. 1986 Thomas 1991
Kahuzi-Biega NP (DRC)	Forest Bamboo Swamp	77.6% forest, 17.6% bamboo, and 4.8% swamp.	25.7km^2 forest, 5.8km^2 bamboo, and 1.6km^2 swamp.	87.45%	Yumoto et al. 1994 Yamagiwa et al. 1996 Basabose 2005
Kalinzu FR (Uganda)	Forest Bushland Savannah Grassland	75% forest, 15% savannah grassland and bushland.[2]	Not specified.	57.01%	Howard 1991 Hashimoto et al. 1999 Furuichi et al. 2001
Kasakati (Tanzania)	Forest Woodland Savannah Grassland	10% forest, 59% woodland, 32% savannah grassland.	Not specified.	53.69%	McGrew et al. 1981
Kibale NP (Uganda)	Forest Swamp Woodland Savannah Grassland	77% forest, 6% woodland, 15% savannah grassland, and 2% swamp.[2]	Not specified.	50.85%	Howard 1991 Potts et al. 2009 Gilby et al. 2017
Kpala (Liberia)	Forest Cultivated Fields	Not specified.	Not specified.	56.65%	Ohashi 2015
La Belgique (Cameroon)	Forest Swamp	80% forest, 20% swamp.	Not specified.	90.29%	Tagg et al. 2013
Lac Tumba Landscape (DRC)	Forest Swamp Cultivated Fields	35 – 40% forest and 60 – 65% swamp. Coverage of cultivated fields not specified.[2]	Not specified.	77.25%	Inogwabini et al. 2012
Lagoas de Cufada NP (Guinea-Bissau)	Forest Woodland Swamp Mangrove Savannah Grassland Cultivated Fields	44% forest, 54% woodland, and 2% of other vegetation types.[2]	Not specified.	45.79%	Carvalho et al. 2015a Carvalho et al. 2015b
Loango (Gabon)	Forest Swamp Savannah Grassland	79.7% forest, 19.7% swamp and savannah grassland.	Not specified.	60.96%	Head et al. 2011 Head et al. 2012 Estienne et al. 2016
Lopé NP (Gabon)	Forest THV Savannah Grassland	Not specified.	Not specified.	65.57%	Tutin et al. 1997a Tutin et al. 1997b Tutin 1999
Mahale Mountains NP (Tanzania)	Forest Woodland Bamboo Swamp Savannah Grassland	73% forest, 23% woodland and 3.8% swamp. Coverage of other vegetation types not specified.	Not specified.	59.00%	Boesch et al. 2002 Nakamura et al. 2015 Matsumoto 2017
Minkébé NP (Gabon)	Forest Swamp THV	> 60% of forest (only undisturbed forest specified). Coverage of other vegetation types (incl. other forest types) not specified.	Not specified.	90.97%	Huijbregts et al. 2003
Monte Alén NP (Equatorial Guinea)	Forest Cultivated Fields	Not specified.	Not specified.	91.05%	Garcia and Mba 1997
Moukalaba-Doudou NP (Gabon)	Forest	100% forest.[5]	-	83.19%	Wilfried and Yamagiwa 2014
Mount Assirik (Senegal)	Forest Woodland Bamboo	3% forest, 37% woodland, 5% bamboo, and 55%	140 ha of forest (out of 5100 ha area). Area of	12.98%	McGrew et al. 1981 McGrew et al. 2014 McGrew 2015

Site	**Vegetation types -** *present*	**Vegetation types** *– abundance (%)*[1]	**Vegetation types** *– area (km^2/ ha)*[1]	**Tree cover -** *from Landsat*[6]	**References used (major)**
	Savannah Grassland	savannah grassland.	other vegetation types not specified.		
Ndoki-Likouala (Congo)	Forest Swamp THV Savannah Grassland Cultivated Fields	Not specified.	Not specified.	99.38%	Stokes et al. 2010
Ngel Nyaki FR (Nigeria)	Forest	100% forest.[5]	7.5km^2 of forest.	8.45%	Beck and Chapman 2008 Dutton and Chapman 2015 Dutton et al. 2016
Ngotto Forest (CAR)	Forest Swamp	87% forest, and 13% swamp.[2]	Not specified.	85.31%	Bastin 1996 Hicks et al. 2005
Nimba Mountains (Guinea)	Forest THV Savannah Grassland	86% forest and 14% THV. Savannah grassland coverage not specified.	Not specified.	69.00%	Koops et al. 2012a K. Koops[7]
Odzala NP (Republic of Congo)	Forest Swamp THV	95% forest, 4% THV, and 1% swamp.	Not specified.	95.79%	Bermejo 1999 Devos et al. 2008
Sapo (Liberia)	Forest Swamp	87% forest and 13% swamp.	Not specified.	76.37%	Anderson et al. 1983
Semliki WR (Uganda)	Forest Woodland Swamp Savannah Grassland	7.25% of forest. Coverage of other vegetation types not specified.[2]	Not specified	34.03%	Hunt and McGrew 2002 Samson and Hunt 2012 Webster et al. 2014
Taï NP (Ivory Coast)	Forest	100% forest.[5]	Not specified.	76.07%	Boesch and Boesch-Archermann 2000 Kouakou et al. 2009 Janmaat et al. 2013b
Tenkere (Sierra Leone)	Forest Woodland Savannah Grassland Cultivated Field	Not specified.	Not specified.	44.23%	Alp 1993 Alp 1997
Tongo (DRC)	Forest Swamp Woodland Shrubland Bare Land Lava Flows	Not specified.	Not specified.	61.06%	Lanjouw 2002
Ugalla (Tanzania)	Forest Woodland Savannah Grassland	2% forest, 86% woodland, 12% savannah grassland[2]	Not specified.	39.31%	Moore 1994 Ogawa et al. 2014 Moore et al. 2017

[1]Vegetation composition of the study area, and thus the chimpanzee home-range, was used preferably. In case this was not possible, vegetation composition of the whole park was used instead if available; [2]Data on vegetation cover for the whole park; [3]Calculations by KL van Leeuwen based on area in km^2 or ha; [4]Calculations by KL van Leeuwen based on published figures (McLennan and Hill 2012, Bessa et al. 2015); [5]The actual percentage of forest cover is not specified in the literature, however, it is implied that the chimpanzee home-range consists only of forest, and thus 100% forest coverage can be assumed; [6]Analyses of tree cover (%) within a 5km-buffer of the geographical position of the study site, as specified by the relevant papers, based on Landsat satellite imagery (Hansen et al. 2013); [7]Data based on findings from expert-based reviews on the environmental determinants of chimpanzee site selection at a specific study site (Chapter 2).

Climate

In addition to vegetation composition, the 43 chimpanzee study sites showed considerable variation in their climatic conditions (Table 3.8). Some study sites had high mean annual temperatures, low mean annual rainfall and long dry seasons, some had low mean annual temperatures, high mean annual rainfall and short dry seasons, and others were intermediate between these two ‘extremes’. Across the 43 sites, mean annual temperature (T_{ann}) ranged between 16.3 – 29.0 °C, mean annual precipitation (P_{ann}) ranged between 750 – 3244 mm, length of longest consecutive dry season (Dry_{long}) ranged between 1 – 7 months, and total number of dry months (Dry_{all}) ranged between 1 – 7 months (Table 3.8).

Table 3.8. Annual precipitation, temperature, and precipitation seasonality (as measured in length of the dry season) for the chimpanzee study sites encountered in this study. Site list adapted from Inskipp (2005), and Russak (2013). NP = National Park, FR = Forest Reserve, WR = Wildlife Reserve.

Site	**Temperature –** *Annual average/ average range*[1]	**Precipitation –** *Annual average/ average range*	**Dry season**	**Number of dry months (consecutive)**	**References used (major)**
Bafing (Mali)	28.5^{0}C[2]	900 – 1,500 mm *average 1,200 mm*[4]	mid-Dec to Jun	6.5	Duvall, 2000 Duvall 2001
Bakoun (Guinea)	24.0^{0}C	1,585 mm	Nov to May	7	Hijmans et al. 2005[5] Boesch et al. 2017
Bossou (Guinea)	23.6^{0}C	2,272 mm	Nov to Feb	4	Lehmann et al. 2007 Matsuzawa et al. 2011
Budongo FR (Uganda)	17 - 29^{0}C *average 23 °C*[3]	1,780 – 1,900 mm *average 1,840 mm*[4]	mid-Dec to mid-Feb Jun to Jul	2 2	Reynolds 2005 Tweheyo et al. 2006
Bulindi (Uganda)	22.4 ^{0}C	1,461 mm	Dec to Feb Jun to Jul	3 2	Hijmans et al. 2005[5] McLennan 2015
Bwindi-Impenetrable NP (Uganda)	16.3^{0}C	1,100 – 2,400 mm *average 1,750 mm*[4]	Dec to Feb May to Jul	3 3	Kajobe and Roubik 2006 Stanford and Nkurunungi 2008
Caiquene-Cadique (Guinea-Bissau)	27.5^{0}C	1,964 mm	Nov to mid-May	6.5	Bessa et al. 2015
Comoé (Ivory Coast)	27^{0}C	1,010 mm	Nov to Apr	6	Fisher et al. 2002 Lapuente et al. 2016
Dzanga-Ndoki NP (CAR)	26.4^{0}C	1,365 mm	Dec to Feb Jun to Jul	3 2	Blom et al. 2001
Fongoli (Senegal)	28.4^{0}C[4]	900 mm	Nov to Apr	6	Lindshield et al. 2017 Pruetz et al. 2017
Gashaka Gumti NP (Nigeria)	20.9 – 31.9^{0}C *average 26.4 °C*[3]	1,973 mm	Nov to Apr	6	Fowler et al. 2011 Pascual-Garrido et al. 2013
Gishwati (Rwanda)	15.7 – 24.2^{0}C[4] *average 20°C*[3]	1,884 mm	Jun to Aug	3	Chancellor et al. 2012b Chancellor et al. 2017
Gombe NP (Tanzania)	19 – 28^{0}C[4] *average 23.5°C*[3]	1,321 – 1,710 mm *average 1,516 mm*[4]	May to Oct	6	McGrew et al. 1981 Foerster et al. 2016
Goualougo Triangle (Republic of Congo)	21.5 – 24.2^{0}C *average 22.9°C*[3]	1,650.3 – 1,675.7mm *average 1,663 mm*[4]	Dec to Apr Jun to Jul	5 2	Morgan et al. 2006 Sanz et al. 2014
Ishasha River (DRC)	23.2^{0}C	750 mm	Dec to Mar Jun to Aug	4 3	Schoeninger et al. 1999 Hijmans et al. 2005[5]
Issa Valley (Tanzania)	11 – 35^{0}C *average 23°C*[3]	900 – 1,400 mm *average 1,150 mm*[4]	May to Sep	5	Stewart et al. 2011 Wondra et al. 2016
Ituri FR (DRC)	23.7^{0}C	1,839 mm	Dec to Feb	3	Hijmans et al. 2005[5]
Kahuzi-Biega NP (DRC)	20.1^{0}C[2]	1,586 mm	Jun to Aug	3	Basabose and Yamagiwa 2002 Basabose 2005
Kalinzu FR (Uganda)	14 – 28^{0}C *average 21 °C*[3]	1,584 mm	Jan to Mar Jun to Aug	3 3	Howard 1991 Kagoro-Rugunda and Kayanja 2011
Kasakati (Tanzania)	19 – 28^{0}C *average 23.5°C*[3]	962 mm	May to Oct	6	Moore 1992 Hijmans et al. 2005[5]
Kibale NP (Uganda)	14 – 27^{0}C[2] *average 20.5 °C*[3]	1,492 – 1,622 mm *average 1,557 mm*[4]	Dec to Feb Jun to Jul	3 2	Howard 1991 Lwanga 2003
Kpala (Liberia)	24.7^{0}C	2,204 mm	Dec to Feb	3	Hijmans et al. 2005[5]
La Belgique (Cameroon)	19.5 – 26.3^{0}C[4] *average 22.9 °C*[3]	1,638 mm	Dec to Feb Jul	3 1	Hijmans et al. 2005[5] Tagg et al. 2013

Site	**Temperature –** *Annual average/ average range*[1]	**Precipitation –** *Annual average/ average range*	**Dry season**	**Number of dry months (consecutive)**	**References used (major)**
Lac Tumba Landscape (DRC)	25 ^{0}C[4]	1,500 – 1,600 mm *average 1,550 mm*[4]	Feb Jul to Aug	1 2	Serckx et al. 2014
Lagoas de Cufada NP (Guinea-Bissau)	26^{0}C	2,200 mm	Nov to May	7	Carvalho et al. 2015a Carvalho et al. 2015b
Loango (Gabon)	22.9 – 27.2^{0}C[4] *average 25.1°C*[3]	2,215 mm	Dec to Jan May to Sep	2 5	Head et al. 2012 Estienne et al. 2016
Lopé NP (Gabon)	20.5 – 30.8^{0}C[2] *average 25.7°C*[3]	1,548 mm	Jun to Sep	4	Tutin et al. 1997a Tutin et al. 1997b
Mahale Mountains NP (Tanzania)	18.4 – 28.9^{0}C[2] *average 23.7°C*[3]	1,751 mm	May to Sep	5	Nakamura et al. 2013 Nakamura et al. 2015
Minkébé NP (Gabon)	24^{0}C	1,500 – 1,800 mm *average 1,650 mm*[4]	Dec to Feb Jun to Aug	3 3	Huijbregts et al. 2003 Hijmans et al. 2005[5]
Monte Alén NP (Equatorial Guinea)	19.5 – 21.9^{0}C *average 20.7°C*[3]	2,000 – 3,000 mm *average 2,500 mm*[4]	Dec to Feb Jun to Aug	3 3	Garcia and Mba 1997 Kumpel et al. 2008
Moukalaba-Doudou NP (Gabon)	25.7^{0}C	1,777 mm	May to Sep	5	Hijmans et al. 2005[5] Wilfried and Yamagiwa 2014
Mount Assirik (Senegal)	23 – 35^{0}C[2] *average 29 °C*[3]	885 mm	Nov to May	7	McGrew et al. 1981 McGrew 2015
Ndoki-Likouala (Congo)	24.7^{0}C	1,653 mm	Dec to Mar Jun to Jul	4 2	Hijmans et al. 2005[5] Stokes et al. 2010
Ngel Nyaki FR (Nigeria)	25.8^{0}C	1,800 mm	Nov to mid-Apr	5.5	Akinsoji 2013 Dutton and Chapman 2015
Ngotto Forest (CAR)	24.9^{0}C	1,740 mm	Nov/Dec to Feb/Mar	3 – 5	Hicks et al. 2009 Freycon et al. 2015
Nimba Mountains (Guinea)	21^{0}C	3,244 mm	Nov to Feb	4	Hijmans et al. 2005[5] Koops et al. 2012a
Odzala NP (Republic of Congo)	20.4 – 31.5^{0}C *average 26°C*[3]	1,957 mm	Dec to Apr Jun to Jul	5 2	Devos et al. 2008
Sapo (Liberia)	25.4^{0}C	3,043 mm	Jan	1	Hijmans et al. 2005[5]
Semliki WR (Uganda)	18 – 33^{0}C[2] *average 25.5°C*[3]	1,352 mm	Jan to Feb May to Jul	2 3	Hunt and McGrew 2002 Webster et al. 2014
Taï NP (Ivory Coast)	24 – 30^{0}C *average 27°C*[3]	1,800 mm	Nov to Feb Jul to Aug	4 2	Kolongo et al. 2006 Kouakou et al. 2009
Tenkere (Sierra Leone)	27^{0}C	2,223 mm	mid-Nov to mid-May	6	Alp 1993 Hijmans et al. 2005[5]
Tongo (DRC)	17^{0}C	1,753 mm	Dec to Feb May to Aug	3 4	Lanjouw 2002 Hijmans et al. 2005[5]
Ugalla (Tanzania)	14 – 34^{0}C[4] *average 24°C*[3]	980 mm	May to Oct	6	Ogawa et al. 2014

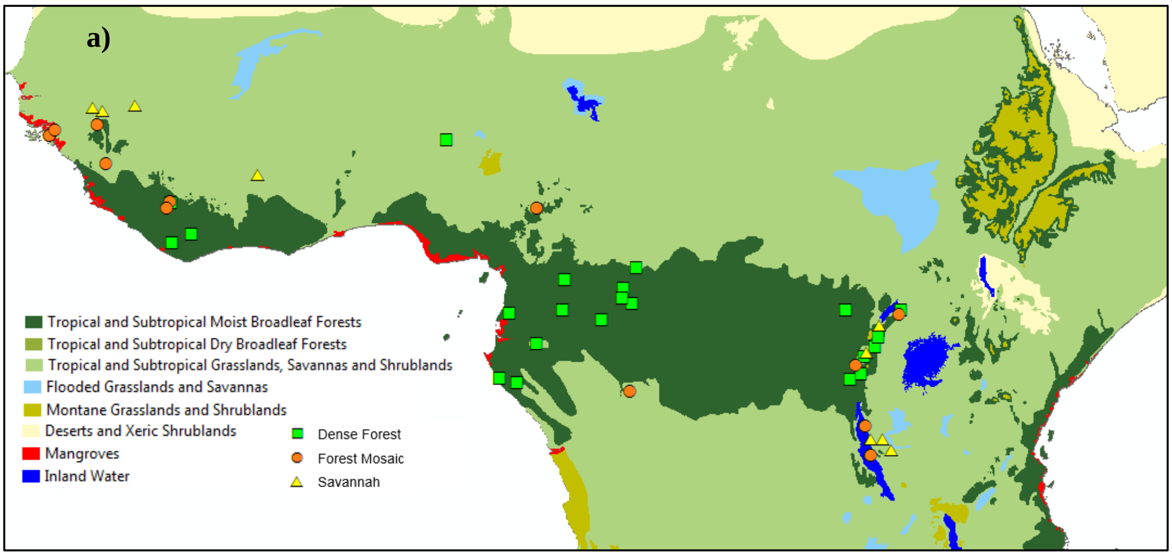
[1] Annual average temperature/ average temperature range was used preferably. In case this was not possible, monthly or daily average temperatures/ average temperature range were used; [2] Data for mean monthly temperature/ temperature range; [3] Calculations by KL van Leeuwen based on temperature and/or precipitation range; [4] Data for mean daily temperature/ temperature range; [5] Data based on analyses of the WorldClim – Global Climate Data database (Hijmans et al. 2005).

Existing biome, vegetation and climate classification schemes

To quantitatively separate chimpanzee dense forest, forest mosaic and savannah sites based on traditional biome classification schemes, the 43 chimpanzee study sites were plotted onto three selected biome classification schemes (Figure 3.2). The WWF terrestrial ecoregions (WWF 2018), White's Vegetation Map of Africa (White 1983) and the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008) all showed slight variations in environments and distinctions between landscapes (Figure 3.2). All three classification schemes placed the chimpanzee study sites differently, and lacked sufficient detail to quantitatively separate forest from savannah sites as outlined in chimpanzee literature (Figure 3.2 and Table 3.9): chimpanzee dense forest, forest mosaic and savannah sites were placed in various, not mutually exclusive habitat classes across the three maps. This illustrative example thus shows that chimpanzee researchers' landscape classifications of study sites differ from the ecological definitions set out by three selected biome classification schemes.

Table 3.9. Chimpanzee study sites, labelled by their literature-based landscape class (i.e. dense forest, forest mosaic and savannah), in comparison to the landscape classes of three existing biome, vegetation and climate classification schemes: WWF terrestrial ecoregions (WWF 2018), the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008), and White's Vegetation Map of Africa (White 1983).

Vegetation/ Climate Map	**Habitat Class**	**Chimpanzee literature-based landscape class**			
		Savannah	***Forest Mosaic***	***Dense Forest***	***Total***
WWF Terrestrial Ecoregions	Tropical and subtropical moist broadleaf forest	0	5	17	22
	Tropical and subtropical grasslands, savannas and shrublands	9	6	5	20
	Mangroves	0	1	0	1
	TOTAL	**9**	**12**	**22**	**43**
Whittaker Biome Diagram	Tropical rainforest	0	0	3	3
	Tropical deciduous forest	0	12	17	29
	Temperate deciduous forest	0	0	1	1
	Tropical grassland	9	0	1	10
	TOTAL	**9**	**12**	**22**	**43**
White's Vegetation Map of Africa	Tropical lowland rainforest	0	2	10	12
	Dry forest and thicket	0	1	1	2
	Swamp forest and mangrove	0	2	0	2
	Mosaics of forest	0	5	2	7
	Arid-fertile savanna	1	0	2	3
	Moist-infertile savanna	8	1	1	10
	Unpalatable grassland	0	1	4	5
	Anthropic landscapes	0	0	2	2
	TOTAL	**9**	**12**	**22**	**43**



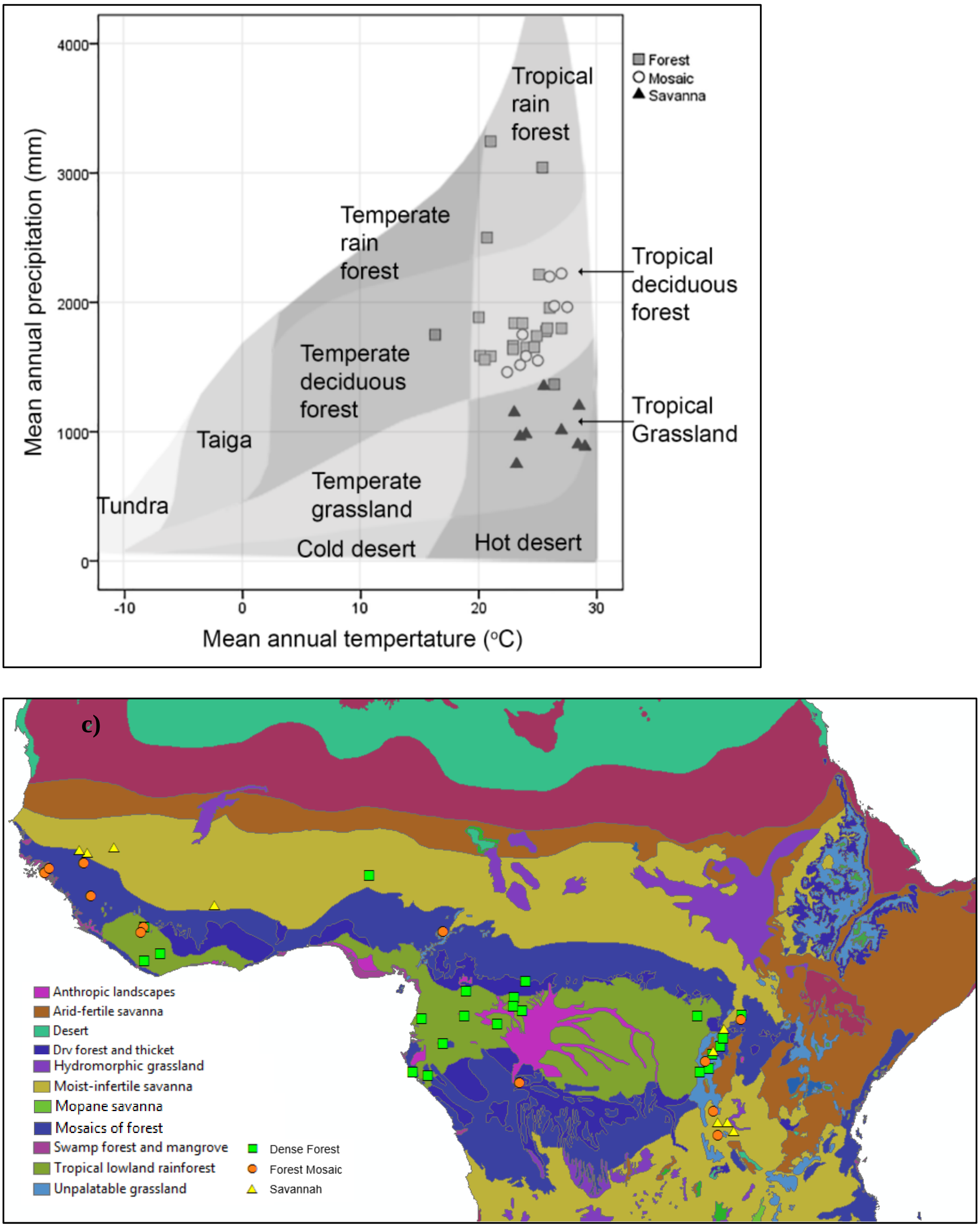


Figure 3.2. The 43 chimpanzee study sites encountered in this study, labelled by their literature-based landscape class, plotted on **a)** WWF terrestrial ecoregions map (WWF 2018), **b)** the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008), and **c)** White's Vegetation Map of Africa (White 1983).

Quantitative definitions of chimpanzee environments

To quantitatively separate chimpanzee dense forest, forest mosaic and savannah sites based on published climate and vegetation cover data, data range tables, boxplots and scatterplots are shown in Table 3.10, Figure 3.3 and Figure 3.4. Data from published literature showed that chimpanzee forest (i.e. dense forest and forest mosaic sites combined) and savannah sites could be separated based on forest cover and annual rainfall (Table 3.10, Figure 3.3 and Figure 3.4). Chimpanzee forest landscapes could therefore be quantitatively defined as environments with ≥1360 mm annual rainfall and ≥15% forest cover, and chimpanzee savannah landscapes as environments with <1360 mm annual rainfall and < 15% forest cover (Table 3.10, Figure 3.3b, Figure 3.3e, and Figure 3.4c). Values for annual temperature, total number of dry months, length of the longest consecutive dry season and woody tree cover overlapped between chimpanzee forest and savannah environments, albeit that savannah sites generally had higher mean annual temperatures, longer consecutive dry seasons, more overall dry months, and lower percentages of tree cover than forest sites (Table 3.10 and Figure 3.3).

Within forest environments, dense forest and forest mosaic sites showed overlap in the ranges of all six environmental variables assessed (i.e. annual temperature, annual rainfall, total number of dry months, length of the longest consecutive dry season, forest cover and tree cover; Table 3.10 and Figure 3.3). Statistical differences in environmental variables between chimpanzee dense forest and forest mosaic sites are shown in Table 3.11. Based on multiple environmental variables, however, published literature data showed that dense forest and forest mosaic sites could be separated based on the relationship between either annual temperature or length of the longest consecutive dry season and forest cover (Figure 3.4a and Figure 3.4e). Unlike the separation of forest from savannah chimpanzee study sites, which could be achieved by applying a simple rainfall or forest cover threshold, here the relationship was slightly more complicated and required the application of an equation:

Forest cover threshold = 8.0 * Length of the longest consecutive dry season + 38

Forest cover threshold = 3.3 * Annual temperature – 5.5

Values below this derived forest cover threshold can be defined as forest mosaic sites and values above this derived forest cover threshold can be defined as dense forest sites (Figure 3.4a and Figure 3.4e). As annual temperature and length of the longest consecutive dry season increased, sites were more likely to be classified as forest mosaics (as compared to dense forests), most likely because they became more open and semi-deciduous, as is reported for some chimpanzee forest mosaic sites (e.g. Matsusaka et al. 2006, Fowler and Sommer 2007, Inogwabini et al. 2012). Semi-deciduous forests likely differ in vegetation structure from evergreen forests, and with semi-deciduous forests shedding their leaves at certain times of year, vegetation features and micro-climates likely change through time and potentially become periodically less valuable to the chimpanzees (derived from e.g. Boubli et al. 2011, Hue et al. 2016, Rakotomalala et al. 2017).

When no data on field-derived forest cover from chimpanzee researchers were available, quantitatively characterising chimpanzee study sites as dense forest or forest mosaics is difficult, as overlap existed in the ranges of all six assessed environmental variables (Table 3.10). Some sites, however, fell within the non-overlapping regions of values for these environmental variables (i.e. mean annual temperature: < 17.0°C or > 27.0°C; mean annual rainfall: < 1460mm or > 2275mm; total number of dry months: < 3.0 months; length of the longest consecutive dry season: < 2.0 months or > 5.5 months; forest cover: < 64.0% or > 85.5%; and/or tree cover: < 23.25% or > 77.3%), and these sites could be matched exclusively with one of the two categories (N = 16 for dense forest, and N = 8 for forest mosaic; Table 3.10 and Figure 3.3). This therefore provides an alternative approach to chimpanzee landscape classifications when forest cover data remain absent.

Thus, quantitative environmental data on vegetation cover and climate from chimpanzee study sites could be used to successfully separate chimpanzee sites into dense forests, forest mosaics and savannahs (Table 3.10, Figure 3.3 and Figure 3.4). Using the proposed definitions, nine literature-based classifications could be matched to chimpanzee savannah sites and 34 to chimpanzee forest sites, with nine forest mosaic sites and 21 dense forest sites. Four forest sites (i.e. for Bossou, Kpala, Lopé, Tongo) could not be matched to either a dense forest or a forest mosaic due to a lack of data on forest cover and overlap in values of all other environmental variables assessed.

K-means clustering analysis

K-means clustering analysis showed a valid distinction between chimpanzee forest (i.e. combining dense forest and forest mosaic sites: Clusters 2 and 3) and savannah (Cluster 1) sites based on their mean annual temperature, mean annual rainfall, total number of dry months, length of the longest consecutive dry season, forest cover and tree cover (Table 3.12 – Table 3.14). Chimpanzee dense forest and forest mosaic sites did not fall into separate clusters during the clustering analysis (Table 3.12 – Table 3.14). Cluster 3 contained two dense forest sites, i.e. Nimba Mountains and Sapo, which have extremely high values for annual rainfall (e.g. Koops et al. 2012a, Greengrass 2015). Cluster 2 incorporated chimpanzee study sites categorised as dense forests and forest mosaics based on author descriptions. Although this initially indicated a difficulty in separating dense forest from forest mosaic sites, inspection of Euclidean distances from cluster centre for each site in Cluster 2 showed that, in general, dense forest sites were located closer to the cluster centre than forest mosaic sites (Table 3.13). Two dense forest sites Kibale and Loango were outliers, being situated relatively far from the cluster centre due to low annual rainfall (Kibale), long dry seasons (Loango), and/or relatively lower forest cover (Kibale and Loango) as compared with other dense forest sites (e.g. Lwanga 2003, Potts et al. 2009, Head et al. 2012). A third outlier was the forest mosaic site Mahale, which has a relatively high forest cover as compared to other forest mosaic sites (e.g. Nakamura et al. 2015). Without these outliers, no overlap exists in Euclidean distance from cluster centre between dense forest and forest mosaic sites in Cluster 2. The k-means clustering analysis showed similarities with plotting the 43 chimpanzee study sites onto the Whittaker Biome Diagram (Table 3.9), with nine chimpanzee savannah sites being placed within the ‘Tropical grassland’ biome (i.e. Cluster 1), three dense forest outliers (i.e. Nimba, Sapo and Monte Alén: Clusters 2 and 3) being placed within the ‘Tropical rain forest’ biome, one dense forest site being placed within the ‘Temperate deciduous forest’ biome (Cluster 2), another dense forest site being placed within the ‘Tropical grassland’ biome (Cluster 2), and all other sites being placed within the ‘Tropical deciduous forest’ biome (Cluster 2).

Table 3.10. Mean and range of vegetation cover and climate at chimpanzee dense forest, forest mosaic and savannah sites using the landscape classifications as described by chimpanzee researchers: mean annual temperature (T_{ann}), mean annual rainfall (P_{ann}), length of longest consecutive dry season (Dry_{long}), total number of dry months (Dry_{all}), forest cover (as defined by chimpanzee researchers), and tree cover (based on Landsat derived maps of global tree cover: Hansen et al. 2013). Non-overlapping environmental variables are in bold.

Variable	**Measure**	**1. Savannah**	**2. Forest**		**2a. Forest Mosaic**	**2b. Dense Forest**
T_{ann} (°C)	*Mean*	25.8	23.6		24.2	23.3
	Range	23.0 – 29.0	16.3 – 27.5		17.0 – 27.5	16.3 – 27.0
P_{ann} (mm)	*Mean*	1,021	1,885		1,871	1,892
	Range	**750.0 – 1,352.0**	**1,365.0 – 3,244.0**		1,461 – 2,272	1,365 – 3,244
Dry_{long} (#)	*Mean*	5.5	4.1		5.0	3.6
	Range	3.0 – 7.0	1.0 – 7.0		2.0 – 7.0	1.0 – 5.5
Dry_{all} (#)	*Mean*	6.1	5.1		5.5	4.9
	Range	5.0 – 7.0	1.0 – 7.0		3.0 – 7.0	1.0 – 7.0
Forest Cover (%)	*Mean*	5.0	76.9		50.7	87.7
	Range	**1.5- 10.0**	**15.0 – 100**		15.0 – 85.5	64.3 – 100
Tree Cover (%)	*Mean*	27.7	65.3		46.7	75.4
	Range	10.7 – 53.7	8.5 – 99.9		23.2 – 77.3	8.5 – 99.9

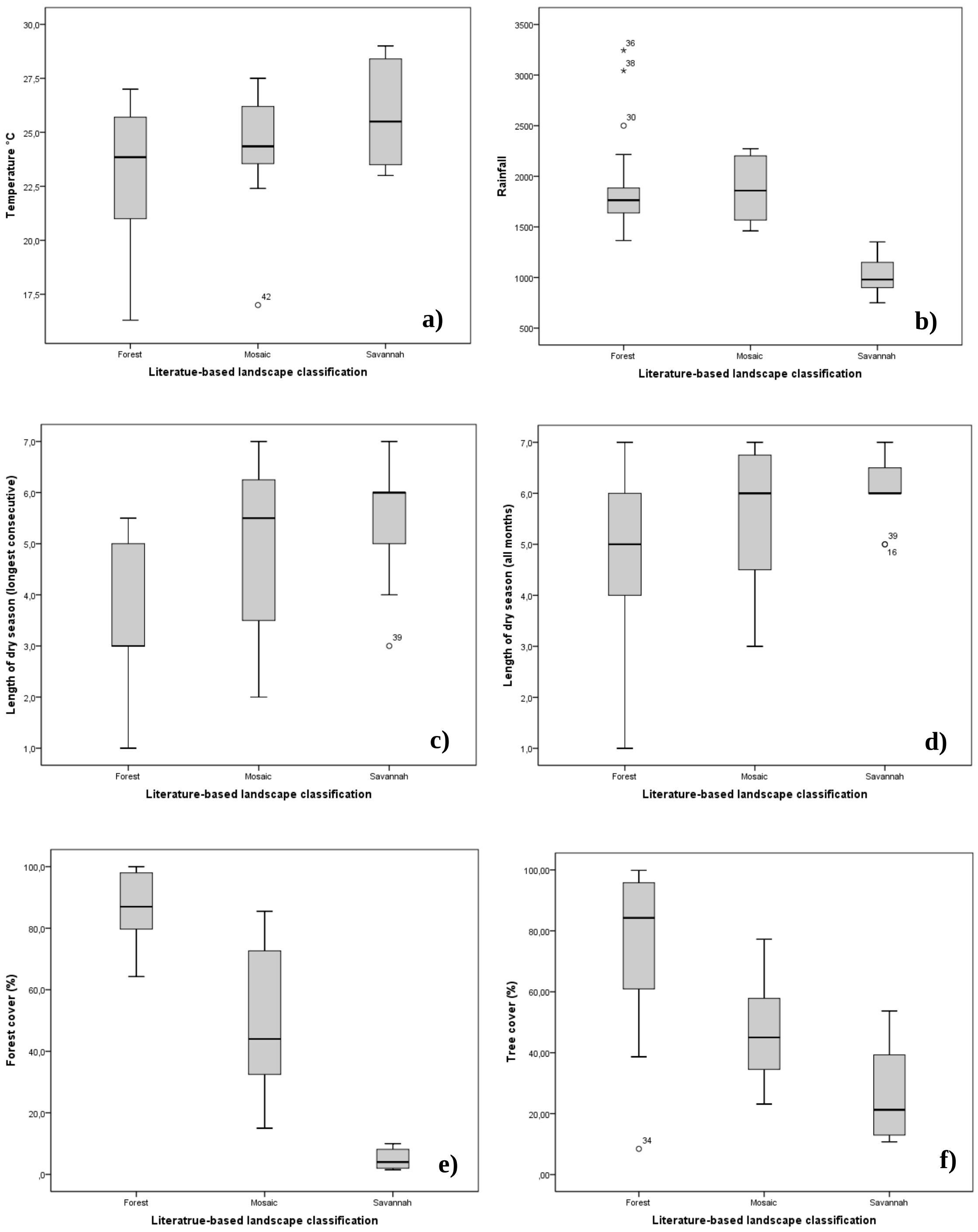
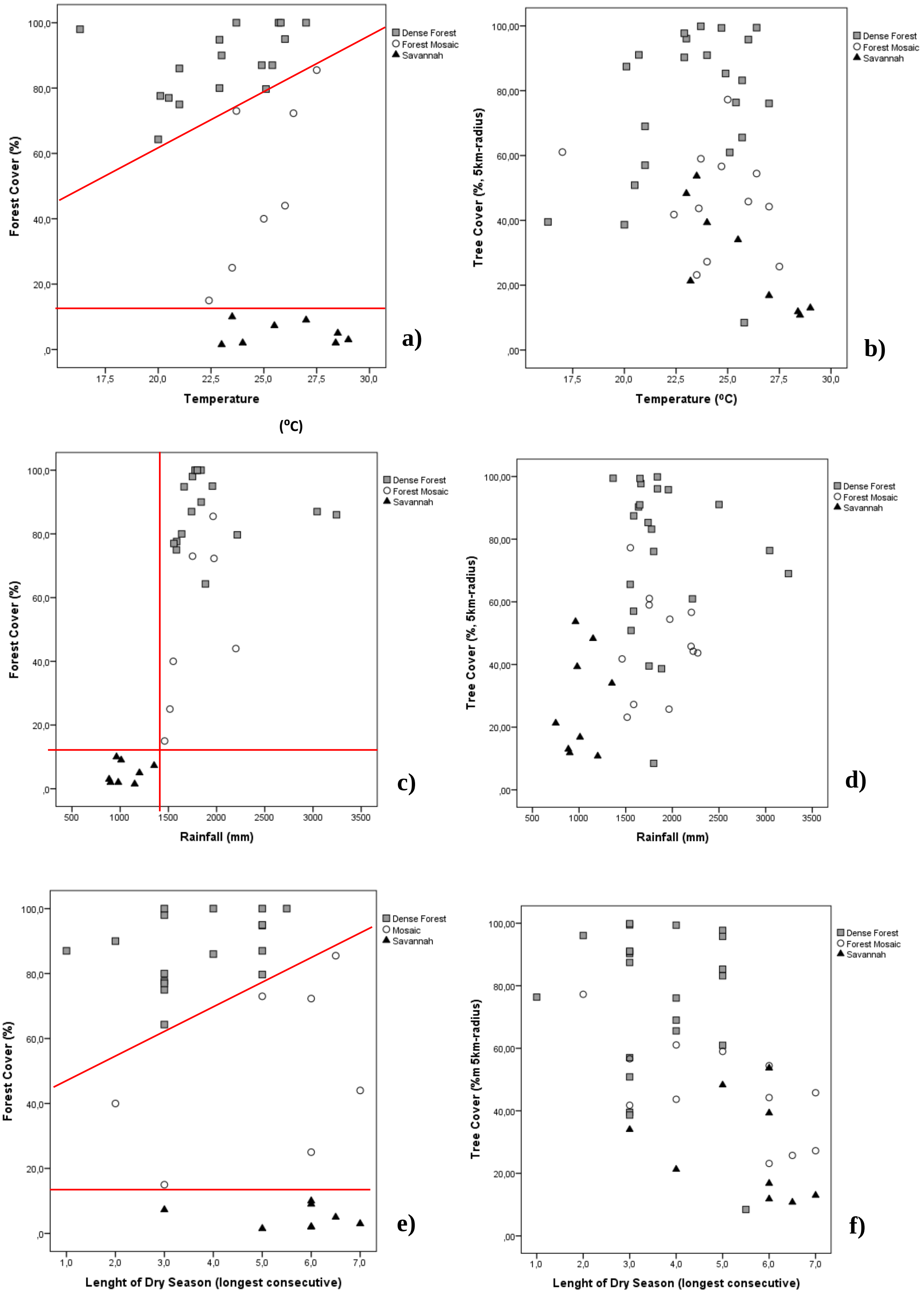


Figure 3.3. Range of vegetation cover and climate across chimpanzee dense forest, forest mosaic and savannah sites as identified by chimpanzee researchers: **a)** mean annual temperature, **b)** mean annual precipitation, **c)** length of the longest consecutive dry season, **d)** total number of dry months, **e)** forest cover, and **f)** tree cover. Black bars depict the mean, gey boxes indicate the upper and lower quartiles, and the whiskers depict the range of these environmental variables.


Forest Cover (%)
100,0
80,0
60,0
40,0
20,0
,0
17,5
20,0
22,5
25,0
27,5
30,0
Temperature
(ºC)
Dense Forest
Forest Mosaic
Savannah
a)
Tree Cover (%, 5km-radius)
100,00
80,00
60,00
40,00
20,00
,00
Temperature (ºC)
b)
Rainfall (mm)
500
1000
1500
2000
2500
3000
3500
c)
d)
Lenght of Dry Season (longest consecutive)
1,0
2,0
3,0
4,0
5,0
6,0
7,0
Mosaic
e)
Tree Cover (%m 5km-radius)
f)

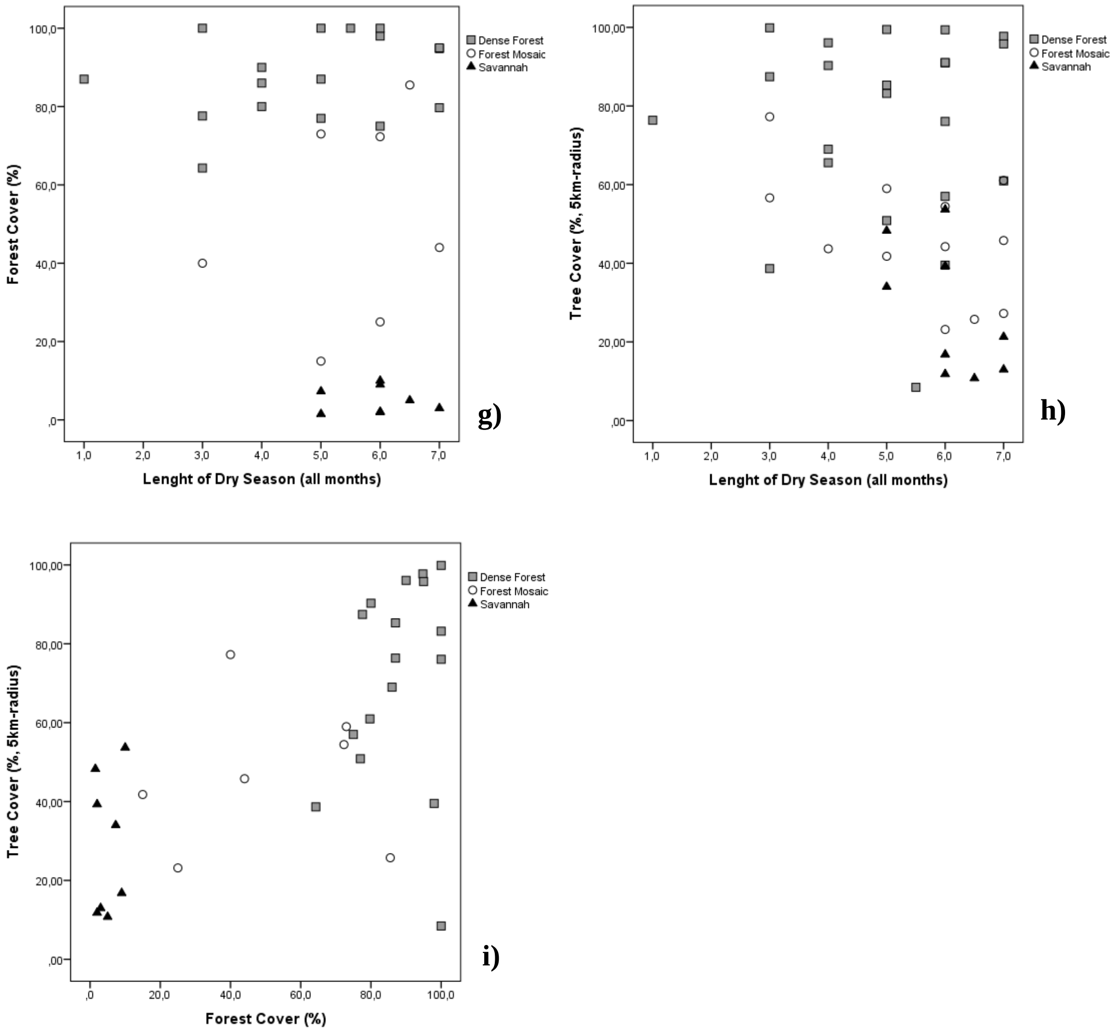


Figure 3.4. Relationships of vegetation cover and climate at each chimpanzee study site, labelled by their current literature-based landscape classification: **a)** temperature vs. forest cover; **b)** temperature vs. tree cover; **c)** rainfall vs. forest cover; **d)** rainfall vs. tree cover; **e)** length of the longest consecutive dry season vs. forest cover; **f)** length of the longest consecutive dry season vs. tree cover; **g)** total number of dry months vs. forest cover; **h)** total number of dry months vs. tree cover; and **i)** tree cover vs. forest cover. Figure 3.4c shows that chimpanzee forest and savannah sites can be separated from each other based on forest cover and annual rainfall, as indicated by the red line. Figure 3.4a and 3.4e show that chimpanzee dense forest and forest mosaic sites can be separated based on the relationship between annual temperature and forest cover (i.e. Forest Cover Threshold = 3.3 * Annual temperature - 5.5) and/or between length of the longest consecutive dry season and forest cover (i.e. Forest Cover Threshold = 8.0 * Length of the longest consecutive dry season + 38), as indicated by the red lines.

Table 3.11. Statistical difference in environmental variables for annual temperature (T_{ann}), annual rainfall (P_{ann}), length of the longest consecutive dry season (Dry_{long}), total number of dry months (Dry_{all}), forest cover (as described by chimpanzee researchers), and tree cover (based on Landsat derived maps of global tree cover: Hansen et al. 2013) between chimpanzee study sites identified as dense forests (F), forest mosaics (M) and savannahs (S) in chimpanzee literature. *Post-hoc* Mann-Whitney U tests had a significance level α of 0.05 / 3 = 0.0167 (Bonferroni correction).

	Statistical differences		
	F vs. M	**F vs. S**	**M vs. S**
T_{ann} (°C)	Kruskal-Wallis: $N_1 = 9$, $N_2 = 12$, $N_3 = 22$, $H = 4.1$, $df = 2$, $p = 0.131$		
	-	-	-
P_{ann} (mm)	Kruskal-Wallis: $N_1 = 9$, $N_2 = 12$, $N_3 = 22$, $H = 20.9$, $df = 2$, $p < 0.001$		
	F = M U = 124.0 Z = -0.3 p = 0.773	F > S U = 0.0 Z = -4.3 p <0.001	M > S U = 0.0 Z = -3.8 p < 0.001
Dry_{long} (#)	Kruskal-Wallis: $N_1 = 9$, $N_2 = 12$, $N_3 = 22$, $H = 11.8$, $df = 2$, $p = 0.003$		
	F = M U = 70.0 Z = -3.0 p = 0.022	S > F U = 26.5 Z = -3.3 p = 0.001	M = S U = 46.0 Z = -0.6 p = 0.561
Dry_{all} (#)	Kruskal-Wallis: $N_1 = 9$, $N_2 = 12$, $N_3 = 22$, $H = 3.9$, $df = 2$, $p = 0.139$		
	-	-	-
Forest Cover (%)	Kruskal-Wallis: $N_1 = 8$, $N_2 = 7$, $N_3 = 17$, $H = 23.6$, $df = 2$, $p < 0.001$		
	F > M U = 8.0 Z = -3.3 p = 0.001	F > S U = 0.0 Z = -4.0 p <0.001	M > S U = 0.0 Z = -3.2 p < 0.001
Tree Cover (%)	Kruskal-Wallis: $N_1 = 9$, $N_2 = 12$, $N_3 = 22$, $H = 19.9$, $df = 2$, $p < 0.001$		
	F > M U = 44.0 Z = -3.2 p = 0.002	F > S U = 15.0 Z = -3.7 p <0.001	M > S U = 20.0 Z = -2.4 p < 0.001

Table 3.12. Cluster centres of the three clusters identified through k-means clustering analysis. 'T_{ann}' stands for mean annual temperature, 'P_{ann}' is mean annual rainfall, 'Dry_{long}' is length of the longest consecutive dry season, and 'Dry_{all}' is the total number of dry months per year.

	Cluster		
	1	**2**	**3**
T_{ann} (°C)	26.1	23.6	23.2
P_{ann} (mm)	1,055	1,775	3,144
Dry_{long} (#)	5.7	4.2	2.5
Dry_{all} (#)	5.9	5.2	2.5
Forest Cover (%)	5.0	76.1	86.5
Tree Cover (%)	28.5	63.4	72.7

Table 3.13. Membership for all 43 chimpanzee study sites encountered in this study into the three clusters identified through k-means clustering analysis. Sites are grouped based on their mean annual temperature, mean annual rainfall, total number of dry months, length of the longest consecutive dry season, forest cover and tree cover. Sites not included in the k-means clustering analysis lacked available data on forest cover. The column 'Distance' indicates the Euclidean distance from the cluster centre.

Case	**Site**	**Literature-based Classification**	**Cluster**	**Distance**
1	Bafing	Savannah	1	146.225
2	Bakoun	Forest Mosaic		
3	Bossou	Forest Mosaic		

Case	Site	Literature-based Classification	Cluster	Distance
4	Budongo FR	Dense Forest	2	74.331
5	Bulindi	Forest Mosaic	2	320.391
6	Bwindi-Impenetrable	Dense Forest	2	41.475
7	Caiquene-Cadique	Forest Mosaic	2	193.223
8	Comoé	Savannah	1	46.550
9	Dzanga-Ndoki NP	Dense Forest		
10	Fongoli	Savannah	1	155.812
11	Gashaka Gumti NP	Forest Mosaic	2	198.493
12	Gishwati	Dense Forest	2	112.694
13	Gombe NP	Forest Mosaic	2	266.819
14	Goualougo Triangle2	Dense Forest	2	118.440
15	Ishasha River	Savannah		
16	Issa Valley	Savannah	1	97.288
17	Ituri FR	Dense Forest	2	77.699
18	Kahuzi-Biega NP	Dense Forest	2	190.357
19	Kalinzu FR	Dense Forest	2	190.905
20	Kasakati	Savannah	1	96.410
21	Kibale NP	Dense Forest	2	218.161
22	Kpala	Forest Mosaic		
23	La Belgique	Dense Forest	2	139.463
24	Lac Tumba Landscape	Forest Mosaic	2	228.094
25	Lagoas de Cufada NP	Forest Mosaic	2	426.816
26	Loango	Dense Forest	2	440.256
27	Lopé NP	Dense Forest		
28	Mahale Mountains NP	Forest Mosaic	2	24.379
29	Minkébé NP	Dense Forest		
30	Monte Alén NP	Dense Forest		
31	Moukalaba-Doudou NP	Dense Forest	2	31.237
32	Mount Assirik	Savannah	1	170.623
33	Ndoki-Likouala	Dense Forest		
34	Ngel Nyaki FR	Dense Forest	2	65.067
35	Ngotto Forest	Dense Forest	2	42.569
36	Nimba Mountains	Dense Forest	3	100.615
37	Odzala NP	Dense Forest	2	186,.79
38	Sapo	Dense Forest	3	100.615
39	Semliki WR	Savannah	1	297.201
40	Taï NP	Dense Forest	2	37.188
41	Tenkere	Forest Mosaic		
42	Tongo	Forest Mosaic		
43	Ugalla	Savannah	1	75.747

Table 3.14. Summary table of cluster membership for the literature-based landscape classifications by chimpanzee researchers in comparison to the outcomes of the k-means clustering analysis. The table shows how many literature-based savannah, dense forest, and forest mosaic sites (as identified by chimpanzee researchers in Table 3.8) have been assigned to each cluster.

Cluster	'Savannah' sites	'Dense Forest' sites	'Forest Mosaic' sites	Total
1	8	0	0	8
2	0	15	7	22
3	0	2	0	2
Unassigned	1	5	5	11
Total	9	22	12	43

Discussion

This study aimed to provide a quantitatively measurable definition and review of the various landscapes inhabited by chimpanzees, and compared the vegetation and climate characteristics of the main landscape categories used in chimpanzee literature: forest and savannah. It investigated how the landscape classifications used by chimpanzee researchers mapped onto traditional biome, vegetation and climate classification schemes, and identified which vegetation and climate characteristics of 43 chimpanzee field study sites best separated the chimpanzee researcher classifications. The hypothesis that differences in vegetation composition and climatic conditions of different chimpanzee study sites could be used to quantitatively characterise chimpanzees and their environments was supported, and detailed definitions were set out for chimpanzee dense forest, forest mosaic and savannah environments. This study is therefore the first to succeed in formalising what chimpanzee researchers call ‘forest chimpanzees’ and ‘savannah chimpanzees’, and furthermore defined a new class of ‘mosaic chimpanzees’. Chimpanzee researcher definitions did not match with selected traditional biome, vegetation and climate classification schemes.

Classifying chimpanzee landscapes

Chimpanzees have adapted to a wide variety of environmental conditions. Across the 43 chimpanzee study sites reviewed in this study, chimpanzee landscapes differed substantially in their vegetation cover and climate. Following the environmental field site descriptions of McGrew et al. (1981) and Moore (1992) for chimpanzees, this study successfully developed a framework that uses differences in mean annual temperature, mean annual precipitation, forest cover, tree cover, total number of dry months and length of the longest consecutive dry season to separate and classify chimpanzee field sites into dense forests, forest mosaics and savannahs. In general, chimpanzee dense forest environments are cool, wet, and have a high amount of forest cover, chimpanzee savannah environments are hot, dry and have only limited amounts of forest cover, and chimpanzee forest mosaic landscapes are intermediate. Whereas chimpanzee forest and savannah environments could be distinguished from each other based on percentage forest cover and amount of annual rainfall, the distinction between chimpanzee dense forest and forest mosaic landscapes was best described by the observed relationships between forest cover on the one hand, and temperature or rainfall seasonality (i.e. length of the longest consecutive dry season) on the other hand. This study thus used published, qualitative data from various chimpanzee study sites on vegetation cover and climate to provide a first, quantifiable distinction between forest chimpanzees, mosaic chimpanzees and savannah chimpanzees. The proposed chimpanzee landscape classification scheme succeeded in capturing the necessary details for classifying chimpanzees and their environments. At a scale that matters to chimpanzees, this study showed that the main drivers of chimpanzee landscape-based classifications were amount of forest cover, amount of annual rainfall, precipitation seasonality and annual temperature.

In separating forest mosaic from dense forest sites, it was shown that sites with higher temperatures and longer dry seasons were more likely to be classified as forest mosaics as compared to dense forests, even if they had a large amount of forest cover present. This suggests that forests in areas with longer dry seasons are different, and this would be in line with a change from evergreen to deciduous forest types (Saha 2012). Indeed, some (though not all) studies of chimpanzee forest mosaic sites include a reference to the semi-deciduous character of at least part of the forest in their environmental field site descriptions (Caiquene-Cadique: Sa et al. 2013; Gashaka Gumti: Fowler and Sommer 2007; Gombe: Bakuza and Nkwengulila 2009, Gilby et al. 2006; Lac Tumba Landscape: Inogwabini et al. 2012; Mahale: Matsusaka et al. 2006, Nakamura et al. 2013, Kaburu and Newton-Fisher 2015). Thus, when it gets hotter and drier, forests become more deciduous and seasonally shed their leaves. Forest vegetation types shedding their leaves likely provide different micro-habitat characteristics periodically as compared to their ‘in-leaf’ conditions (as derived from e.g. Hue et al. 2016, Rakotomalala et al. 2017). For example, micro-habitat characteristics such as temperatures and luminosities likely increase, and canopy cover, amount of shade and the presence of preferred resources likely decrease, when forests shed their leaves. Therefore, these forests are seasonally less favourable, and perhaps periodically less valuable, for primates (as shown for e.g. howlers and marmosets: Hue et al. 2016; red-tailed sportive lemurs: Rakotomalala et al. 2017; and spider monkeys: e.g. Chapman et al. 1995). Chimpanzee dense forest and forest mosaic sites may therefore sometimes have a similar percentage of forest cover, but the accompanying temperature and rainfall seasonality influence the (semi-)deciduous nature of these forests and make them different as habitat. The exact value (or importance) of different vegetation and landscape types for chimpanzees remains to be studied, but can potentially be addressed with population densities. For example, one could suggest that higher population densities would imply more suitable habitat for chimpanzees. Field observations have shown that chimpanzees in savannah landscapes live at lower population densities than chimpanzees in more forested areas (e.g. Tutin et al. 1983, Piel et al. 2015). Using population density estimates in assessing chimpanzee habitat suitability should, however, be approached with care, as high population densities may also represent overcrowding as a consequence of habitat loss and fragmentation (Asensio et al. 2007, Gabriel et al. 2017), or may be sustained through the use of non-forest (human) food sources (e.g. crop raiding, artificial feeding: e.g. Sugiyama 2015).

Chimpanzee researcher classifications of their sites did not map well onto three selected biome, vegetation and climate classification schemes: the WWF terrestrial ecoregions (WWF 2018), White's Vegetation Map of Africa (White 1983), and the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008). These traditional biome classifications lacked the sufficient amount of detail to quantitatively separate chimpanzee dense forest, forest mosaic and savannah field study sites as identified by chimpanzee researchers. Sites identified by chimpanzee researchers as savannahs generally matched with grassland or savannah classifications of traditional habitat classification schemes, but dense forest and forest mosaic sites inconsistently fell into several, non-corresponding classifications (including grassland and savannah categories) within the WWF terrestrial ecoregions (WWF 2018), White's Vegetation Map of Africa (White 1983), and the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008). Differences are likely due to the scale of measurement and details of the environmental classifications in these often global classification schemes. Whereas existing biome maps focus on quantifying the broad-scale environments of the world, chimpanzee researchers focus on environmental classifications from a chimpanzee perspective at a local scale, i.e. at the scale that matters to chimpanzees.

Chimpanzee researchers can now use the chimpanzee landscape classification scheme of this study to systematically formalise and classify the chimpanzees and their environments at their site, which will bring consistency and transparency to the chimpanzee literature. Researchers should, however, acknowledge that chimpanzee landscape classifications may not always correspond with existing biome, vegetation and climate classification schemes, and a reference to these ecological definitions wherever possible may be worthwhile when putting findings into perspective with, for example, geographical and climatological literature.

Suggestions for future research

Even though chimpanzee landscapes are inherently different, the proposed chimpanzee landscape classification scheme showed that quantifiable distinctions could be made within this natural environmental continuum. Nonetheless, outlined definitions might benefit from adding more detailed data on vegetation and climate, as not all authors reported the same level of environmental detail for specific chimpanzee study sites. Additional data on the vegetation composition of different sites could be gained in several ways. Some methods include local, site-scale measurements of vegetation, such as GPS (Global Positioning System) and GIS (Global Information System) analyses, and the usage of drones or Unmanned Aerial Vehicles (UAVs) to capture aerial images (e.g. Nkurunungi and Stanford 2006, van Andel et al. 2015). Other approaches include global-scale methods, such as using currently available satellite data to assess the landscapes at different sites (e.g. Pintea et al. 2003, Hansen et al. 2013).

The climates of chimpanzee study sites could also be assessed in more diverse ways than by just measuring the mean annual precipitation, mean annual temperature, and length of the dry season. For example, the patterns and distribution of rainfall at particular chimpanzee study sites could be assessed in further detail by also incorporating measurements of the number of rainy days per year (e.g. McGrew et al. 1981, Blasco et al. 2000), number of rainy days per month (e.g. McGrew et al. 1981), rainfall predictability over the years (e.g. McGrew et al. 1981), mean amount of rainfall per month (e.g. McGrew et al. 1981, Lehmann et al. 2007), and mean number of months within a year that the precipitation is more than twice the average monthly temperature (e.g. le Houérou 1984, Blasco et al. 2000, Lehmann et al. 2007). In addition, as disagreement exists on the exact definition of a dry month, more data should be gathered to facilitate incorporation of all existing definitions. Some studies currently define a dry month as a month with less than 100mm of rainfall (e.g. this study, Hunt and McGrew 2002, Matsuzawa et al. 2011, Russak 2013), whereas others define a dry month as a month with less than 30mm of rainfall (e.g. Kortlandt 1983), a month with less than 60mm of rainfall (e.g. van Schaik and Pfannes 2005), or as a month where the rainfall is less than twice its mean temperature (e.g. le Houérou 1984, Blasco et al. 2000). Detailed data should therefore not only be included on the mean number of months with less than 100mm of rainfall (e.g. McGrew et al. 1981, Lehmann et al. 2007), but also on the mean number of months with less than 60mm of rainfall (e.g. Koops et al. 2012a), less than 50mm of rainfall (e.g. Lehmann et al. 2007), and/or less than 30mm of rainfall (e.g. Kortlandt 1983). Only few chimpanzee study sites have currently incorporated this wide arsenal of precipitation characteristics (see McGrew et al. (1981) for a review). Although these data could be obtained through WorldClim – Global Climate Data, these data were interpolated from weather stations based on average monthly climate data (Hijmans et al. 2005), and site-specific data collected at chimpanzee study sites per se might prove more reliable. Which environmental variables have greatest overall influence on chimpanzee landscape classifications remains to be investigated.

Measurements of temperature could be assessed in more detail by also incorporating the mean monthly temperature (e.g. McGrew et al. 1981), highest maximum temperatures (e.g. McGrew et al. 1981), lowest minimum temperatures (e.g. McGrew et al. 1981), mean minimum temperature (e.g. McGrew et al. 1981), mean maximum temperature (e.g. McGrew et al. 1981), mean temperature of the coldest month (e.g. Blasco et al. 2000, Peel et al. 2007), mean temperature of the hottest month (e.g. Peel et al. 2007), mean annual temperature within the different vegetation types (e.g. McGrew et al. 1981, Kortlandt 1983), and mean monthly temperature within the different vegetation types (e.g. McGrew et al. 1981, Kortlandt 1983). Again, only few studies have included these temperature variables in their climate measurements at present (see McGrew et al. (1981) for a review). Similarly to the above, these details could be obtained through WorldClim – Global Climate Data, but locally collected data from specific chimpanzee study sites might provide more detailed insights.

Lastly, the outlined definitions would benefit from more clear and accessible terminologies. Many different terms are currently used to assess different vegetation types at a local scale, and the same is true for assessing global-scale landscapes (e.g. McGrew et al. 1981, White 1983, Moore 1992, Gardner 2006, Torello-Raventos et al. 2013, Dominguez-Rodrigo 2014). For example, identifying a landscape or vegetation type as ‘savannah’ can mean many different things to different researchers (Dominguez-Rodrigo 2014, Gardner 2006, McGrew et al. 1981, Oliveras and Malhi 2016, Torello-Raventos et al. 2013, White 1983). Similarly, although grouped under the single term ‘forest’, forest vegetation types have been described as ranging from rainforests, montane forest and evergreen forest on the one hand, to mixed forest, secondary forest and dry forest on the other hand (Bryson-Morrison et al. 2016, Collins and McGrew 1988, White 1983). It should therefore be acknowledged that it is paramount to establish clearly outlined, realistically scaled definitions for landscapes and vegetation types, preferably with respect to geographical and climatological literature. Although this would be challenging as no universally accepted climate and vegetation classification scheme currently exists, this study argues for the development of a universally accepted climate and vegetation classification scheme across disciplines that encompasses sufficient detail to assess small- and large-scale differences.

Implications and insights

The quantitative framework of this study to classify chimpanzees in terms of their habitat has various implications. First, the exact range of environments inhabited by chimpanzees is now consistently quantified, and shows that chimpanzees have adapted to an exceptionally wide range of environments (e.g. McGrew et al. 1981). Documenting chimpanzees' exact adaptations to most successfully exploit the available resources of these different environments will extend current knowledge on chimpanzee behavioural capacities, and this, in turn, will benefit studies on the sources and functions of behavioural variability across different chimpanzee study sites (e.g. Moore 1992, Hunt and McGrew 2002). Second, the clear overview presented in this study on the environmental conditions of the landscapes that chimpanzees are able to inhabit, provides detailed information into chimpanzee minimal landscape requirements and constraints, which is essential information for predicting how chimpanzees might cope with future habitat changes. It helps in determining when chimpanzees would still be able to cope with environmental degradations, and when changes would impair chimpanzee survival. Third, as chimpanzees are not the only primate species that are categorised in terms of their main preferred natural habitat, the proposed chimpanzee landscape classification scheme of this study may help classifications of the field study sites of other primate species that live in a wide variety of habitats (e.g. Meijaard 2016). Last, insights into chimpanzee dense forest, forest mosaic and savannah landscapes may also yield new understandings of the landscapes that early hominins lived in (e.g. Reed 1997, Hunt and McGrew 2002, White et al. 2009). New insights into the behavioural adaptations of chimpanzees to this variety of environments may further current knowledge to explain observed and implied adaptations in early hominins (e.g. Hunt and McGrew 2002, Pruetz and Bertolani 2009, Piel et al. 2017). Even though these remain questions to be addressed, this study provided an important scheme to use for landscape classifications at the scale that matters to chimpanzees.

Modelling purposes

The lack of exclusive definitions to separate chimpanzee dense forest and forest mosaic landscapes based on forest cover initially presented some difficulties for the modelling purposes of this thesis (Chapter 4 – Chapter 6). For the future modelling purposes, it was important to set out exclusive definitions for dense forests, forest mosaics and savannahs to test the prediction of whether chimpanzees in different landscapes behave differently. As the future individual-based models of this thesis mainly focus on the net effect of differing vegetation cover, have individuals operating over the course of 24 hours within the model, and do not include variability in annual temperature and length of the dry season, specific model rules on the forest cover of each chimpanzee landscape class were needed. Whereas a clear separation between chimpanzee forest and savannah environments was shown based on forest cover (i.e. 15% forest cover), dense forest and forest mosaic landscapes were not so easily distinguished from one another based on forest cover alone. This difficulty was circumvented by introducing some simple modelling example coverages (i.e. some set definitions for vegetation cover in each landscape) for inclusion within the individual-based models. With reference to the annual temperatures and length of the longest consecutive dry seasons outlined in Figure 3.4a and Figure 3.4e, chimpanzee dense forest environments were specified to have 80% forest cover, and chimpanzee forest mosaic environments were outlined to have 45% forest cover. Chimpanzee savannah environments had 10% forest cover. Forest cover was evenly spaced between chimpanzee landscape classes, and fit within the proposed classification scheme proposed in this study. These example coverages equipped this study with the necessary information to outline specific model rules for the individual-based models on chimpanzee landscape use presented in this thesis.

Conclusion

This study provided a detailed review of the environmental conditions at 43 chimpanzee study sites and developed a landscape-based classification of chimpanzees and their environments using a qualitative to quantitative process based on existing biome classification schemes, published field site descriptions and environmental data on mean annual temperature, mean annual rainfall, precipitation seasonality, forest cover and tree cover. Although three selected biome classification schemes lacked sufficient detail to separate chimpanzee dense forest, forest mosaic and savannah field study sites, observed differences in vegetation and climate of chimpanzee study sites could be used to quantitatively characterise chimpanzee environments, and detailed definitions were formalised for chimpanzee dense forest, forest mosaic and savannah environments. The amount of annual rainfall and the relative abundance (%) of forest provided a clear distinction between chimpanzee forest and savannah environments. The proposed chimpanzee landscape classification scheme of this study is therefore the first to provide quantitative definitions of the environmental conditions under which a chimpanzee can be called a ‘forest chimpanzee’ and its landscape a ‘forest’ or a ‘savannah chimpanzee’ and its landscape a ‘savannah' based on published data from various chimpanzee study sites. Within forest landscapes, a further distinction was highlighted between dense forests and forest mosaics, based on identified relationships between annual temperature and length of the longest consecutive dry season on the one hand, and forest cover on the other hand. This study therefore also quantified a new class of ‘mosaic chimpanzees’, and formalised the environmental circumstances under which a landscape can be called a ‘dense forest’ or a ‘forest mosaic’ using literature data. Even though chimpanzee landscapes ultimately form a natural environmental gradient from forest to savannahs, the proposed chimpanzee landscape classification scheme succeeded in labelling separable divisions within this environmental continuum, which provides consistency and clarity. Quantitatively classifying chimpanzees in terms of their environment provides a unique contribution to the field of primatology, which highlights the wide range of environments occupied by chimpanzees and shows which minimal conditions support or constrain chimpanzee survival now and in the future. This has important implications for future research, including extending current knowledge on the underlying reasons of chimpanzee flexibility and variability to different environments and the adaptations of early hominins to similar habitats, and identifying the range of environments used by other primate species. Chimpanzee study sites can now consistently and systematically be classified as dense forests, forest mosaics and savannahs, and new chimpanzee study sites can be categorised whenever details become available.

CHAPTER 4

An individual-based model on chimpanzee landscape use in different environments: The importance of vegetation

Abstract

Considering the rapid decline of primate habitat, it is important to investigate how flexibly primates can adapt to changing landscapes. Landscape-scale studies of primate habitat use are, however, scant. Studying how primate landscape use may be affected by environmental changes is best done through predictive modelling, which allows individuals to virtually interact with different environments based on rules from published data on known primate-habitat relationships. This study investigated how activity budgets, path lengths and internal states changed for chimpanzees in dense forests, forest mosaics and savannahs, using an individual-based modelling approach. The model was developed using NetLogo; environments and individuals followed rules based on chimpanzee literature. Savannah chimpanzees were expected to spend more time feeding, drinking and travelling, and spend less time resting than chimpanzees elsewhere, whereas forest chimpanzees were expected to drink, feed and travel least, and rest most. Chimpanzees in forest mosaics were expected to be intermediate. Whereas model results confirmed these predictions when comparing forest and mosaic chimpanzees, savannah chimpanzees faced increasing challenges and had to exponentially increase their travel time and distance at the cost of feeding, drinking, nesting and resting time. This indicated that additional adaptations were required to safeguard savannah chimpanzee survival. Model results showed that chimpanzees were flexible to adjust their behavioural patterns to fit the resource availability of various environments, but adaptation became increasingly more difficult in more open environments where resources were more scarce. Potential future model applications include predicting chimpanzee responses to future landscape change scenarios, and presenting a referential model and framework for understanding the underlying reasons for adaptation, behavioural innovation and evolution of hominids.

Keywords: agent-based models, habitat selection, activity budgets, daily path lengths, landscape change, energy budgets.

Introduction

Globally, the natural habitat of plants and animals is declining at an alarming rate (e.g. Schwitzer et al. 2011, Estrada et al. 2017). Populations left residing in degraded habitats face particular survival challenges, such as decreased availability of resources, increased vulnerability to predation, and local (micro-)climate changes (e.g. Schwitzer et al. 2011, de Almeida-Rocha et al. 2017). The link of habitat loss and alteration to declining biodiversity stresses the importance of the identification and protection of critical habitat, which is a primary focus of many conservation efforts (e.g. Harvey and Weatherhead 2006, Carretero-Pinzón et al. 2017). Exploring how a species uses its environment and identifying how selective it is in choosing specific types of vegetation is a first step towards determining the parts of the landscape that are most essential for a species' survival (e.g. Harvey and Weatherhead 2006). Investigating the spatial patterns of an animal's habitat use and the underlying mechanisms that shape these patterns will facilitate the current understanding of the complexities in animal behaviour, ecology and evolution (Deppe and Rotenberry 2008, Fan and Jiang 2008). Apart from determining a species' habitat preference, this will provide insights into the behavioural adaptability and flexibility of a species, and the ecological determinants of its abundance and distribution (e.g. Rovero and Struhsaker 2007, Deppe and Rotenberry 2008). These insights will facilitate predictions of how a particular species would have coped with past landscape changes, how it will cope with future landscape changes, and what their tipping points would be of coping versus non-coping with environmental change, which may be extended to other, closely related species.

At a landscape scale, habitat use is guided by an animal's metabolic needs and the ability of the environment to provide the necessary requirements to adhere to these needs (e.g. Deppe and Rotenberry 2008, Gibson and Koenig 2012, Sutton et al. 2017). How a species uses its overall environment to forage most efficiently for food and water, and to find safe sleeping sites, determines how likely it is able to survive at any particular location and how susceptible it is to change (e.g. Deppe and Rotenberry 2008, Dunbar et al. 2009). Specific locations are selected based on preferred and required micro-habitat characteristics, such as vegetation features (e.g. tree height, tree density, canopy cover, understory density, food and water availability) and micro-climates (e.g. local temperature, luminosity) (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017).

Even though landscape-wide inferences of species' habitat use are few, there is a growing body of evidence on species' habitat use patterns across large spatial scales (e.g. Arroyo-Rodriguez et al. 2013b, Carretero-Pinzón et al. 2017). Landscape use can be considered as a multi-scaled practice: a species is not only influenced by the structural characteristics of individual patches or vegetation types, but also by the overall composition and spatial arrangement of these vegetation types across the landscape (e.g. Arroyo-Rodriguez and Fahrig 2014, Carretero-Pinzón et al. 2017). Landscape use is, therefore, a hierarchical process, where an animal first decides on its subsequent behaviour based on its metabolic needs and internal physiological state (e.g. Sutton et al. 2017). The animal then selects the most suitable habitat, or vegetation type, for this behaviour, and then additionally within this chosen habitat selects the micro-habitat that best fits its needs (e.g. Harvey and Weatherhead 2006, Sutton et al. 2017). A species' landscape use is thus primarily determined by the spatial distribution of resources within an environment, such as food, water, vegetation features, and micro-climates (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Landscape-scale studies of species' habitat use include investigations across a wide variety of environments in order to determine the effects of change across large, relevant, and independently meaningful scales (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a).

Given the multi-level spatial scale of landscape use studies and the complexity of species-habitat interactions, studying species' landscape use under field conditions can be a challenging and time-consuming process (e.g. Dunbar 2002, Arroyo-Rodriguez et al. 2013a, Bialozyt et al. 2014). These scales and complexities can be dealt with by using a predictive modelling approach (e.g. Dunbar 2002; Chapter 1). Individual-based, or agent-based, models are mathematical representations, or simulations of the interactions between individuals and their environments (e.g. Grimm et al. 2006, Railsback and Grimm 2012). Unique, virtual individuals are placed within a virtual environment where they behave and interact subject to a predefined set of (knowledge-based) rules (e.g. Dunbar 2002, Sellers et al. 2007, van der Vaart et al. 2016). Individuals have goals, are able to sense their surrounding environment and neighbouring individuals, and choose their activities based on an internal decision-making process (e.g. Dunbar 2002, Sellers et al. 2007, van der Vaart et al. 2016). A model keeps track of the decisions for each individual over time, and produces collective output with respect to the purpose of the simulation (e.g. Dunbar 2002, Sellers et al. 2007). Even though models are always simplified representations of real-life systems, models are tested and calibrated against field observations in order to verify and validate their results (e.g. Sellers et al. 2007, van der Vaart et al. 2016). Current models on species' landscape-scale habitat use are few (e.g. Sellers et al. 2007), yet developing landscape use models can have various implications. First, 'null models' of a species' landscape use can explain how habitat use patterns will vary across realistic, present-day environments (e.g. Ramos-Fernandez et al. 2006). Results of these models can be used to predict critical habitat and priority areas for conservation. Furthermore, findings of such models can aid in predicting species' responses to future scenarios (e.g. Jepsen et al. 2005, Bonnell et al. 2010). For example, they can predict the effects of future climate and landscape changes, and can assist in identifying species' tipping points for coping with environmental alterations. Individual-based modelling therefore provides a powerful and valuable tool in exploring the landscape-scale habitat use of species across a wide range of different environments, and provide potential for scenario testing.

Species that are relatively generalised in their behavioural requirements for vegetation features and micro-climate characteristics (i.e. generalists) may be able to adapt to a wide range of different landscapes, whereas specialist species may struggle to survive after habitat loss and degradation (e.g. Venier and Fahrig 1996). Primates are among the species most affected by landscape change, which is partly due to their dependence on tropical forests (e.g. de Almeida-Rocha et al. 2017). Primate responses to habitat disturbances include changes in activity budgets, ranging patterns, occupancy, abundance, distribution, health status, and, in some cases, behavioural innovations (e.g. Kelley et al. 2013, de Almeida-Rocha et al. 2017). Innovations can simply be referred to as something new, and in order to be adaptive, behavioural innovations need to be successfully (socially) transmitted throughout the population (e.g. Coward and Grove 2011).

The common chimpanzee (*Pan troglodytes*) is a highly flexible primate species that inhabits a wide range of environments across equatorial Africa (e.g. Hunt and McGrew 2002, Inskipp 2005). Chimpanzees are, however, threatened with extinction throughout their range, mainly due to the loss and degradation of their natural habitat (e.g. Humle et al. 2016b, Estrada et al. 2017). This makes chimpanzees an ideal species for studying behavioural adaptability and flexibility to an extensive range of landscapes, which may highlight their susceptibility to change. Chimpanzee environments range from dense tropical rainforests to open and marginal savannahs (e.g. Hunt and McGrew 2002, Inskipp 2005). Each landscape differs substantially in its vegetation cover and configuration, climate, and resource quality, abundance, and distribution (Hunt and McGrew 2002, Arroyo-Rodríguez and Fahrig 2014). Furthermore, the various vegetation types within a landscape (e.g. forest, woodland, savannah grassland, swamp) differ markedly in their structural vegetation features and micro-climate characteristics (e.g. White 1983). Open and marginal savannah environments are generally considered as being hotter, drier, and more scarce and seasonal as compared to more forested landscapes (e.g. Moore 1996, Hunt and McGrew 2002).

Chimpanzee landscapes can be divided into three typical environments: dense forests, forest mosaics and savannahs, based on mean annual temperature, precipitation, rainfall seasonality and forest cover (Chapter 3). Within this classification dense forests are cool, wet and consist mainly of the vegetation type forest, savannahs are hot, dry and have only a minimal percentage of forest cover, and forest mosaics are intermediate. Within their environments, chimpanzees select specific types of vegetation for different behavioural activities and at different times of day based on micro-climate and vegetation characteristics (e.g. Pruetz 2007, Koops et al. 2012a, Duncan and Pillay 2013). Chapter 2 showed some of the minimal landscape requirements and constraints for chimpanzees in site selection for five key daily activities: feeding, drinking, nesting, resting (including social time), and travel. These findings provide insights into the (relative) importance of various micro-climates and vegetation features in deciding *where* and *when* chimpanzees should perform their behaviours. Even though detailed information on chimpanzee behaviour and ecology is present, their landscape-scale habitat use and how this changes when their landscape changes remains to be investigated. Chimpanzees' susceptibility and adaptability to change, therefore, remain currently unknown. Other primate species have been shown to increase their time spent feeding and travelling, decrease their time spent resting, and increase their daily path lengths after deforestation and habitat loss due to reduced resource availability (e.g. Clarke et al. 2002, Asensio et al. 2007, Ruppert et al. 2018).

This study therefore aims to provide insights into how chimpanzee behaviour varies when their landscapes differ along an environmental gradient from forest to savannah in order to highlight their adaptability, flexibility, and susceptibility to change using an individual-based modelling approach. Specifically, it will investigate the differences and similarities in activity budgets, energy budgets, daily path lengths, overall and behaviourally preferred vegetation, and site selection for chimpanzees in dense forests, forest mosaics and savannahs. It is hypothesised that: ***i)*** The presence of preferred vegetation features and micro-climate characteristics makes forest vegetation types most ideal for chimpanzees in all landscapes (Chapter 3). Other vegetation types, such as woodland, swamp, bamboo, and savannah grassland are increasingly less ideal; ***ii)*** Chimpanzees in dense forest (i.e. forest chimpanzees) use only optimal forest vegetation types for their daily activities, as these are highly available to them.

Consequently, forest chimpanzees can be very specific in their site selection for particular activities. In forest mosaics (i.e. mosaic chimpanzees) and savannahs (i.e. savannah chimpanzees), optimal forest vegetation types are used as much as possible, but forests are generally not widely available. Compared to forest vegetation types, other vegetation types such as woodland and savannah grassland have a wider range of vegetation structures and micro-climates (Chapter 3). However, mosaic and savannah chimpanzees will limit their use of suboptimal vegetation types in such a way that they do not experience environmental conditions beyond those encountered in forest, e.g. using savannah grassland areas only in the cooler times of day, and/or using locations with the tallest trees and highest tree densities when in woodland; ***iii)*** Daily travel distances are longest for chimpanzees in savannah landscapes, shortest in dense forests and intermediate in forest mosaics due to the differences in overall resource availability and distribution within the different landscapes; and ***iv)*** Time spent nesting is similar in all landscapes, due to the general inability to perform other activities at night (i.e. chimpanzees are a mostly diurnal species). Time spent travelling, feeding, and drinking is greatest for savannah chimpanzees, least in forest chimpanzees, and intermediate in forest mosaics, due to the quality, availability and distribution of resources within the different landscapes. Time spent resting is greatest in dense forests, least in savannahs and intermediate in forest mosaics, due to the differences in amount of time available after performing their other daily activities. The individual-based simulation model on chimpanzee landscape use in different environments developed for this purpose follows specific rules on chimpanzee behaviour and landscapes based on published literature outlined in Chapter 2 and Chapter 3. Thereby, the model presents a null model of current chimpanzee landscape use. Model findings can be used to predict chimpanzees' critical habitat and the impacts of future landscape change scenarios on chimpanzee behaviour and survival. Findings can furthermore be used to present a framework for understanding the underlying reasons of behavioural innovation and adaptation to specific landscapes in hominid evolution, and to provide a referential model for the landscape use of closely related early hominins.

Methods

Study species and data collection

This study focused on the landscape-scale habitat use of chimpanzees (*Pan troglodytes*) across a wide range of environments within their geographical range throughout equatorial Africa. As such, the four chimpanzee subspecies (i.e. *P. t. verus*, *P. t. ellioti*, *P. t. troglodytes*, and *P. t. schweinfurthii*) were analysed equally. Data on chimpanzee landscapes, behaviour and site selection were collected and analysed in Chapter 2 and Chapter 3. These data formed the basis for the model rules for the individual-based simulation model on chimpanzee landscape use created in this study.

Model building

The individual-based model was developed using NetLogo software (version 5.2.1; Willensky 1999). The description of the model follows the ODD (i.e. Overview, Design concepts, and Details) protocol for communicating individual-based models (Grimm et al. 2006, Grimm et al. 2010; Appendix 4.1). Input parameters for the model are outlined in Appendix 4.2, and the final model code and an overview of the model's 'interface' are presented in Appendix 4.3 – 4.4. The rationale behind model rules, decisions and design are outlined in Appendix 4.5.

Purpose

The purpose of the generic chimpanzee landscape use model developed here was to simulate how chimpanzee behaviour changed when their environments differed along an environmental gradient from forest to savannahs. In particular, it aimed to assess the daily activity budgets, path lengths, energy budgets, food intake, water intake, hydration budgets, fatigue budgets, overall preferred vegetation, behaviourally preferred vegetation, and site selection for chimpanzees in (dense) forest, (forest) mosaic, and savannah landscapes. Individual-based simulation models can be seen as computer-based experiments, where the state of one 'independent' variable is changed, and the states of other 'controlled' variables are kept constant, in order to test the effects of the independent variable on model output. As chimpanzees are mainly threatened with habitat loss and degradation throughout their range (e.g. Humle et al. 2016b, Estrada et al. 2017), the independent variable was vegetation cover in this study. By changing only the percentage of vegetation cover across different model runs and keeping all other environmental variables (e.g. home-range size, fragmentation, temperature, rainfall) equal, the model aimed to explore the net effect of differing vegetation cover on chimpanzee survival abilities (Figure 4.1).

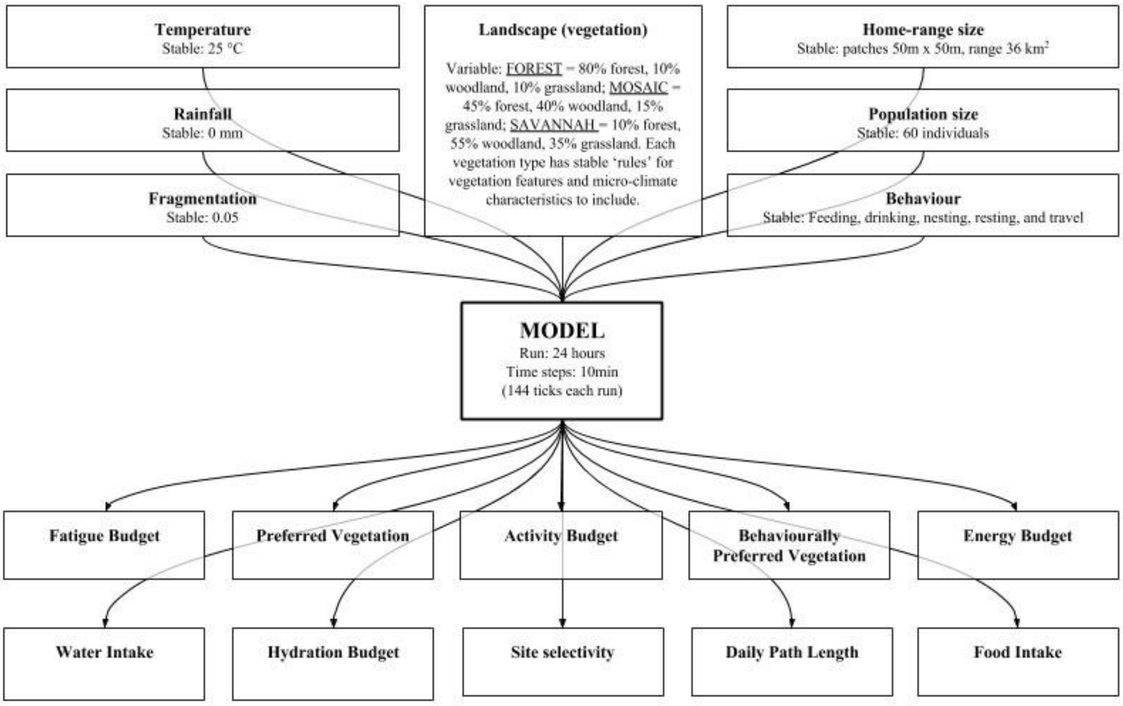


Figure 4.1. Conceptual flowchart of the chimpanzee individual-based model developed in this study. The model aims to investigate the net effect of changing vegetation cover on chimpanzee behaviour and survival, and thus explores how chimpanzee landscape use differs within different environments.

Entities, state variables and scales

The generic chimpanzee landscape use model is comprised of two entities: the landscape and the chimpanzees (Figure 4.1 and Appendix 4.5). The landscape was simulated as 36 km^2, i.e. the average chimpanzee home-range size (based on published data for the study sites encountered in Chapter 3[2]), and is represented by 14,400 cells, henceforward called 'patches', of 50m x 50m. Within the model, wrapping was turned off, meaning that the model boundaries were absolute. Landscapes were simulated as either being a forest, mosaic or savannah environment, with relative proportions of different vegetation types set out accordingly. Values for overall temperature (25°C), rainfall (0mm) and fragmentation (0.05) were kept constant across landscapes. Within each landscape, three different vegetation types were simulated: forest, woodland, and (savannah) grassland. Each patch was first randomly assigned a vegetation type and was then, accordingly, assigned a specific set of vegetation features and micro-climate characteristics: tree height, tree density, food tree density, canopy cover, canopy

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[2] References used: Bessa et al. 2015, Boesch and Boesch-Archerman 2000, Fowler et al. 2011, Furuichi et al. 2001, Goodall 1986, Koops et al. 2012a, Matsuzawa et al. 2011, McGrew et al. 2014, McLennan 2015, Morgan et al. 2006, Nakamura et al. 2015, Oelze et al. 2014, Reynolds 2005, Samson and Hunt 2012, Stanford and O'Malley 2008, Stewart and Pruetz 2013, Watts and Mitani 2002, Yamagiwa et al. 2012.

connectivity, understory density, food availability, water availability, local temperature day, local temperature night, local luminosity day, and local luminosity night (Table 2.3, Chapter 2). Values for number of fruits and amount of water changed after consumption by the chimpanzees, whereas all other vegetation and micro-climate features remained stable throughout each model run.

Within each landscape, a population of 60 chimpanzees, i.e. the approximate average chimpanzee community size across sites and studies (based on published data for the study sites used in Chapter 3[3]), was parameterised. Each chimpanzee, represented as a point within the landscape, was placed randomly within the model environment. Individuals were parameterised to possess internal states for energy (kCal), fatigue (unitless measure), hydration (unitless measure), current activity, current vegetation type, food intake (# food items, or edible grams dry weight), water intake (unitless measure), and distance travelled (m). Chimpanzees were simulated to perform five daily activities, i.e. feeding, drinking, nesting, resting and travel, and were guided by their internal states and their main goal of maintaining homeostasis. As such, chimpanzees' internal states changed throughout the model run at each time step. Every chimpanzee had the ability to assess the vegetation features and micro-climates of its current patch and its neighbouring patches within a radius of 100m, i.e. the maximum direct sighting distance. No memory or pre-knowledge of the environment was included for individuals within the model. Each time step in the model represented 10 minutes and a total model run simulated a single day, i.e. 24 hours; This equalled 144 time steps (or 'ticks'), of which the first 72 time steps were characterised as 'day', and the following 72 time steps were characterised as 'night'.

Process overview and scheduling

At the onset of each time step, chimpanzees lost energy and hydration, and gained fatigue simply by existing (i.e. through basic metabolic processes). As the model simulated chimpanzee landscape use over the course of 24 hours, at each time step individuals had to decide which behaviour to perform based on their current internal states for energy, hydration and fatigue, and their aim to maintain homeostasis (Figure 4.2 and Appendix 4.5). During daytime, individuals could choose to feed, drink or rest,

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[3] References used: Schoeninger et al. 1999, Lanjouw 2002, Stanford and O'Malley 2008, Hockings et al. 2009, Kosheleff and Anderson 2009, Murray et al. 2009, Chancellor et al. 2012a, Watts 2012, Stewart and Pruetz 2013, Samson and Hunt 2014, Basabose et al. 2015, Bessa et al. 2015, Eckhardt et al. 2015, Hashimoto et al. 2015, McLennan 2015, Nakamura et al. 2015, Pruetz et al. 2015, Sommer et al. 2016, Sanz et al. 2016.

whereas at nighttime, individuals could only choose to nest. Throughout the active day, resting had priority over all other behaviours, and an individual rested when it was too tired, or when it was too hot or too rainy[4] for other activities (i.e. enforced resting, *sensu* Korstjens et al. 2010). Feeding had priority over drinking when an individual was more hungry than thirsty, and drinking had priority over feeding when an individual was more thirsty than hungry. When an individual was neither hungry nor thirsty, it rested (i.e. 'free' resting time, e.g. Dunbar 1996). Once a chimpanzee had decided on an activity, it had to assess whether this behaviour could be performed at its current patch, or whether it had to travel to find a suitable location. The site-specific details (i.e. vegetation features, micro-climate, amount of food and water) of the patch currently occupied by each individual were outlined at the start of a model time step to explore this decision-making process. Only one activity could be performed at each time step. Drinking made an individual gain hydration and water intake, whereas feeding made an individual gain energy and food intake. Nesting and resting made a chimpanzee lose fatigue, and travel made an individual lose energy and hydration, and gain fatigue. Whereas travel within 100m of the current patch was directed towards a suitable location for the chosen behaviour, travelling more than 100m was done at a random bearing. Drinking made a patch lose water, and feeding made a patch lose fruit. At the end of each time step, and thus after a chosen behaviour was performed, each individual's current activity, vegetation type, travel distance, food intake, water intake, energy level, hydration level, and fatigue level were updated, as well as the vegetation features of each patch.

Design concepts

As the model investigates chimpanzee landscape use in different environments, it focused on how the composition and spatial structure of a landscape affect chimpanzee behavioural patterns. As such, the model included eight out of eleven design concepts (Appendix 4.1 and 4.5): *Basic principles* – Based on the extensive literature reviews of Chapter 2 and Chapter 3, the basic concept that underlies the development and design of the model is the prediction that chimpanzees behave and adapt differently in different environments. *Emergence* – Emergent outputs of the model that were not simply

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[4] Within the model, overall temperature (25°C) and precipitation (0mm) were kept constant and it was never too hot and/or too rainy to impair chimpanzees' daily activities. These rules (Table 4.2) were, however, included in the model for the sake of completeness, and for potential future modelling purposes. Note that overall temperature is different from local micro-climate temperature per vegetation type (scaled).

imposed by model rules alone include chimpanzees' daily path lengths, overall and behaviourally preferred vegetation, activity budgets, energy budgets, fatigue budgets, hydration budgets, and food and water intake. *Adaptation* – Chimpanzees adapted their behaviour with regards to their internal variables for energy, hydration, and fatigue. Behavioural priorities, criteria, and consequences are shown in Figure 4.2. *Objectives* – The primary goal of each chimpanzee in the model was to maintain homeostasis, and individuals adapted their activity selection accordingly. By the end of the model run (i.e. 24 hours), chimpanzees aimed to have a positive to neutral energy and hydration balance, and a neutral to negative fatigue balance. *Sensing* – Within the model, chimpanzees were able to assess their internal states for energy, hydration, and fatigue and then based their activity selection on these internal states. Individuals were furthermore able to assess the vegetation features and micro-climate of their current patch, as well as their neighbouring patches within 100m. These environmental variables allowed an individual to decide whether a chosen behaviour could be performed at the current patch, whether it had to travel within 100m for this, or whether it had to travel further to find a suitable location. Chimpanzees could furthermore judge the time of day as measured in the number of time steps. *Interaction* – Chimpanzees interacted with their simulated environment by exploring the vegetation features and micro-climates of their current and surrounding patches and the time of day. Knowledge of these variables guided chimpanzees in their decision-making process of where and when to perform their daily activities. *Stochasticity* – Stochasticity played a significant role in the initial set up of the model. Initial values for patches' vegetation features and micro-climates, and chimpanzees' initial values for energy, hydration and fatigue, were set randomly within a specified range of values to model realistic diversity. Furthermore, when an individual decided it was necessary to travel further than 100m within a single time step, the amount to travel was specified randomly between 100 – 300m, i.e. the maximum amount of travel within a 10min time frame at average speed (following calculations of Bates and Byrne 2009). *Observation* – At each time step and for each individual, data were recorded on current activity, current vegetation type, energy, hydration, fatigue, daily path length, food intake, water intake, and current patch specifics (i.e. vegetation features and micro-climates). These data were saved to an external file (.csv) at the end of each model run and were used to calculate daily activity budgets, daily path lengths, overall preferred vegetation, behaviourally preferred vegetation, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, and site selection for chimpanzees in different landscapes.

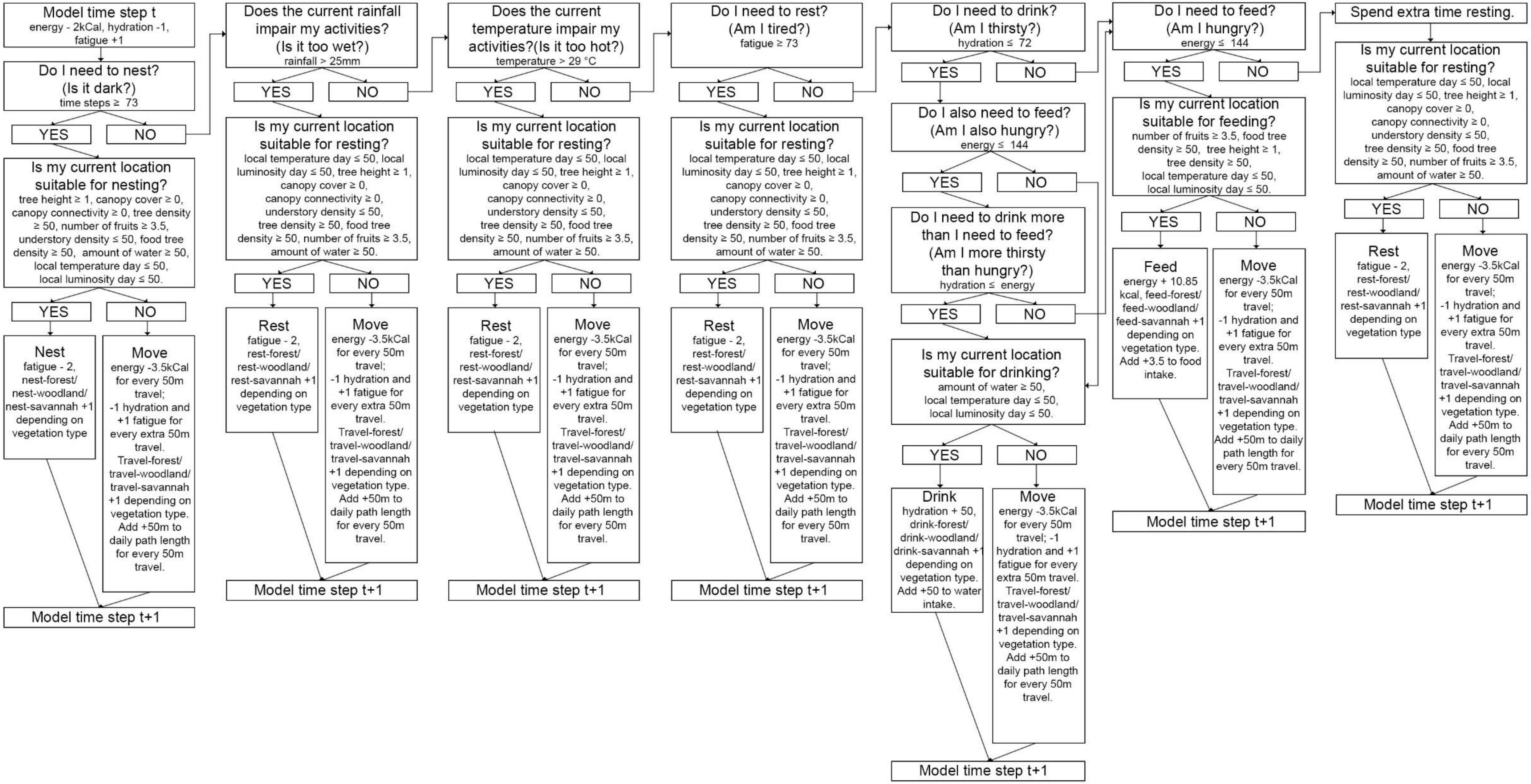

Figure 4.2. Model flowchart of the chimpanzee landscape use model, which specifies the decisions that have to be made by each individual at each time step, and its consequences.

Initialisation

At the onset of a model run, it was first specified whether the simulation should represent chimpanzee landscape use in a forest, mosaic, or savannah landscape. The vegetation cover for each landscape was set out as follows[5]: Forests were simulated as landscapes with 80% forest, 10% woodland, and 10% grassland; Mosaic landscapes had 45% forest, 40% woodland and 15% grassland; and savannahs had 10% forest, 55% woodland, and 35% grassland (Figure 4.1 and Appendix 4.5). With regards to these proportions, patches were randomly assigned a vegetation type, and accordingly, a set of landscape-scale vegetation features and a micro-climate (Chapter 2). The ranges of vegetation features and micro-climate characteristics for each vegetation type are based on findings from Chapter 3 and are outlined in Table 4.1.

Sixty virtual chimpanzee individuals were created and placed within the landscape at random. Each individual was randomly assigned an initial level of energy, hydration and fatigue between 0 – 10, which guided their behaviour (Appendix 4.5). Internal state variables for daily path length, food intake and water intake were set at 0, current activity was set to ‘none’, and current vegetation type was set with respect to the patch the individual occupied at the onset of the model run. Individuals were parameterised to lose two energies, lose one hydration and gain one fatigue at each time step to simulate metabolic processes (Appendix 4.5). For daily feeding, drinking, nesting, resting, and travel activities, specific model rules were outlined on *how much* energy, hydration, fatigue, food and water were gained and/or lost at each time step for these behaviours, as well as on *where* and *when* these behaviours could be performed (Appendix 4.5). As such, behaviours were parameterised to only be performed at suitable times of day and at locations with suitable vegetation features and micro-climate characteristics. Model rules are based on findings from Chapter 2 and are outlined in Table 4.2. Multiple individuals could be present on the same patch, as long as this patch abided to the outlined criteria for the specific behaviour performed. Simulated individuals started off their day with feeding and/or drinking activities, in accordance with chimpanzee observations from the field (Chapter 2).

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[5] Simulated vegetation covers for each landscape are simple modelling example coverages that fall within ranges outlined for chimpanzee dense forest, forest mosaic and savannah environments as outlined in Chapter 3. Although the model only runs over the course of 24 hours and thus no rainfall seasonality is included, the length of the longest consecutive dry season for these landscapes can be deduced from Figure 3.4e (Chapter 3). Mean annual temperature for all model landscapes was set as 25°C (Figure 3.4a).

Table 4.1. Range of vegetation features and micro-climates simulated for each vegetation type within the individual-based model on chimpanzee landscape use. For rationale, see Appendix 4.5.

Characteristic	**Forest**	**Woodland**	**Savannah Grassland**
Tree height	10 – 50m	8 – 20m	3 – 15m
Canopy cover	75 – 100% (i.e. dense/ closed)	25 – 75% (i.e. medium)	0 – 25% (i.e. sparse/ open)
Canopy connectivity	75 – 100%	25 – 75%	0 – 25%
Understory density	0 – 25%	25 – 75%	75 – 100%
Tree density	75 – 100%	25 – 75%	0 – 25%
Food tree density	75 – 100%	25 – 75%	0 – 25%
Local temperature daytime	0 – 25 (i.e. cold - scaled)	25 – 75 (i.e. medium - scaled)	75 – 100 (i.e. hot - scaled)
Local temperature nighttime	75 – 100	25 – 75	0 – 25
Luminosity daytime	0 – 25 (i.e. shaded - scaled)	25 – 75 (i.e. medium - scaled)	75 – 100 (i.e. bright - scaled)
Luminosity nighttime	0 – 25	0 – 25	0 – 25
Number of fruits	0 – 21 fruits (i.e. edible grams)	0 – 14 fruits	0 – 7 fruits
Amount of water	0 – 100 hydrations	0 – 75 hydrations	0 – 50 hydrations

Submodels

The individual-based model developed in this study consisted of four submodels: feeding, drinking, resting and nesting. Travel was included within all four submodels.

Model understanding and testing

Testing of the model code and its implementation was done throughout the model building phase. Upon model completion, the final model was tested as a whole and checked for typographical errors, syntax errors, misunderstandings of code ‘primitives’, run-time errors, logic errors and formulation errors (Railsback and Grimm 2012). Incongruences found were corrected and included in the final code. The model was also subjected to a thorough review of model understanding. It was assessed whether the final model followed the conceptual model and model question, whether the code was accurately implemented according to the model flowchart, and whether the model ran and produced output as expected (e.g. Railsback and Grimm 2012). Improvements were made whenever necessary.

Model calibration and verification

As not all model parameters could be quantified empirically, upon completion of the final model, output was calibrated against literature-based knowledge on the activity budgets of forest chimpanzees (e.g. Raislback and Grimm 2012, Bates and Byrne 2009, Potts et al. 2011, Doran 1997, Boesch and Boesch-Achermann 2000, Lehmann and Boesch 2004). The values for a total of six parameter combinations (i.e. *when* to feed, *when* to drink, *where* to perform daily activities, energy lost per time step, amount fruit per vegetation type, and number fruits eaten per time step; Table 4.3 and Appendix 4.2) were varied over large scales (i.e. > 50%) to assess which parameter combination could predict the activity budgets of forest chimpanzees within 5% of their observed range. The model was run once for each combination of parameter settings, and model and empirical data output were compared. The parameter combination that correctly predicted the observed activity budgets of forest chimpanzees within 3% was selected. A model is said to be verified when its outputs match real-world observations (e.g. Railsback and Grimm 2012).

Table 4.2. Model rules for the chimpanzee landscape use model on *how much* energy, hydration, fatigue, food and water to gain/ lose at each time step for each behaviour, as well as *where* and *when* behaviours could be performed. For rationale, see Appendix 4.5.

Behaviour	**Where**	**When**	**How much to gain/ lose per time step**
Feeding	Patches with number fruit ≥ 3.5 fruits (equals 3.5 grams edible dry weight), food tree density ≥ 50%, tree height ≥ 1m, tree density ≥ 50%, local temperature day ≤ 50 (scaled), and local luminosity day ≤ 50 (scaled).	Energy ≤ 144 kCal (i.e. when it is hungry) and energy < hydration (i.e. when an individual is more hungry than thirsty).	Gain 3.1 kCal per fruit eaten (i.e. per edible gram dry weight) and eat 3.5 fruits per time step. Patches lose 3.5 fruits.
Drinking	Patches with amount water ≥ 50 hydrations, local temperature day ≤ 50 (scaled), and local luminosity day ≤ 50 (scaled).	Hydration ≤ 72 (i.e. when it is thirsty) and hydration < energy (i.e. when an individual is more thirsty than hungry).	Gain 50 hydrations. Patches lose 50 hydrations.
Nesting	Patches with tree height ≥ 1m, canopy cover ≥ 0%, canopy connectivity ≥ 0%, tree density ≥ 50%, number fruit ≥ 3.5 fruits (equals 3.5 grams edible dry weight), understory density ≤ 50%, food tree density ≥ 50%, amount water ≥ 50 hydrations, local temperature (day) ≤ 50 (scaled), and local luminosity (day) ≤ 50 (scaled).	Time steps > 72 (i.e. the second half of the 24-hour day, and thus when it is night).	Lose 2 fatigues.
Resting	Patches with local temperature (day) ≤ 50 (scaled), local luminosity (day) ≤ 50 (scaled), tree height ≥ 1m, canopy cover ≥ 0%, canopy connectivity ≥ 0%, tree density ≥ 50%, number fruit ≥ 3.5 fruits (i.e. equals 3.5 grams edible dry weight), understory density ≤ 50%, food tree density ≥ 50%, and amount water ≥ 50 hydrations.	Fatigue ≥ 73 (i.e. when it is too tired), or rainfall ≥ 25mm (i.e. when it is too wet)*, or overall temperature ≥ 29°C (i.e. when it is too hot)*, or energy > 144 and hydration > 73 (i.e. 'free' resting).	Lose 2 fatigues.
Travel	No rules set out on where to travel; travel is directed towards a suitable location for the selected activity.	No specific rules, but travel when a current patch is not suitable for the chosen activity. In this case, first assess the suitability of neighbouring patches within 50m, then assess the patches within 100m, and if a suitable location is then still not be found, jump at random between 3 – 6 patches (i.e. 150 – 300m).	Lose 3.5 kCal for every 50m of travel (i.e. one patch), and lose 1 additional hydration and gain 1 additional fatigue for every extra 50m of travel (i.e. when travelling more than 50m in one time step).

*Within the model, rainfall and overall temperature never reached above 25mm and 29°C; Overall temperature and rainfall are, however, included in model rules for the sake of completeness.

Model sensitivity analysis

This study conducted a local sensitivity analysis on the final calibrated model to assess the effect of small changes in parameter settings on model output (e.g. Railsback and Grimm 2012, Muko et al. 2014). This study selected 26 parameters for sensitivity analysis (Table 4.3 and Appendix 4.2), varied the target parameter values by +/- 10%, and checked for changes in the simulated activity budgets. Parameters were varied one-at-a-time, and the model was run once for each parameter combination. Final sensitivities (S^+ and S^-) were calculated by dividing the percentage of change in the output by the percentage of change in the input, with low values for S indicating low sensitivities (EduPristine 2018). A low sensitivity indicates that a parameter has a small effect on model output, whereas a high sensitivity highlights that a parameter has a strong influence on model output; high or low sensitivities are not necessarily good or bad, it is the relative differences in sensitivities that emphasise how a model works (Railsback and Grimm 2012).

Model output analyses and statistics

The model was run 30 times for each landscape, i.e. forests, mosaics and savannahs (e.g. Crawley 2005). Model data for each simulated individual were averaged per model run and analyses were conducted on the mean values of output variables over the 30 runs per simulated environment. In most analyses, therefore, N = 30. The following output variables were analysed: frequencies of activities; usage of vegetation types overall and per behaviour; final total energy, hydration and fatigue budgets; total food and water intake; site selections with regards to vegetation features and micro-climates; and total daily path lengths. Values are presented as mean ± standard deviation. Differences in landscape use patterns for chimpanzees in forests, mosaics and savannahs were assessed visually using graphs and data range tables, and statistically using Kruskal-Wallis tests in IBM SPSS Statistics (version 22). Correlations were performed using Spearman’s rank correlation coefficient. All tests were performed two-tailed and the significance level alpha (α) was set at 0.05. *Post-hoc* Mann-Whitney U tests were performed whenever a significant difference was found (Kruskal-Wallis tests); the Bonferroni correction was applied to control for multiple comparisons (Field 2009), resulting in a significance level α of $0.05 / 3 = 0.0167$. Preferences for specific types of vegetation were assessed using chi-square goodness of fit tests with a significance level α of 0.05, and were based on the number of time steps spent in each vegetation type across individuals over the 30 model runs per landscape (i.e. N = 30 runs x 60 individuals x 144 time steps = 259,200). Total frequencies of ‘0’ were replaced with ‘1’ to produce reliable output.

Results

Sensitivity analysis

Local sensitivity analysis showed that model output was robust to small changes in parameter settings (Table 4.3). With 10% changes in input parameters, the model output was never more than 10% different from the baseline output (i.e. the output when using only target values for the calibrated parameters). The low sensitivity of the model to small changes in the input parameters did not indicate model overfitting, i.e. fine-tuning a model in such detail that only a few patterns are matched closely at the cost of other patterns (Railsback and Grimm 2012), as large changes in parameter settings (> 50%) had a significant effect on the model output during the calibration process.

Activity budgets

Chimpanzee daily activity budgets (24 hours) differed significantly between forest, mosaic and savannah landscapes (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 15.7$, df = 2, $p < 0.001$; Table 4.4 and Figure 4.3). Chimpanzees in mosaic landscapes spent significantly more time feeding and drinking than chimpanzees in forests and savannahs, and chimpanzees in savannah landscapes spent significantly less time feeding and drinking than chimpanzees in forests (Table 4.5). Forest chimpanzees spent significantly more time nesting and resting than mosaic and savannah chimpanzees, and savannah chimpanzees rested and nested for significantly less time than mosaic chimpanzees. Chimpanzees in savannahs travelled for significantly more time than chimpanzees in forest and mosaic landscapes, and chimpanzees in mosaics spent more time travelling than chimpanzees in forests (Table 4.5).

Daily path lengths

Daily path lengths differed significantly between landscapes for chimpanzees (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 79.1$, df = 2, $p < 0.001$; Table 4.4 and Figure 4.4). Savannah chimpanzees had significantly longer daily path lengths than forest and mosaic chimpanzees, and mosaic chimpanzees travelled significantly longer distances than forest chimpanzees (Table 4.5).

Table 4.3. Sensitivity (S) of model output of the generic chimpanzee model to small (i.e. +/- 10%) changes in input parameter values. 26 parameters were selected for sensitivity analysis. Sensitivities were calculated by dividing the percentage of change in the output by the percentage of change in the input; Low values for S indicated low sensitivities. The rationale behind the baseline values for all parameters is outlined in Appendix 4.5. Within the table, 'random' indicates that a value was randomly assigned between 0 and 'number'.

Parameter	**Base value**	**+10% value**	**S+**	**-10% value**	**S-**
number of fruit forest*	random 21	random 23.1	0.24	random 18,9	0.53
number of fruit woodland*	random 14	random 15.4	0.13	random 13.6	0.07
number of fruit savannah*	random 7	random 7.7	0.01	random 6.3	0.09
amount of water forest	random 100	random 110	0.06	random 90	0.26
amount of water woodland	random 75	random 82.5	0.12	random 67.5	0.03
amount of water savannah	random 50	random 55	0.09	random 45	0.09
where - understory density criterion*	<50	<55	0.04	<45	0.22
where - tree density criterion*	>50	>55	0.03	>45	0.19
where - food tree density criterion*	>50	>55	0.01	>45	0.09
where - local temperature criterion*	<50	<55	0.07	<45	0.27
where - local luminosity criterion*	<50	<55	0.22	<45	0.14
when - feeding criterion*	<144	< 158.4	0.35	<129.6	0.22
when - drinking criterion*	<72	< 79.2	0.23	< 64.8	0.27
when - resting criterion	>73	>80.3	0.2	>65.7	0.04
Initial - energy	random 10	random 11	0.07	random 9	0.13
Initial - hydration	random 10	random 11	0.02	random 9	0.06
Initial - fatigue	random 10	random 11	0.16	random 9	0.19
Step – energy*	-2	-2.2	0.52	-1.8	0.18
Step - hydration	-1	-1.1	0.24	-0.9	0.02
Step - fatigue	+1	1.1	0.09	0.9	0.33
Feeding - number fruits eaten*	3.5	3.85	0.41	3.15	0.54
Drinking - amount water drunk	50	55	0.1	45	0.93
Resting - fatigue	-2	-2.2	0.13	-1.8	0.23
Nesting - fatigue	-2	-2.2	0.07	-1.8	0.12
Travel - hydration	-1 per 50m	-1.1	0.15	-0.9	0.29
Travel - fatigue	+1 per 50m	+1.1	0.05	+0.9	0.23

* Used for model calibration (i.e. six parameter combinations: *when* to feed / drink, *where* to perform activities, energy lost per time step, amount fruit per vegetation type, and number fruits eaten per time step; Appendix 4.2).

Energy budgets

Final total energy budgets were significantly different for forest chimpanzees, mosaic chimpanzees, and savannah chimpanzees (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 78.1$, df = 2, $p < 0.001$; Table 4.4 and Figure 4.5). Chimpanzees in savannahs had significantly lower energy budgets than chimpanzees in forests and mosaics, and chimpanzees in mosaics had significantly lower energy budgets than chimpanzees in forests (Table 4.5).

Hydration budgets

Chimpanzee daily hydration budgets differed significantly between forest, mosaic and savannah landscapes (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 60.1$, $df = 2$, $p < 0.001$; Table 4.4 and Figure 4.6). Savannah chimpanzees had significantly lower hydration budgets than forest chimpanzees and mosaic chimpanzees, but hydration budgets did not differ significantly between mosaic and forest chimpanzees (Table 4.5).

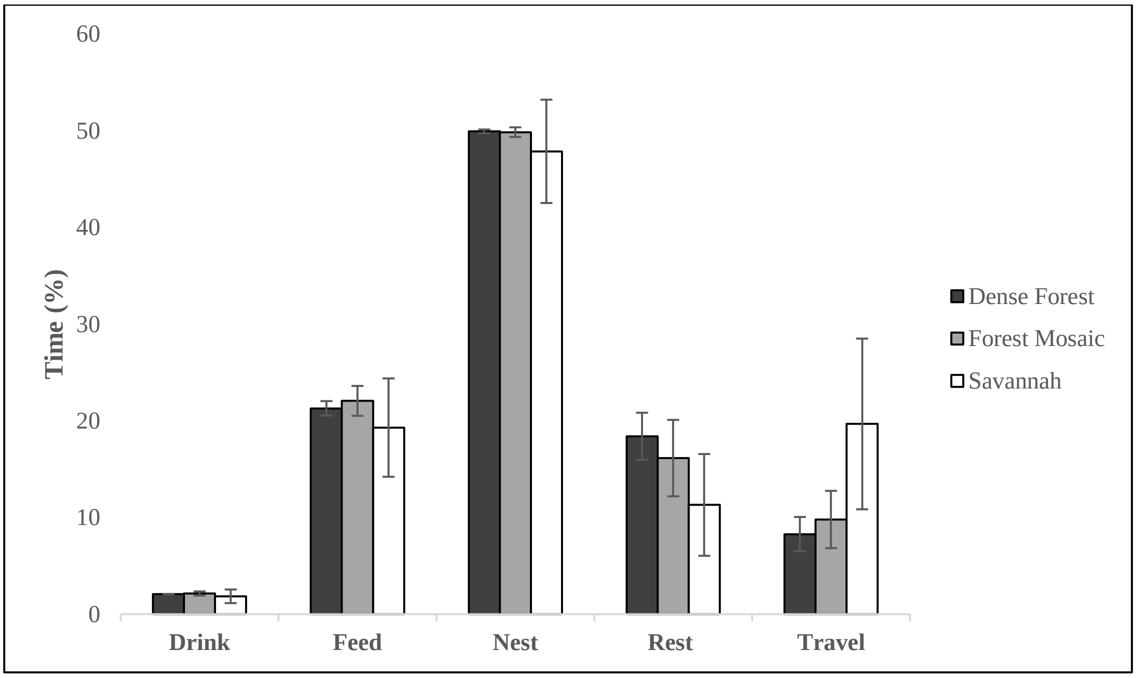

Figure 4.3. Model output of the daily activity budgets (24 hours) for chimpanzees in forests, mosaics and savannahs.

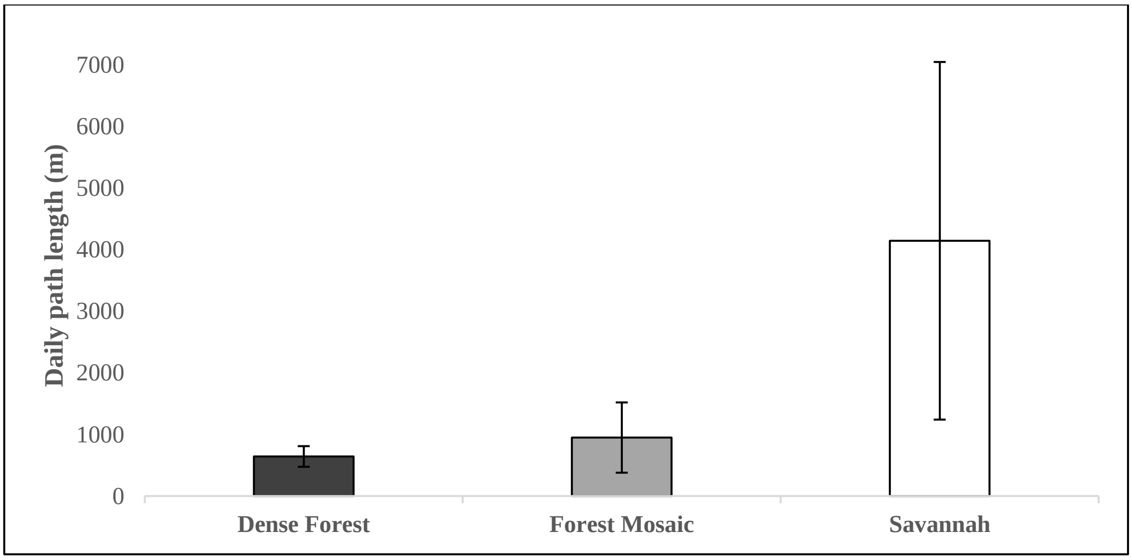

Figure 4.4. Model output of the daily path lengths (24 hours) for chimpanzees in forests, mosaics and savannahs.

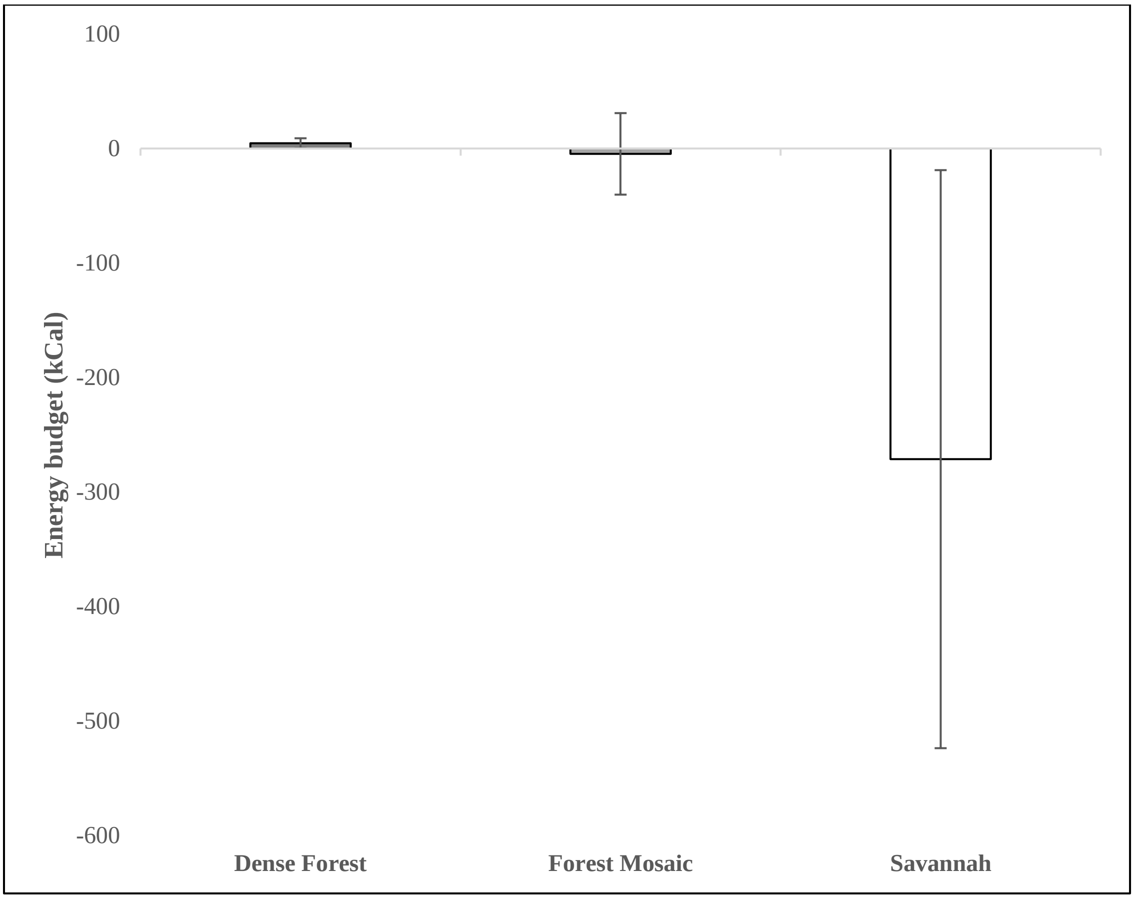

Figure 4.5. Model output of the daily energy budgets (24 hours) for chimpanzees in forests, mosaics and savannahs.

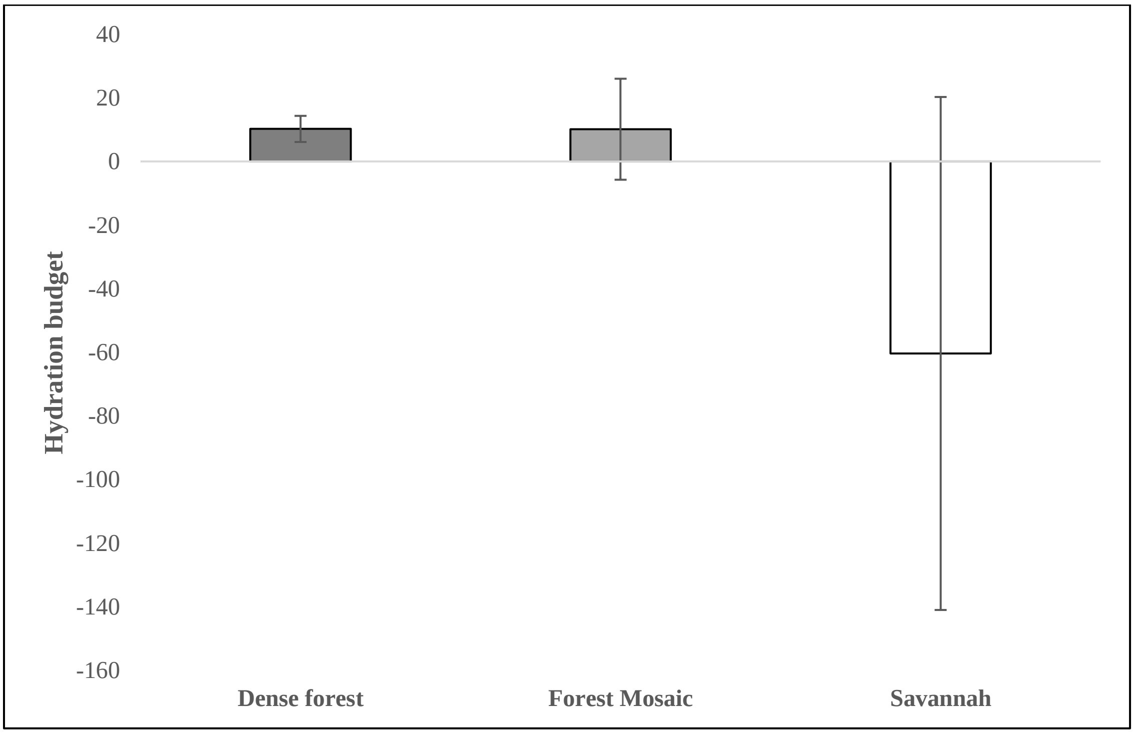

Figure 4.6. Model output of the daily hydration budgets (24 hours) for chimpanzees in forests, mosaics and savannahs.

Fatigue budgets

Chimpanzee daily fatigue levels differed significantly between environments (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 79.1$, $df = 2$, $p < 0.001$; Table 4.4 and Figure 4.7). Savannah chimpanzees had significantly higher fatigue levels than forest and mosaic chimpanzees, and forest chimpanzees had significantly lower fatigue budgets than mosaic chimpanzees (Table 4.5).

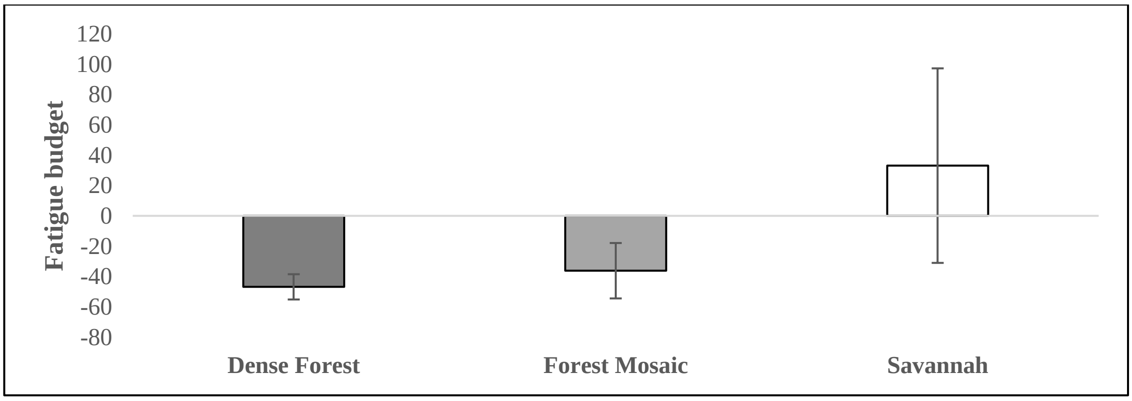

Figure 4.7. Model output of the daily fatigue budgets (24 hours) for chimpanzees in forests, mosaics and savannahs.

Food intake

Food intake differed significantly for chimpanzees between landscapes (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 75.1$, $df = 2$, $p < 0.001$; Table 4.4 and Figure 4.8). Mosaic chimpanzees had significantly higher food intake than forest and savannah chimpanzees, and savannah chimpanzees had significantly lower food intake than forest chimpanzees (Table 4.5).

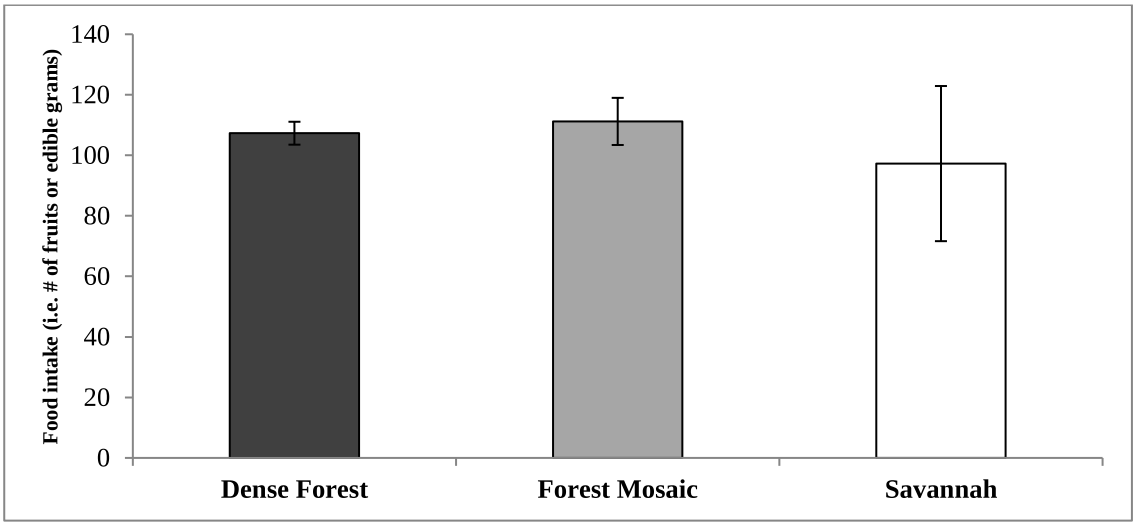

Figure 4.8. Model output of daily food intake (24 hours) for chimpanzees in forests, mosaics and savannah landscapes.

Water intake

Daily water intake was significantly different between environments for chimpanzees (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 64.9$, $df = 2$, $p < 0.001$; Table 4.4 and Figure 4.9). Water intake was significantly higher for mosaic chimpanzees as compared to forest chimpanzees and savannah chimpanzees, and forest chimpanzees had significantly higher water intake than savannah chimpanzees (Table 4.5).

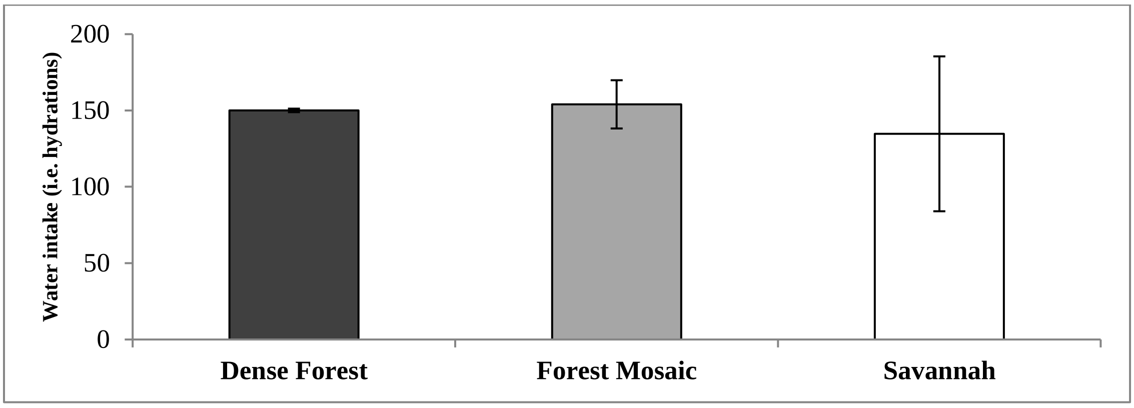

Figure 4.9. Model output of daily water intake (24 hours) for chimpanzees in forests, mosaics and savannahs.

Table 4.4. Model output (i.e. mean ± standard deviation) of the daily activity budgets (% time of 24-hours), path lengths (m), food intake (# of fruits or edible grams), water intake (hydrations), energy budgets (kCal), hydration budgets (hydrations), and fatigue budgets (fatigues) for chimpanzees in forest, mosaic and savannah landscapes.

	Dense Forest	Forest Mosaic	Savannah
Time spent feeding	21.3±0.8%	22.1±1.5%	19.3±5.1%
Time spent drinking	2.1±0.0%	2.1±0.2%	1.8±0.7%
Time spent nesting	49.9±0.2%	49.9±0.5%	47.9±5.3%
Time spent resting	18.4±2.4%	16.1±4.0%	11.3±5.3%
Time spent travelling	8.3±1.8%	9.8±3.0%	19.7±8.8%
Daily path length	642.6±167.4m	949.1±570.2m	4,142.3±2,901.4m
Food intake	107.3±3.8 fruits	111.2±7.8 fruits	97.3±25.6 fruits
Water intake	150.1±1.2 hydrations	154.0±15.8 hydrations	134.7±50.7 hydrations
Energy budget	4.6±4.3kCal	-4.7±35.6kCal	-271.4±252.5kCal
Hydration budget	10.2±4.1	10.1±15.9	-60.4±80.7
Fatigue budget	-46.8±8.3	-36.2±18.3	33.1±64.2

Preferred vegetation

Daily vegetation type usage differed significantly for chimpanzees in forest, mosaic and savannah landscapes (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 78.0$, $df = 2$, $p < 0.001$; Table 4.6 and Figure 4.10). Chimpanzees in forests spent significantly more time in forest patches than chimpanzees in mosaics and savannahs, and chimpanzees in savannahs spent significantly less time in forest patches as compared to chimpanzees in mosaics (Table 4.7). Savannah chimpanzees spent significantly more time in woodland

and grassland patches as compared to forest and mosaic chimpanzees, and forest chimpanzees spent significantly less time in woodland and grassland patches than mosaic chimpanzees (Table 4.7). When checking vegetation type usage against vegetation type availability for each landscape (Figure 4.11), it was shown that forest vegetation types were preferred in all environments, and woodland and grassland were avoided (dense forests: $\chi^2 = 61,807.3$, df = 2, $p < 0.001$; forest mosaics: $\chi^2 = 282,964.5$, df = 2, $p < 0.001$; savannah: $\chi^2 = 1,224,101.3$, df = 2, $p < 0.001$).

Table 4.5. *Post-hoc* Mann-Whitney U tests statistics for the comparisons of activity budgets, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, and daily path lengths for chimpanzees in dense forests (F), forest mosaics (M) and savannahs (S). An ‘*’ denotes a significant difference. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** (N$_{1,2}$ = 30 in all cases)		
	Dense Forest (F) vs Forest Mosaic (M)	**Dense Forest (F) vs Savannah (S)**	**Forest Mosaic (M) vs Savannah (S)**
Time spent feeding	M > F, Z = -6.5*	F > S, Z = -6.3*	M > S, Z = -6.6*
Time spent drinking	M > F, Z = -4.4*	F > S, Z = -6.3*	M > S, Z = -6.3*
Time spent nesting	F > M, Z = -3.9*	F > S, Z = -6.8*	M > S, Z= -6.7*
Time spent resting	F > M, Z = -6.7*	F > S, Z = -6.7*	M > S, Z = -6.7*
Time spent travelling	M > F, Z = -6.6*	S > F, Z = -6.7*	S > M, Z = -6.7*
Daily path length	M > F, Z = -6.7*	S > F, Z = -6.7*	S > M, Z = -6.7*
Energy budget	F > M, Z = -6.5*	F > S, Z = -6.7*	M > S, Z = -6.7*
Hydration budget	F = M, Z = -1.3**	F > S, Z = -6.7*	M > S, Z = -6.7*
Fatigue budget	M > F, Z = -6.7*	S > F, Z = -6.7*	S > M, Z = -6.7*
Food intake	M > F, Z = -6.4*	F > S, Z = -6.2*	M > S, Z = -6.6*
Water intake	M > F, Z = -6.9*	F > S, Z = -5.8*	M > S, Z = -5.8*

*significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$); **no significant difference, i.e. $p > 0.0167$.

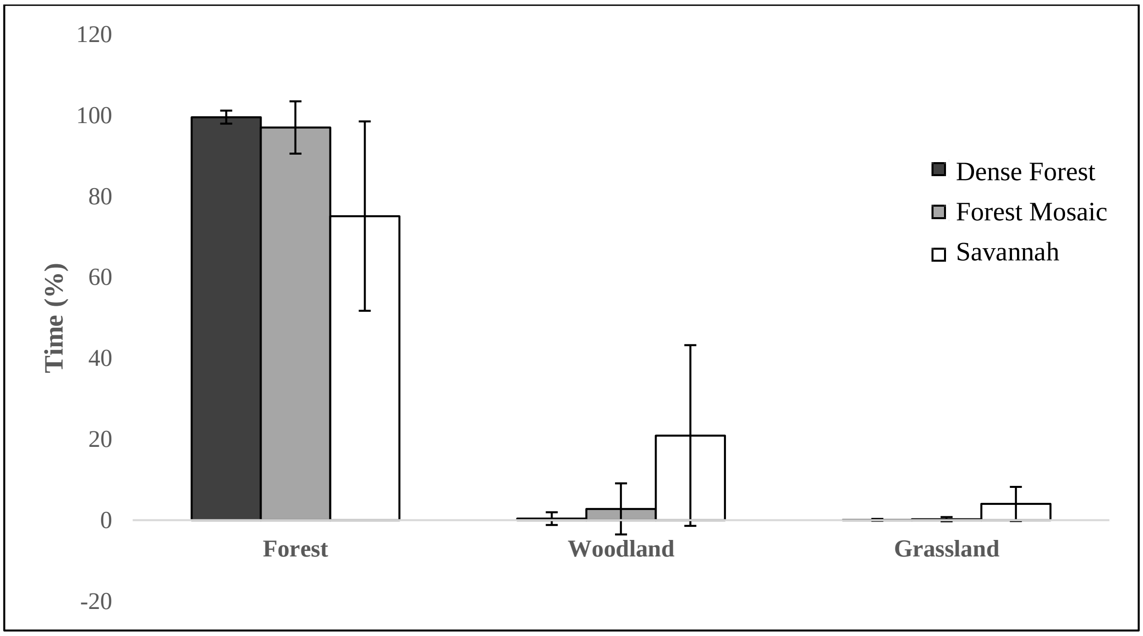

Figure 4.10. Model output on daily vegetation type usage (24 hours) for chimpanzees in forests, mosaics and savannah landscapes.

Table 4.6. Model output (i.e. mean ± standard deviation) of the vegetation type usage (i.e. % time of 24-hours spent in forest, woodland and grassland) for chimpanzees in forest, mosaic and savannah landscapes.

	Dense Forest	**Forest Mosaic**	**Savannah**
Time spent in forest	99.5±1.6%	97.0±6.5%	75.1±23.4%
Time spent in woodland	0.4±1.6%	2.8±6.3%	20.9±22.3%
Time spent in grassland	0.1±0.2%	0.2±0.5%	4.0±4.2%

Table 4.7. *Post-hoc* Mann-Whitney U tests statistics for the comparisons of vegetation type usage for chimpanzees in dense forest (F), forest mosaic (M) and savannah (S) landscapes. An '*' denotes a significant difference. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)		
	Dense Forest (F) vs Forest Mosaic (M)	**Dense Forest (F) vs Savannah (S)**	**Forest Mosaic (M) vs Savannah (S)**
Time spent in forest	F > M, Z = -6.7*	F > S, Z = -6.7*	M > S, Z = -6.7*
Time spent in woodland	M > F, Z = -6.6*	S > F, Z = -6.7*	S > M, Z = -6.7*
Time spent in grassland	M > F, Z = -6.4*	S > F, Z = -6.9*	S > M, Z = -6.7*

*significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$).

Behaviourally preferred vegetation

Time spent in different vegetation types (i.e. forest, woodland and grassland) was spent on different activities (i.e. feeding, drinking, nesting, resting, and travelling), and this differed significantly for chimpanzees in forest, mosaic and savannah environments (in all cases, Kruskal-Wallis: $N_1 = 30$, $N_2 = 30$, $N_3 = 30$, $H \geq 29.2$, df = 2, $p < 0.001$; Table 4.8 and Figure 4.12). Across environments, savannah chimpanzees spent significantly more time feeding, drinking, nesting and resting in woodland as compared to forest and mosaic chimpanzees, and mosaic chimpanzees spent more time feeding, drinking, nesting and resting in woodland than forest chimpanzees (Table 4.9). Similarly, savannah chimpanzees spent significantly more time travelling in woodland and grassland as compared to forest and mosaic chimpanzees, and forest chimpanzees spent significantly less time travelling in woodland and grassland than mosaic chimpanzees (Table 4.9). Mosaic chimpanzees spent significantly more time feeding and travelling in forest as compared to forest and savannah chimpanzees, and savannah chimpanzees spent significantly less time feeding and travelling in forest than forest chimpanzees (Table 4.9). Forest chimpanzees spent significantly more time drinking, nesting and resting in forest as compared to mosaic and savannah chimpanzees, and mosaic chimpanzees spent significantly more time drinking, nesting and resting in forest than savannah chimpanzees (Table 4.9). Chimpanzees in forest, mosaic and savannah landscapes were never observed to feed, rest, drink or nest in grassland. Forest was the preferred vegetation type for each behaviour, and woodland and grassland were avoided (in all cases: $\chi^2 \geq 1,244.6$, df = 2, $p < 0.001$).

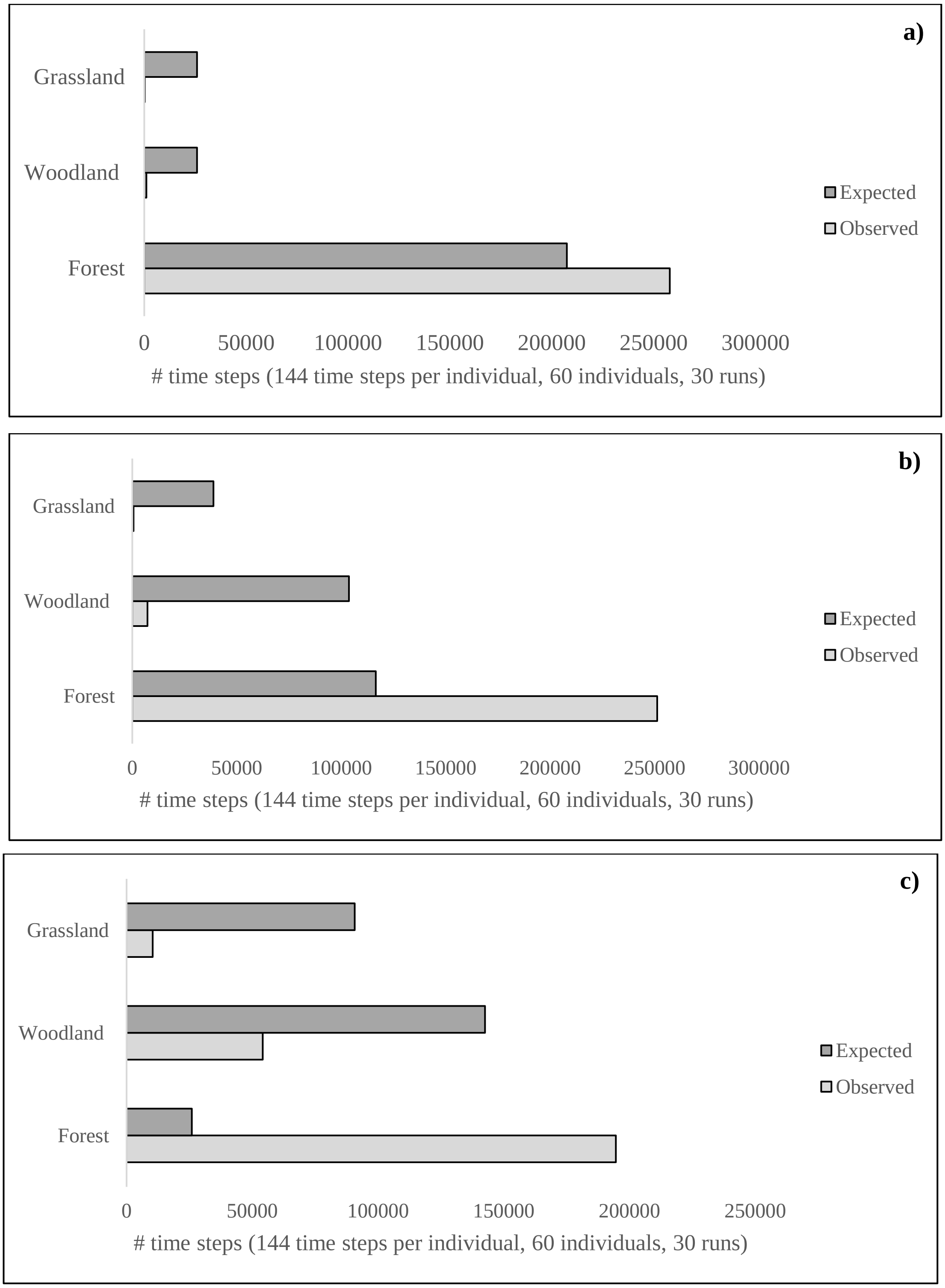

Figure 4.11. Observed vs expected vegetation type usage for chimpanzees simulated in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs. Total frequency is calculated across individuals and landscapes, i.e. 60 individuals x 144 time steps per model run x 30 model runs = 259,200). Expected frequencies followed from the vegetation cover as outlined for the model (i.e. p. 101), whereas observed frequencies followed from actual usage by the simulated model individuals.

Table 4.8. Model output (i.e. mean ± standard deviation) of time spent on different activities (i.e. feeding, drinking, nesting, resting and travelling) in different vegetation types (i.e. forest, woodland and grassland) for chimpanzees in forests, mosaics and savannahs.

	Dense Forest			**Forest Mosaic**			**Savannah**		
	Forest	***Woodland***	***Grassland***	***Forest***	***Woodland***	***Grassland***	***Forest***	***Woodland***	***Grassland***
Feeding	21.1±0.8%	0.1%±0.4%	-	21.3±1.9%	0.8±1.5%	-	16.0±6.1%	3.3±2.8%	-
Drinking	2.1±0.1%	0.0±0.1%	-	2.0±0.3%	0.1±.03%	-	1.5±0.8%	0.4±0.4%	-
Nesting	49.8±0.9%	0.1±0.7%	-	49.3±4.2%	0.5±4%	-	40.3±18.1%	7.6±17.4%	-
Resting	18.4±2.5%	0.0±0.1%	-	16.0±4.0%	0.1±0.6%	-	9.8±5.8%	1.5±3.8%	-
Travel	8.1±1.7%	0.1±0.4%	0.1±0.2%	8.3±2.1%	1.2±1.8%	0.2±0.5%	7.6±3.0%	8.1±6.2%	4.0±4.2%
Total	99.5±1.6%	0.4±1.6%	0.1±0.2%	97.0±6.5%	2.8±6.3%	0.2±0.5%	75.1±23.4%	20.9±22.3%	4.0±4.2%

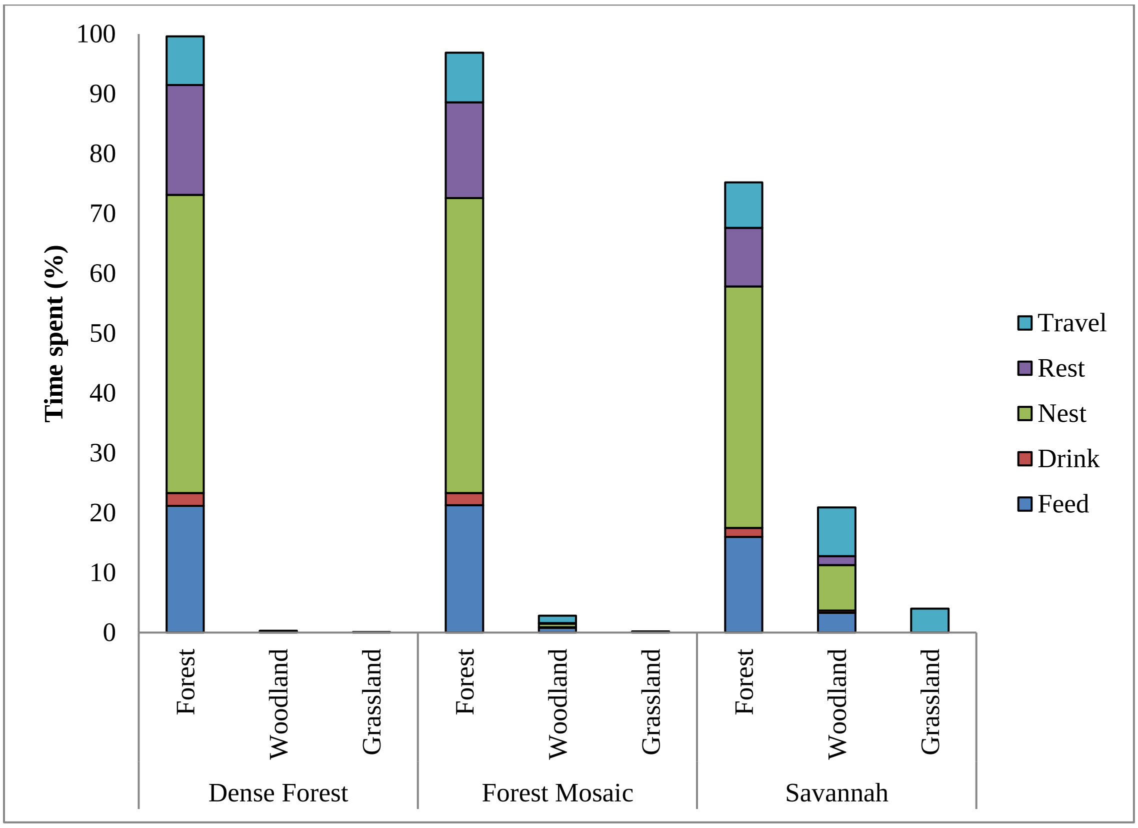

Figure 4.12. Model output of daily activities performed in forest, woodland and grassland vegetation (24 hours) for chimpanzees in forest, mosaic and savannah landscapes.

Site selectivity

Following model rules, chimpanzees in forests, mosaics and savannahs used the complete range of vegetation features and micro-climates found in forest, woodland and grassland for travel (Table 4.1 and Table 4.2). For feeding, drinking, nesting and resting, chimpanzees were more restrictive in their site selection across environments, and included the total range of micro-climates and structural vegetation features observed in forest and only a part of the range found in woodland (Table 4.1 and Table

4.2). The median and interquartile ranges of vegetation features and micro-climates used for the different activities, however, showed that chimpanzees in forest, mosaic and savannah environments predominantly used the range of vegetation features and micro-climates found in forest vegetation types (Table 4.10). When chimpanzee environments changed from forests to more open mosaic and savannah landscapes, medians and interquartile ranges of the vegetation features and micro-climates used gradually became wider and shifted more towards the micro-climate and structural vegetation ranges observed in woodland. This pattern was especially evident for chimpanzee travel (Table 4.10).

Table 4.9. *Post-hoc* Mann-Whitney U test statistics for the comparisons of time spent on different activities within different vegetation types for chimpanzees in forests, mosaics and savannahs. An '*' denotes a significant difference. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)		
	Dense Forest (F) vs Forest Mosaic (M)	**Dense Forest (F) vs Savannah (S)**	**Forest Mosaic (M) vs Savannah (S)**
Feed – forest	M > F, Z = -3.2*	F > S, Z = -6.7*	M > S, Z = -6.7*
Feed – woodland	M > F, Z = -6.7*	S > F, Z = -6.7*	S > M, Z = -6.7*
Feed - grassland	-	-	-
Drink – forest	F > M, Z = -5.6*	F > S, Z = -7.0*	M > S, Z = -6.8*
Drink – woodland	M > F, Z = -7.1*	S > F, Z = -7.2*	S > M, Z = -6.9*
Drink - grassland	-	-	-
Nest – forest	F > M, Z = -4.7*	F > S, Z = -6.7*	M > S, Z = -6.7*
Nest – woodland	M > F, Z = -3.7*	S > F, Z = -7.0*	S > M, Z = -6.7*
Nest - grassland	-	-	-
Rest – forest	F > M, Z = -6.7*	F > S, Z = -6.7*	M > S, Z = -6.7*
Rest – woodland	M > F, Z = -3.5*	S > F, Z = -6.9*	S > M, Z = -6.7*
Rest - grassland	-	-	-
Travel – forest	M > F, Z = -3.6*	F > S, Z = -3.3*	M > S, Z = -4.6*
Travel – woodland	M > F, Z = -6.8*	S > F, Z = -6.8*	S > M, Z = -6.7*
Travel - grassland	M > F, Z = -6.4*	S > F, Z = -6.9*	S > M, Z = -6.7*

* significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$).

Inter-individual variability

Within each environment, inter-individual variability between chimpanzees was observed across model runs and was particularly evident for chimpanzees' internal states. In forests, for example, even though average energy budgets were positive, daily energy budgets across individuals and model runs ranged between -143.5 and 10.8 kCal, with 98.4% of the individuals having positive energy budgets and 1.6% of the individuals having negative energy budgets (Figure 4.13). In mosaic landscapes, energy budgets across individuals and model runs ranged between -1,025.9 and 10.8 kCal, and 87.5% of the individuals had positive energy budgets and 12.5% of the individuals had negative energy budgets (Figure 4.13). In savannahs, daily energy budgets ranged between -1,661.4 and 10.8 kCal across individuals and model runs, with 13.8% of the individuals having positive energy budgets and 86.2% of the individuals having negative energy budgets (Figure 4.13). Similar patterns were observed for hydration budgets (forest: range = -69 – 49 hydrations, percent positive individuals = 99.9%; mosaic: range = -318 – 50 hydrations, percent positive individuals = 96.1%; savannah: range = -420 – 50 hydrations, percent positive individuals = 28.8%) and fatigue budgets (forest: range = -67 – 2 fatigues, percent positive individuals = 0.1%; mosaic: range = -68 – 178 fatigues, percent positive individuals = 5.7%; savannah: range = -63 – 459 fatigues, percent positive individuals = 74.9%).

Inter-individual variability across model runs was also observed for other model output, including daily path lengths (forest: range = 300 – 2,600m; mosaic: range = 300 – 11,500m; savannah: range = 450 – 22,650m) and forest use (forest: range = 40.3 – 100.0% of time spent in forest vegetation; mosaic: range = 0.0 – 100.0% of time spent in forest vegetation; savannah: range = 0.0 – 100.0% of time spent in forest vegetation). Daily path length and time spent in forest vegetation showed a significant negative correlation for chimpanzees in mosaic landscapes ($N = 30$, $r_s = -0.530$, $p = 0.003$) and in savannah environments ($N = 30$, $r_s = -0.732$, $p < 0.001$; Figure 4.14). No significant correlation was observed between daily path length and forest use for chimpanzees in forests ($N = 30$, $r_s = -0.252$, $p = 0.180$).

Discussion

Using an individual-based modelling approach, this study explored chimpanzee landscape use patterns in different environments. Specifically, it investigated how chimpanzees adapted their activity budgets, daily path lengths, food intake, water intake, vegetation type usage, site selection, and consequently their energy, hydration and fatigue budgets to inhabit dense forest, forest mosaic and savannahs. Model output showed that chimpanzees in different environments used different behavioural strategies to balance their energy, hydration and fatigue budgets, and chimpanzees generally increased their feeding time, drinking time, travel time and travel distance, decreased their resting time, and used more suboptimal woodland and grassland vegetation types more often when the environment was more open. In savannahs, however, travel time and distance increased exponentially at the cost of feeding, drinking, nesting and resting, indicating that additional adaptations were necessary to safeguard savannah chimpanzee survival.

Table 4.10. Interquartile range and median of the vegetation features and micro-climates most frequently used by forest, mosaic and savannah chimpanzees for performing their daily feeding, drinking, nesting, resting and travel activities: **a**) tree height, canopy cover, canopy connectivity and understory density, **b**) tree density, food tree density, food availability and water availability, and **c**) temperature and luminosity at daytime. Q_1 stands for the lower quartile of the range used, i.e. 25%, and Q_3 stands for the upper quartile of the range used, i.e. 75%. As published literature has not presented quantitative data on micro-climates, these variables are presented on a 0-100 scale, with 0 being cold/dark and 100 being hot/light.

a)		**Tree height (m)**			**Canopy cover (%)**			**Canopy connectivity (%)**			**Understory density (%)**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Dense Forest	Feeding	20	30	40	81	87	94	81	88	94	6	13	19
	Drinking	20	30	40	81	87	94	81	88	94	6	12	19
	Nesting	19	30	40	80	87	94	81	88	94	5	13	19
	Resting	19	30	41	81	87	94	81	88	94	6	12	19
	Travel	19	29	40	80	87	94	80	87	94	6	13	20
Forest mosaic	Feeding	19	29	40	80	87	94	80	87	94	6	13	20
	Drinking	18	29	39	80	86	93	80	87	93	6	13	20
	Nesting	20	30	40	80	88	94	81	87	94	6	13	19
	Resting	19	30	40	81	87	94	81	87	94	6	13	19
	Travel	16	27	39	78	85	93	78	85	93	7	15	22
Savannah	Feeding	16	26	38	77	85	93	77	85	93	7	15	23
	Drinking	16	25	38	76	84	93	76	84	92	7	16	24
	Nesting	17	26	38	78	85	93	77	85	93	7	15	23
	Resting	17	26	38	78	85	92	78	85	93	7	15	22
	Travel	11	15	24	30	61	84	30	61	84	16	39	70

b)		**Tree density (%)**			**Food tree density (%)**			**Number fruit**			**Amount water**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Dense Forest	Feeding	81	87	94	81	87	94	6	9.5	13.5	27	53	77
	Drinking	81	87	94	81	88	94	3.5	8	13	62	75	88
	Nesting	81	88	94	81	87	93	5.5	8.5	12.5	63	75	88
	Resting	81	87	94	81	87	94	6	8.5	12.5	62	75	88
	Travel	80	87	94	80	87	94	0.5	2	3	20	41	67
Forest mosaic	Feeding	80	87	94	80	87	94	6	9.5	13.5	25	50	75
	Drinking	80	87	94	80	87	94	3.5	7.5	12.5	61	73	87
	Nesting	81	87	93	81	87	93	6	9	13	61	73	88
	Resting	81	87	94	81	87	94	6	8.5	12.5	62	75	87
	Travel	78	85	93	78	85	93	1	2	3	19	39	64
Savannah	Feeding	77	85	93	77	85	93	6	9	13	21	44	69
	Drinking	76	82	92	76	82	92	2.5	6.5	11.5	60	71	84
	Nesting	77	85	93	77	85	93	7	10.5	14.5	61	72	86
	Resting	78	85	93	78	85	93	6.5	10	14	62	72	86
	Travel	32	64	84	32	63	84	1	3	6	16	34	52

c)		**Temperature day**			**Luminosity day**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Dense Forest	Feeding	6	12	19	6	13	19
	Drinking	6	13	19	6	13	19
	Nesting	5	12	18	6	13	20
	Resting	6	12	19	6	13	19
	Travel	6	13	20	6	13	19
Forest mosaic	Feeding	6	13	20	6	13	20
	Drinking	6	13	20	7	13	20
	Nesting	6	13	19	6	12	19
	Resting	6	13	19	6	12	19
	Travel	7	15	22	7	15	22
Savannah	Feeding	7	15	23	7	15	23
	Drinking	8	16	24	7	16	24
	Nesting	8	15	23	7	14	22
	Resting	7	14	22	8	15	22
	Travel	16	36	68	16	36	67

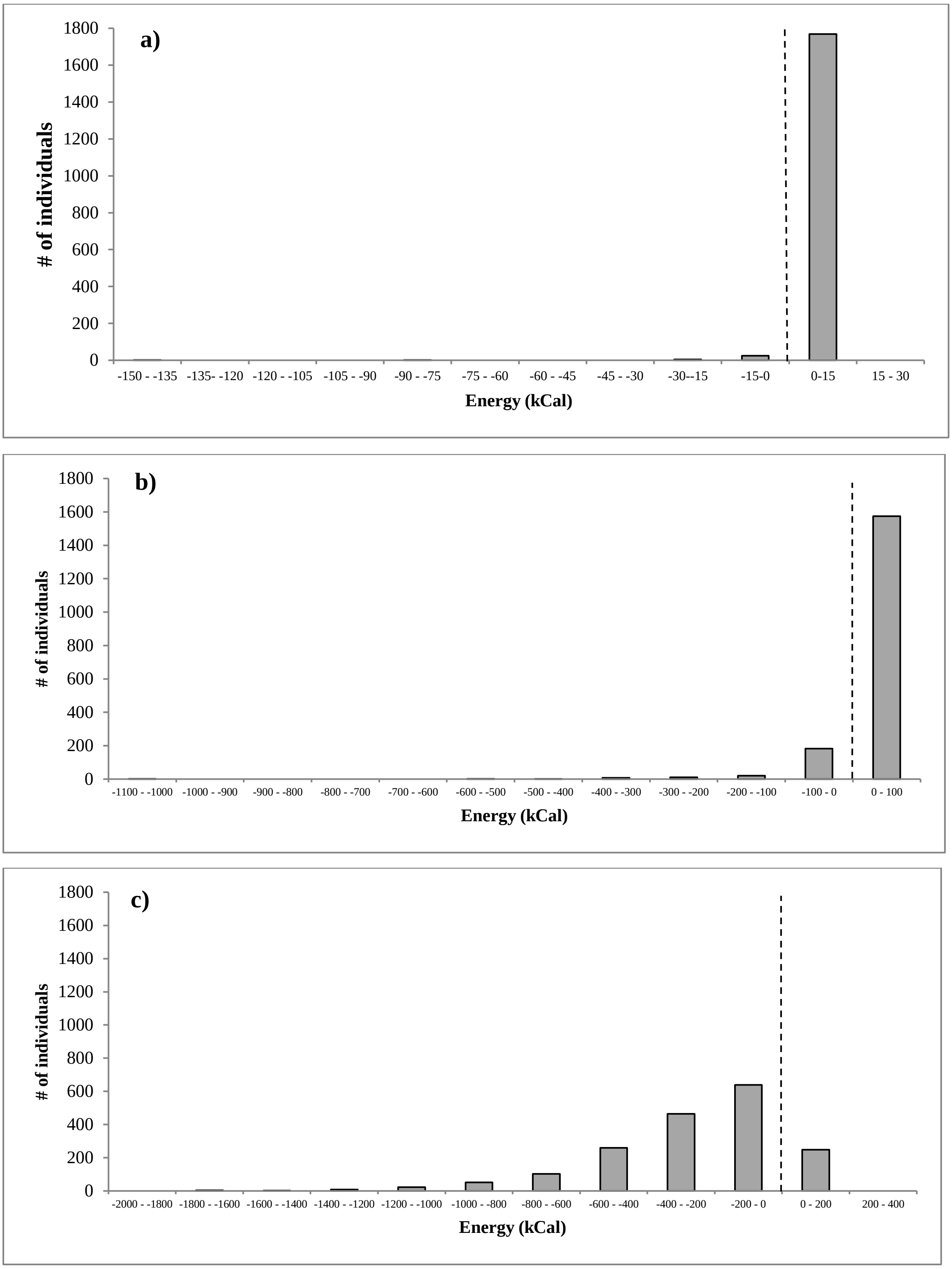

Figure 4.13. Frequency distribution of the final energy budgets (24 hours) for chimpanzees in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs. The total number of individuals equals 1,800 individuals per landscape (i.e. 60 individuals per model run, 30 model runs per landscape). Note that scaling is different between graphs (i.e. chimpanzee energy budgets are grouped in classes of 15kCal for forest chimpanzees (**a**), in classes of 100kCal for mosaic chimpanzees (**b**), and in classes of 200kCal for savannah chimpanzees (**c**)). The dotted line indicates the cut-off between positive and negative energy budgets.

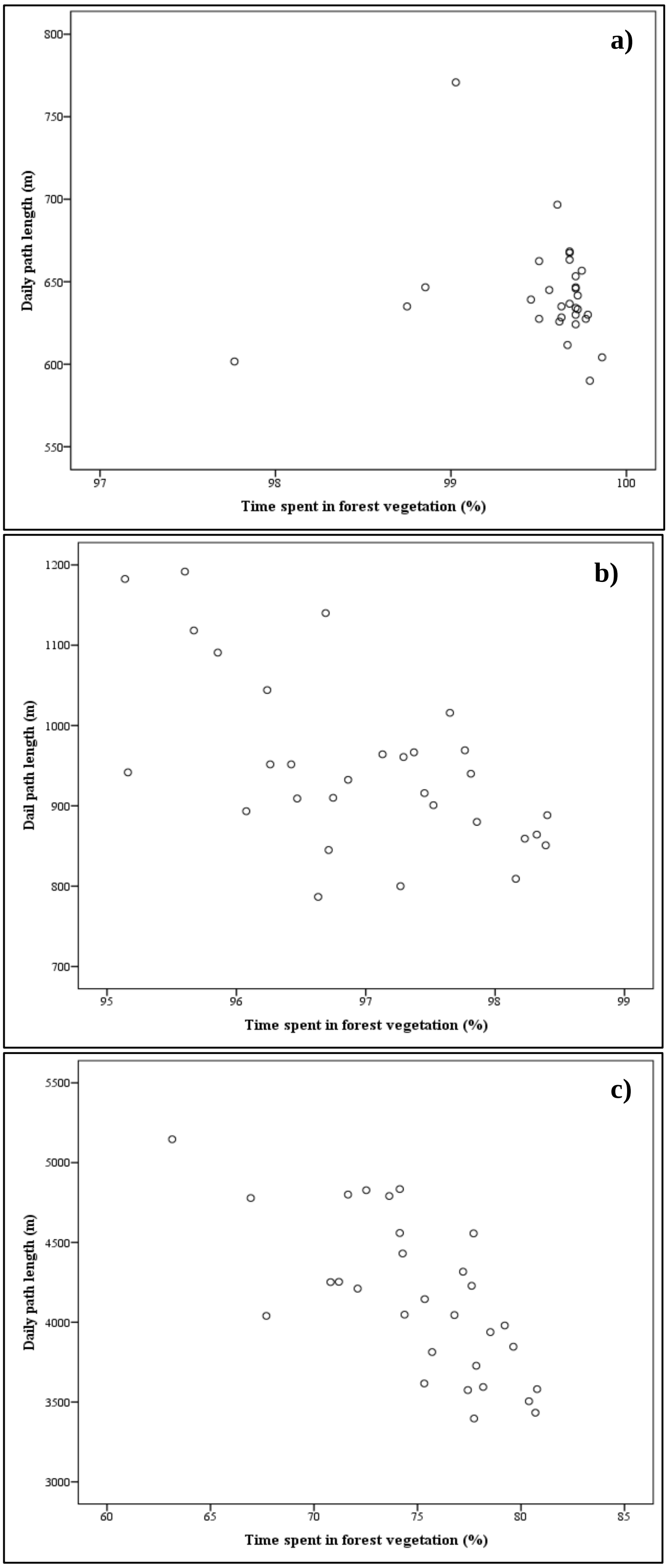

Figure 4.14. Scatterplot of time spent in forest vegetation (%, 24 hours) against daily path lengths for chimpanzees in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs. Significant negative correlations were observed for forest mosaics (N = 30, r_s = -0.530, p = 0.003) and savannahs (N = 30, r_s = -0.732, p < 0.001), but no significant correlation was observed for dense forests (N = 30, r_s = -0.252, p = 0.180).

Chimpanzee time budgets, energy budgets and survival across environments

Considering the decline of chimpanzee habitat across equatorial Africa (e.g. Humle et al. 2016b), it is important to discuss this study's results in light of how flexibly chimpanzees can adapt to changing environments. Model results showed that mosaic chimpanzees spent more time travelling, feeding and drinking, less time resting and nesting, and used woodland and grassland vegetation types more often, whilst food intake, water intake and fatigue budgets were higher and energy and hydration budgets were lower as compared to forest chimpanzees. By contrast, savannah chimpanzees spent more time travelling, less time feeding, drinking, nesting and resting, had longer daily path lengths, used woodland and grassland vegetation types more often, had lower energy and hydration budgets, higher food and water intake, and higher levels of fatigue as compared to forest and mosaic chimpanzees. Similar responses to habitat alterations have been observed for other primate species. For example, Clarke et al. (2002) found that mantled howlers (*Alouatta palliata*) in Costa Rica increased their feeding time and travel distance in response to deforestation. Asensio et al. (2007) showed that howlers (*Alouatta palliata mexicana*) in south-eastern Mexico adapted their foraging strategies to degraded environments with scarce resources and high population densities by increasing their travel time, decreasing their resting time, and including a wider range of different food items. Similarly, Jung et al. (2015) showed dietary shifts, increased feeding and travel times, and decreased resting times for brown howler monkeys (*Alouatta clamitans*) in a regenerating habitat in Brazil as compared to pristine habitat. For macaques (*Macaca fascicularis*), Sha and Hanya (2013) showed that resting time decreased and travel time increased in more anthropogenic landscapes in Singapore. The time budget models on (future) great ape distribution of Lehmann et al. (2008, 2010) found that travel time is a main limiting factor in geographical chimpanzee distribution, together with ultimately increasing resting times as a result of global warming. Findings link to a marked impact of frugivory and (food) resource availability on travel distance, and thus travel time (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005, Coward and Grove 2011).

The current chimpanzee landscape use model was verified to accurately predict the activity budgets of forest chimpanzees, mosaic chimpanzees and savannah chimpanzees within 3%, 13% and 25% of their observed range, respectively (Table 4.11). Whereas the activity budgets of forest chimpanzees were used for model calibration, model output for the daytime activity budgets (i.e. the entire day minus time spent nesting) of mosaic and savannah chimpanzees showed some variation with current studies (Table 4.11). Differences could potentially be attributed to the limited amount of published work on mosaic and savannah chimpanzee activity budgets (Table 4.11), but findings may also be attributed to other explanations. For example, the finding that mosaic chimpanzees in the field were observed to spend more time resting than feeding, whereas modelled mosaic chimpanzees spent more time feeding than resting, could be the result of mosaic chimpanzees in the field choosing more energy-rich food items such as human-introduced cultivars (e.g. Humle 2015), which may require less time for the necessary energy gains. Similarly, chimpanzees in the field may include more fibrous food items, such as leaves, that require more resting time for digestion (e.g. Korstjens et al. 2010). Leaves in environments with higher temperatures have lower protein-to-fibre ratios than those in areas with lower temperatures (e.g. Rothman et al. 2014, Korstjens and Hillyer 2016). Differences in energy between food items and digestion time are not yet incorporated in the current model and feeding was considered based on fruit eating. The finding that savannah chimpanzees in the field (at Fongoli) were observed to rest more and travel less than simulated savannah chimpanzees could presumably be attributed to the more ‘extreme’ climatic conditions at Fongoli that require the chimpanzees to rest more and travel less as an energy saving strategy (Pruetz and Bertolani 2009), and/or are a result of Fongoli chimpanzees using a wider range of food items (Wessling et al. 2018a), allowing them to travel less. ‘Extreme’ climates and varying food items are not yet included in the current model. Simulated chimpanzee daily path lengths were much shorter than observed daily travel distances for chimpanzees across landscapes (Table 4.11). Although this indicates that the model is not currently validated to correctly predict chimpanzee travel distances, model results did repeat the general trend observed in published data, with longer daily path lengths in more open habitat as compared to forested environments (Table 4.11). Incongruences may potentially be attributed to lack of rules on grouping patterns in the current model. Primate travel times are generally expected to increase with group size as a result of intra-group competition and faster patch depletion time (Janson and van Schaik 1988, Chapman and Chapman 2000). In their time budget models, Lehmann et al. (2007, 2008, 2010) found that chimpanzee party size had a significant positive effect on moving time, and thus distance. Indeed, moving time increased with party size in most of the time-budget models across primate genera (*Ateles*, *Gorilla*, *Piliocolobus*, and *Papio* sp.: Dunbar et al. 2009, and *Cercropithecus*: Korstjens et al. 2018). Model output on energy, hydration, fatigue, food intake and water intake could not currently be validated due to lack of quantitative data in published literature. The current model therefore presents a first attempt in identifying quantitative differences and similarities in internal states for chimpanzees in dense forests, forest mosaics and savannahs. Similar to model findings, low hydration and energy budgets were observed for chimpanzees across environments (Wessling et al. 2018a, Wessling et al. 2018b). Generally, the current model is thus validated to correctly predict chimpanzee landscape use patterns in different landscapes.

Table 4.11. Published activity budgets and daily path lengths for chimpanzees at known dense forest, forest mosaic and savannah sites as identified in this thesis (Chapter 3), in comparison to model findings of this study. Here, modelled activity budgets represent the active day range only, i.e. the entire day minus the time spent nesting. Drinking time is not included, as this is not specified in published literature.

Landscape	Site	Feeding (%)	Resting (%)	Travel (%)	DPL (km)	Specifics	Reference
Dense Forest	Budongo	39.0	44.0	17.0	2.7	Males	Bates and Byrne 2009
		44.0	47.0	9.0	1.2	Lactating females	
		27.0	53.0	20.0	2.2	Receptive females	
	Taï	43.0	39.0	12.0	2.4	-	Doran 1997
	Taï	50.0	31.0	19.0	-	-	Lehmann and Boesch 2004
	Kibale	47.0	34.0	14.0	-	Ngogo community	Potts et al. 2011
		44.0	45.0	11.0	-	Kanyawara community	
	Taï	54.0	22.0	22.0	-	-	Boesch & Boesch-Achermann 2000
	Taï	-	-	-	2.5	Saco season (low fruit)	N'guessan et al. 2009
		-	-	-	2.8	Coula season	
		-	-	-	3.1	PariDialium season	
		-	-	-	1.8	Inter-season	
	Kibale	-	-	-	2.4	Males	Pontzer and Wrangham 2004
		-	-	-	2.0	Females	
	AVERAGE	**43.5**	**39.4**	**15.5**	**2.3**	-	-
	MODEL	*42.6*	*36.8*	*16.6*	*0.6*	-	*This study*
Forest Mosaic	Mahale	35.8	31.9	32.3	6.2	Early dry season	Matsumoto-Oda 2002
		26.1	41.4	32.5	4.7	Late dry season	
		23.6	51.2	25.2	4.4	Early wet season	
		24.9	51.1	24.0	2.1	Late wet season	
	Gombe	47.0	-	13.0		Males and females	Goodall 1986
		-	-	-	4.9	Males	
		-	-	-	3.0	Females	
	AVERAGE	**31.5**	**43.9**	**25.4**	**4.2**	-	-
	MODEL	*44.2*	*32.2*	*19.6*	*0.9*	-	*This study*
Savannah	Fongoli	25.0	62.0	11.0	-	-	Pruetz and Bertolani 2009
	Fongoli	40.0	40.0	20.0	-	Burned conditions	Pruetz and Herzog 2017
		33.0	58.0	9.0	-	Unburned conditions	
		47.0	40.0	13.0	-	Partially burned conditions	
	AVERAGE	**36.3**	**50.0**	**13.3**	-	-	-
	MODEL	*37.1*	*27.1*	*37.7*	*4.1*	-	*This study*

Model output on the daily activity budgets, path lengths, energy budgets, hydration budgets, fatigue budgets, food intake and water intake of chimpanzees in different environments can be used to test this study's predictions and put observed differences and similarities into perspective. Time spent nesting was expected to be similar across landscapes, but differences emerged from model output and indicated that forest chimpanzees spent significantly more time nesting than mosaic and savannah chimpanzees, and mosaic chimpanzees nested for longer periods of time than savannah chimpanzees. These findings may indicate an increasing difficulty in finding a suitable nesting location in more open habitats. Whereas this may be true, i.e. forest mosaics and savannahs are considered more scarce and seasonal in their resources (e.g. McGrew et al. 1981, Hunt and McGrew 2002, Arroyo-Rodríguez and Mandujano 2009), observed nesting times are generally similar (i.e. ~12 hours per night) for chimpanzees across environments (e.g. Anderson 1984, Matsumoto-Oda 2002, Bates and Byrne 2009), which may indicate pre-knowledge of the home-range and suitable nesting locations in real-life systems. Pre-knowledge and memory are not currently included within the model. Model output on variable nesting times may additionally explain the finding of infrequently observed nightly activities for chimpanzees in the field (Pruetz and Bertolani 2009, Tagg et al. 2018). Feeding time, drinking time, travel time and travel distance were expected to increase when chimpanzee environments became more open, and resting time was expected to decrease. Whereas this prediction could be confirmed for mosaic chimpanzees as compared to forest chimpanzees, it could only partly be confirmed for savannah chimpanzees. Savannah chimpanzees indeed travelled longer times and distances, and rested shorter times than forest and mosaic chimpanzees, but feeding times and drinking times were significantly lower. When combining these findings with increasingly negative energy and hydration budgets, and increasingly positive fatigue budgets for mosaic and savannah chimpanzees, it becomes clear that forest chimpanzees were most successful in maintaining homeostasis. As their forested environments were rich in preferred resources (e.g. food, water, sleeping sites), forest chimpanzees only spent short amounts of time on travel and had to travel only short distances to meet their daily requirements. Daily food and water intake were sufficient to maintain positive hydration and energy balances, even though time investments were relatively small and intake rates were lower for forest chimpanzees than for mosaic chimpanzees. The ease with which forest chimpanzees acquired their necessary resources left more time for resting, which could, for example, be used to engage in social activities (i.e. ‘free’ resting time, e.g. Dunbar 1996). Maintaining homeostasis became increasingly more difficult for chimpanzees in forest mosaics, which were scarcer in their resources than dense forests (e.g. Arroyo-Rodríguez and Mandujano 2009). Mosaic chimpanzees had to travel for longer times and distances to find their necessary resources, and, as a consequence, lost more energy and hydration. To maintain homeostasis, this loss had to be accompanied by an increase in food and water intake, and thus an increase in time spent feeding and drinking. This happened at the cost of resting time. Although mosaic chimpanzees partly succeeded in compensating for their increased loss of energy and hydration, the maintenance of positive energy budgets, positive hydration budgets, and negative fatigue budgets remained difficult after increasing travel time, and balances were not as ‘ideal’ as those of forest chimpanzees. As compared to forest mosaics, resources in savannah landscapes were even more scarce, seasonal and widely distributed (e.g. McGrew et al. 1981, Moore 1996, Hunt and McGrew 2002). Consequently, travel time and distance increased even more for savannah chimpanzees to acquire their necessary resources, which happened at the cost of feeding, drinking, nesting and resting time. This led to highly negative energy and hydration budgets, and highly positive fatigue budgets, and savannah chimpanzees were unable to maintain homeostasis. As predicted by Lehmann et al. (2010), further environmental changes may additionally lead to increases in (enforced) resting time. As shown by Dunbar (1992), these time constraints may be dealt with by travelling faster; differences in travel speed are not currently included within the model. Model output thus showed that chimpanzees were able to adapt to a wide range of environments, but results implied that the more open environments became, the more difficult it was for chimpanzees to retain their homeostasis, and thus their fitness, due to the reduced availability of resources. Survival challenges are thus expected for chimpanzees when their environments change from forest to more open landscapes.

Inter-individual variability was shown in daily activity budgets, path lengths, energy budget, hydration budgets, fatigue budgets, food intake, water intake, and vegetation type usage across environments, with some individuals being better able to successfully inhabit (i.e. maintain homeostasis in) dense forest, forest mosaic and savannah landscapes than others. Part of this inter-individual variability may be attributed to stochasticity in model environments: As vegetation types were distributed randomly within the model environment for each model run and vegetation features and micro-climates were selected randomly for each patch within a specified range according to the vegetation type, some landscapes were ‘better’, ‘worse’, or ‘more suitable’ for chimpanzees than others. However, inter-individual variability was also observed within single model runs, and this pattern was increasingly evident in more open environments. Only ~14% of simulated chimpanzees were able to maintain homeostasis in marginal savannah landscapes. This result may be due to the random initial placement of simulated individuals within the model: Individuals that were placed on, or in close proximity to, forest patches were better able to acquire their necessary daily resources, as indicated by the observed positive correlation of daily path length and forest use. Model results additionally suggested that resource abundance and distribution in savannah environments as simulated in the model were insufficient to provide for a community of 60 chimpanzees. Limited resource availability may indicate that marginal environments may only provide enough resources for a certain number of individuals. This would imply that, for chimpanzees to survive in savannahs, more than just behavioural adaptations are necessary: Adjustments in home-range size, population size, and thus in population density, may also be required, which provides an additional challenge. In the field, savannah chimpanzees indeed occupy larger ranges and live at lower population densities than chimpanzees in more forested environments (e.g. Hunt and McGrew 2002, Piel et al. 2015). Reduced community sizes for chimpanzees as a result of future climate change are also predicted by Lehmann et al. (2010). Within the model, more variability for chimpanzees simulated in savannah environments may imply stronger selective pressures in these marginal landscapes.

In sum, model results on time budgets, energy budgets and survival showed that chimpanzees were flexible to adjust their behavioural patterns to fit the resource availability and distribution of various environments. This argues in favour of chimpanzee behavioural adaptability to a wide variety of landscapes, although model results also showed that in some situations (e.g. marginal savannahs) adaptations to activity budgets and daily path lengths alone were insufficient to safeguard chimpanzee survival. With these results, the current chimpanzee landscape use model presents a null-model of landscape-scale chimpanzee habitat use across realistic, present-day environments. Results provide new insights into chimpanzee susceptibility, behavioural flexibility and adaptability to future landscape change scenarios.

Chimpanzee vegetation use and preferences in different environments

Modelled chimpanzees used more open vegetation types such as woodland and savannah grassland increasingly more often when their environments became more open, but forest was the preferred vegetation type overall and for each behaviour across environments. In selecting a site for a specific activity, chimpanzees therefore predominantly included vegetation features and micro-climates observed in forest vegetation types. When chimpanzee environments differed from dense forests to forest mosaics and savannahs, site selection gradually included a wider range of vegetation features and micro-climates, and interquartile ranges shifted towards the inclusion of woodland. These findings are in accordance with published literature. For example, chimpanzees generally use all vegetation types available to them for their daily activities across field study sites (e.g. Basabose 2005, Pruetz et al. 2008, Bryson-Morrison et al. 2017). Forest is furthermore often assumed as the most important vegetation type for chimpanzees (e.g. Hunt and McGrew 2002), and field studies generally show that forest vegetation types are used disproportionally to their availability, and are thus preferred (e.g. Tutin et al. 1983, Pascual-Garrido et al. 2013, Wood et al. 2017). For specific behaviours, the preference for forest vegetation types in nesting activities is highlighted for chimpanzees in dense forest, forest mosaic and savannah environments (e.g. Tagg et al. 2013, Carvalho et al. 2013, Hernandez-Aguilar 2009). Forest preferences for feeding, resting and travel activities are emphasised for mosaic and savannah chimpanzees (e.g. Russak 2014, Bryson-Morrison et al. 2017, Lindshield et al. 2017), but no data exist for forest chimpanzees. Preferences for specific vegetation types in drinking activities, as well as differences in the usage of specific vegetation features and micro-climates across environments, remain to be investigated, and the model therefore presents a first attempt in quantifying differences and similarities for chimpanzees in dense forests, forest mosaics and savannahs. The current chimpanzee landscape use model is thus validated to accurately predict chimpanzee vegetation type usage, although results should be approached with care, as findings may follow in part from model rules.

With respect to the hypotheses set out in this study, model output thus confirmed that forest was the preferred vegetation type for chimpanzees across environments. Based on the vegetation features and micro-climates present for each vegetation type within the model, woodland and savannah grassland were increasingly less ideal. It was expected that forest chimpanzees would only use forest vegetation types for their daily activities and would be selective in their choice of specific locations. Model output only partly confirmed this prediction, as it showed that forest chimpanzees used both forest, woodland and savannah grassland for their daily activities, but a specific range of vegetation features and micro-climates observed in forest was predominantly used for feeding, drinking, nesting, resting and travel. Mosaic and savannah chimpanzees, on the other hand, were predicted to use forest vegetation types whenever possible, but would otherwise use woodland and savannah grassland when their environmental variables were comparable to those found in forest. Model output showed that mosaic and savannah chimpanzees did not generally restrict their daily activities to forest locations or locations that had vegetation features or micro-climates comparable to forest. Rather, they included a large range of the vegetation features and micro-climates found in forest and woodland for their daily feeding, drinking, nesting, and resting activities, and even used the entire range of environmental variables found in forest, woodland and savannah grassland for travelling. However, when inspecting the vegetation features and micro-climates most frequently used, it could be observed that these predominantly included the ranges observed in forest and the upper ranges found in woodland, and ranges were only slightly wider than those observed for forest chimpanzees. Savannah chimpanzees, however, used an exceptionally wide range of vegetation features and micro-climates for travel. This indicates that chimpanzees in forest mosaic and savannah landscapes predominantly selected similar locations for their daily activities as chimpanzees in dense forests wherever possible, and chose locations that closely resembled these sites otherwise. These model results imply that even though chimpanzees were able to adapt their behavioural patterns to varying environments, they did not immensely alter their site selectivity, and minimal landscape requirements and constraints therefore remained constant. Results should, however, be taken with caution, as these might be influenced by the specificity of the model rules on site selection and the environmental variables present within different vegetation types.

In sum, the model highlighted the importance of forest vegetation for chimpanzees. Overall, forest vegetation types were preferred across environments, and forest became increasingly more important when it became scarcer. This reliance on forest implies that forest vegetation types can be regarded as critical habitat for chimpanzees, i.e. forest vegetation types are most important for chimpanzee survival, which is in support of the general literature-based assumption (e.g. Hunt and McGrew 2002). Conservation efforts should therefore highlight forest vegetation types as priority areas for chimpanzee conservation, and should focus on the protection of forested habitat within chimpanzee environments. The more forest can be preserved, the easier it will be for chimpanzees to adapt and survive. This suggestion, however, by no means indicates that protection of other types of habitat should be discarded. Especially where forest was scarce, model results showed that chimpanzees had to rely increasingly on other vegetation types for their survival, and without the presence of these additional vegetation types, meeting their daily requirements would have been a challenging task. Habitat protection strategies should therefore be site-specific, and the current chimpanzee landscape use model could facilitate this.

Model limitations and implications

Although model outcomes resembled reality well, the model also had certain limitations, as models are always simplified representations of real-life systems (e.g.

van der Vaart et al. 2016). Certain model improvements could be proposed to make the current model predictions even more accurate. For example, the current model could not yet validate chimpanzee daily path lengths. In dense forests, forest mosaics, and savannahs, chimpanzee travel distances were shorter than the observed daily path lengths in these environments. This could potentially be improved by updating the current movement codes, extending current model run times (i.e. > 24 hours), adding model codes on grouping patterns (i.e. fission-fusion social systems), adding model codes on seasonality (i.e. adapting parameter values for vegetation features, micro-climates, amount of food and amount of water of different vegetation types to simulate different times of year, e.g. wet vs. dry season, low vs. high food abundance, etc.), adding model codes on travel speed, and/or adding model codes on varying food quality (i.e. adding different chimpanzee food items, such fruit, meat, leaves, insects, human-introduced cultivars and underground storage organs (USOs), and adding variations in energy gains within and between food items) based on published data and knowledge-based considerations. Observed circularity in movement patterns may potentially be improved by updating and/or including model codes on foresight (i.e. how far can individuals 'see ahead' in general and in different vegetation types), memory (i.e. what are individuals able to remember and for how long) and pre-knowledge (i.e. what do individuals already know about their environments and conspecifics). Incorporating these code updates may change model output on chimpanzee daily path lengths, and may provide additional insights into chimpanzee patterns of landscape use. Additional model improvements include changes in overall temperature, amount of rainfall, fragmentation, home-range size, population size, and morning locations (i.e. the site from which individuals start off their day). The model could also benefit from adding more detailed model rules on *where* and *when* chimpanzees perform their daily activities (i.e. with regards to vegetation characteristics, micro-climates, time of day, internal states, etc.), on *how much* energy, hydration, fatigue, food and water is gained and lost per unit time and by performing different behaviours, as well as on food (e.g. fruit, meat, insects, USOs) and water distribution per vegetation type and number of fruits per feeding tree. Models may additionally be improved by adding details on macronutrient (e.g. protein, fat) gain, loss and balancing, and energy saving strategies. Model codes could also be adapted to suit a particular chimpanzee study site (Chapter 5), and/or to focus on a specific behaviour of interest (e.g. separating enforced resting time from free resting time, separating resting time from social time, separating arboreal from terrestrial travel). Whilst keeping all else equal, adapting these model parameters one-by-one might reveal more detailed insights into the effect of these (individual and environmental) variables on chimpanzee activity budgets, energy budgets and survival in different landscapes. Lastly, model codes could also be updated by adding the behaviour, characteristics and range use of sympatric species, in order to assess the effects that other species may have on chimpanzee landscape use. Code updates, improvements and additions are not currently included within the model due to time constraints and/or data shortages, or may be beyond the scope of this study. Guidelines for model development exist (e.g. Grimm et al. 2006, Railsback and Grimm 2012), but implementation varies across published research (e.g. Jepsen et al. 2005, Sellers et al. 2007, Bialozyt et al. 2014).

The generic chimpanzee landscape use model provides important implications for future research. First, for example, model output highlighted that, as compared to dense forests and forest mosaics, savannah landscapes were particularly harsh and imposed specific survival challenges on savannah chimpanzees. Inter-individual variability was large across model runs, and only a small number of individuals were able to maintain homeostasis in marginal savannahs. Results could only partly be attributed to model stochasticity, which raised the question of what exactly is happening to chimpanzees in savannah landscapes. As savannah chimpanzee studies remain limited to date (e.g. Hunt and McGrew 2002, Pruetz and Bertolani 2009, Piel et al. 2017), it is currently impossible to solve this problem. Chapter 5 will therefore address this question using an individual-based modelling approach based on field collected data from a chimpanzee savannah landscape in Issa Valley, Tanzania.

Second, the current chimpanzee landscape use model facilitates predictions on the effects of future climate and landscape change scenarios on chimpanzee behaviour and survival. Model results on chimpanzees’ current adaptations to a wide variety of present-day environments can be extrapolated to provide insights into what would happen to chimpanzee behaviour and survival abilities in case of future changes. Scenario testing can be used to test these predictions. With scenario testing, small modifications to the current model code allows the setup of slightly different virtual environments. Model outputs on time budgets, energy budgets, and survival for chimpanzees in these altered environments can then be compared with the current baseline outputs of this study, and the influence of the environmental change can be assessed. In this way, the current chimpanzee landscape use model can be used to predict and test the effects of, for example, global warming and drying, increasing loss or fragmentation of habitat (e.g. forest, woodland), and/or habitat alterations (e.g.

Arroyo-Rodriguez and Mandujano 2006, Korstjens et al. 2010, Arroyo-Rodriguez and Fahrig 2014). The model can also be used to predict and test the relative importance of various environmental changes, for example whether habitat loss per se is more damaging than fragmentation (e.g. Fahrig 2003, Arroyo-Rodriguez et al. 2013a). Furthermore, the model may aid in assessing chimpanzees' tipping points for coping versus non-coping with environmental change. For instance, it can be used to test and predict under which future climate and landscape change scenarios an entire original chimpanzee population is still able to survive, when additional adaptive patterns become necessary, and when chimpanzee behavioural flexibility becomes insufficient to deal with further landscape changes. Exploring these prominent questions would be of great benefit to chimpanzee conservation.

Last, the current chimpanzee landscape use model can be used as a referential model for the landscape use of early hominins, i.e. humans' earliest fossil relatives (e.g. Simpson 2013, Hammond and Ward 2013), and as a framework for understanding the underlying reasons of behavioural innovation and adaptation to specific environments in the evolution of hominids, i.e. modern and extinct great apes including humans (e.g. Blaxland 2016). One of the most daunting challenges in the study of human origins is the reconstruction of early hominin behaviour, as, unlike skeletal remains, behaviour does not fossilise (e.g. Mitani 2013, Plavcan 2013, Carlson and Kingston 2014). Chimpanzees provide one of the best extant models for behavioural reconstructions, not only due to their close phylogenetic relatedness to hominins, but also due to their many morphological similarities and the finding that savannah and mosaic chimpanzees inhabit similarly challenging forest mosaic and savannah environments (e.g. Moore 1996, Mitani 2013). Throughout the evolutionary time frame, Africa had to cope with tremendous environmental changes (e.g. Vrba 1999, Bobe et al. 2002). Amongst others, environments became dryer, cooler, hotter, and changed in vegetation cover (e.g. Potts 2007, Aronson et al. 2008, Boyd and Silk 2012). Hominids thus had to adapt to many environmental variations (e.g. Vrba 1999, Potts 2007, Boyd and Silk 2012). Using a referential modelling approach and adapting the current chimpanzee landscape use model to suit the characteristics of hominids based on available (fossil) evidence will highlight new insights into how hominids may have used their landscapes differently or similarly to extant chimpanzees, how they may have responded to environmental changes in their habitats, when novel behaviours (such as dietary and locomotor adaptations; Doran 1996, Ungar and Daegling 2013, Ward 2013, Carlson and Kingston 2014) may have become advantageous, and how they would have been able to adapt and survive in even more open areas (e.g. Sponheimer et al. 2006). Chapter 6 will address this question for early hominins (i.e. *Ardipithecus* and early *Australopithecus*) using an individual-based modelling approach combining early hominin evidence with findings from chimpanzees (Chapter 2 – Chapter 5).

Conclusion

Considering the rapid decline of chimpanzee habitat, this study developed an individual-based model to identify how activity budgets, energy budgets and daily path lengths changed for chimpanzees when their landscapes differed along an environmental gradient from forest to savannahs. This study showed that landscape-scale habitat use patterns for chimpanzees differed between environments due to the availability of resources. Model results showed that chimpanzees increased their feeding time, drinking time, travel time and travel distance, decreased their nesting time and resting time, and subsequently had lower energy and hydration budgets, and higher food intake, water intake and fatigue levels when environments changed from dense forests to forest mosaics. Although more open vegetation types such as woodland and grassland were used more often, reliance on forest vegetation types increased in forest mosaic environments. Whereas a continuation of this trend was predicted when environments changed from forest mosaics to marginal savannahs, model output showed that travel time and distance increased extensively for savannah chimpanzees at the cost of feeding, drinking, nesting and resting time, which led to reduced food and water intake, highly negative energy and hydration budgets, and highly positive fatigue budgets. Savannah chimpanzees thus faced particular survival challenges, indicating that additional adaptations were necessary to safeguard their survival. Overall, findings thus showed that chimpanzees were able to adapt their activity budgets, daily path lengths and vegetation type usage to suit their environments, although behavioural adaptation became increasingly more difficult when landscapes became more open. As a null-model of chimpanzee landscape use and behavioural flexibility across realistic, present-day environments, specific behavioural patterns, adaptations and challenges to different landscapes were identified, and forest vegetation was highlighted as chimpanzee critical habitat. These findings have important implications for chimpanzee conservation, and will aid in the development of new chimpanzee protection strategies. Through scenario testing, the model can be used to outline the specific survival challenges faced by savannah chimpanzees (Chapter 5), to predict the impacts of future landscape change scenarios on chimpanzee behaviour and survival, and to present a referential model and framework for understanding the underlying reasons of behavioural innovation and adaptation to specific landscapes in hominin evolution (Chapter 6). Additionally for future purposes, the current chimpanzee landscape use model can be updated and extended to also assess the net effects of other environmental changes.

CHAPTER 5

Modelling chimpanzee landscape use in savannahs: A case study for Issa Valley, Tanzania

Abstract

As primate habitat is degrading rapidly, it is important to assess primate flexibility to changing environments. Primates living at the edge of their ecological niche may form the key to understanding how the species will cope with increasing landscape changes. Whilst modelling chimpanzee landscape use in dense forests, forest mosaics and savannahs, Chapter 4 found that, even though chimpanzees were able to cope with different environments and adjusted their behavioural patterns to fit their landscape, savannah chimpanzees faced increasing survival challenges. As current knowledge on savannah chimpanzees remains limited, this study aimed to explore savannah chimpanzee landscape use in Issa Valley, Tanzania, using an individual-based modelling approach based on literature and field-collected data to create a realistic picture of Issa chimpanzee behavioural patterns, adaptations and challenges to marginal savannahs and to evaluate how well the generic model of Chapter 4 was able to accurately assess these circumstances. The Issa model was developed using NetLogo. Model results showed that simulated Issa chimpanzees travelled long distances, spent relatively large amounts of time on travel and small amounts on feeding, drinking, nesting, and resting, were reliant on forest and selective in their site choice for different activities, had negative energy and hydration budgets, low food and water intake, and positive fatigue budgets. Whereas the generic model was able to accurately identify these general trends, the Issa model showed more detailed landscape use patterns for chimpanzees at Issa Valley. Issa is a more marginal environment (i.e. less forest vegetation and resources) than the savannah landscape simulated in the generic model, and this accurately resulted in greater difficulties for chimpanzees in managing their time and energy budgets. In their marginal landscapes, savannah chimpanzees are challenged for survival and are especially susceptible for future habitat degradations and climate change. Through scenario testing, potential future model applications include identifying priority habitat for savannah chimpanzee conservation, predicting responses to future landscape changes, and providing a referential model for hominins.

Keywords: savannah chimpanzees, GMERC, individual-based models, habitat change.

Introduction

As primate habitat across the globe is declining at a rapid rate due to continued deforestation, habitat fragmentation, habitat degradation and climate change, primates have to survive in these changing landscapes and have to adapt to new environmental conditions (e.g. Saunders et al. 1991, Arroyo-Rodriguez and Fahrig 2014, Estrada et al. 2017). As primate life histories are slow, rapid environmental changes may not provide sufficient time for evolutionary level adaptations in primates (e.g. Ross 1989, Charnov and Berrigan 1993). Hence, it is paramount to investigate how flexibly primates can adapt their behavioural patterns to changing environments to assess their susceptibility and vulnerability to change (e.g. Dunbar et al. 2009, Arroyo-Rodriguez and Fahrig 2014, Wong and Candolin 2015). Primate species living at the edge of their ecological niche in challenging landscapes (e.g. chimpanzees in savannahs: e.g. Pruetz 2018; black-and-white snub-nosed monkey at high altitudes in cold climates: e.g. Xiang et al. 2007) may be especially susceptible to climate change and further degradation of their habitat, as they already inhabit marginal environments. At the same time, primates at the edge of their niche may form the key to understanding how primate species will cope with increasing landscape changes throughout their range (e.g. Pruetz 2018). As landscape-scale studies of primate habitat use are scant, Chapter 4 addressed this question using an individual-based modelling approach for chimpanzees (*Pan troglodytes*). Using behavioural rules based on general chimpanzee literature, it tested how chimpanzee landscape use patterns differed between dense forest, forest mosaic and savannah environments. Whereas the model showed that chimpanzees were able to adjust their activity budgets, daily path lengths and vegetation type usage to suit the resource distribution of their landscape, it was more difficult for chimpanzees to cope (i.e. to keep energy and hydration balances positive, and fatigue balances negative) with marginal and more open environments (especially savannahs) if they continued to use the model rules set out based on extensive literature on generalised chimpanzee preferences.

Landscape use studies focus on how a species uses the habitats and micro-habitats within its environment to find its necessary resources, such as food, water and safe sleeping locations (Chapter 4; Deppe and Rotenberry 2008, Sutton et al. 2017). Landscape use is presumably a hierarchical process regulated by an individual's physiological state: based on its metabolic needs, an individual selects its behaviour and, accordingly, the most suitable habitat (e.g. vegetation type) and micro-habitat (e.g.

micro-climate, vegetation features) for this activity (e.g. Harvey and Weatherhead 2006, Sutton et al. 2017). A species' landscape use is, therefore, primarily determined by the spatial arrangement of resources across its environment, as well as by the climatic conditions at temporal and spatial scales (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Due to the challenges faced when studying landscape use under field conditions, i.e. relevant spatial scales, time commitments, complexities in species-habitat interactions, and difficulties in observing direct responses to landscape changes, potential changes in species' landscape use patterns are best investigated using a predictive modelling approach (Chapter 1; e.g. Dunbar 2002, Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014). Using individual-based models, simulated individuals interact virtually with different environments based on published species-habitat relationships without actually altering existing habitat (e.g. Dunbar 2002, Sellers et al. 2007). Thereby, landscape use models present a platform for exploring species' habitat use patterns across realistic, present-day environments, for identifying key areas for species conservation, and for predicting the effects of past and future landscape changes (and associated changes in overall resource abundance and distribution) on species' behaviour and survival (e.g. Jepsen et al. 2005, Ramos-Fernandez et al. 2006).

With regards to these implications, the generic chimpanzee landscape use model of Chapter 4 thus showed that especially savannah chimpanzees faced particular survival challenges. As modelled savannah landscapes were particularly scarce in their resources, additional adaptations, such as a decrease in population size, an increase in home-range size and/or behavioural innovations, seemed necessary to safeguard savannah chimpanzee survival. Model results also showed that individuals' decision-making processes and local circumstances had a major effect on their success. Especially for savannah chimpanzees, modelled individuals showed great variability in internal states (e.g. energy, hydration), and thus fitness, at the end of a 24-hour model run, and findings could only partly be attributed to model stochasticity. As current knowledge from the field on savannah chimpanzee behaviour and ecology remains limited (e.g. Pruetz and Bertolani 2009, Piel et al. 2017), it is difficult to identify the present-day situation and challenges faced by chimpanzees in savannahs. It therefore remains unclear how well the generic chimpanzee landscape use model of Chapter 4 is able to accurately predict the behavioural patterns of savannah chimpanzees.

Considering the wide variety of landscapes inhabited by chimpanzees (e.g. Hunt and McGrew 2002, Inskipp 2005), it is surprising that most studies highlight the behaviour, ecology and characteristics of chimpanzees in forested environments (i.e.

dense forests and/or forest mosaics). Of the 43 chimpanzee study sites encountered in Chapter 3, only nine focused on chimpanzees in savannah landscapes, and only three of these savannah chimpanzee study sites are engaged in current mid- to long-term research (Piel et al. 2017). As a consequence, compared to the wealth of information that currently exists on forest chimpanzees, relatively little is still known about the behavioural ecology of savannah chimpanzees (e.g. Hunt and McGrew 2002, Pruetz et al. 2002, Russak 2013). Savannah chimpanzees inhabit landscapes that are hot, dry and have only a minimal percentage of forest cover (Chapter 3). Savannah landscapes are furthermore marginal and seasonal in resource abundance and distribution (McGrew et al. 1981, Moore 1996, Hunt and McGrew 2002). Behavioural studies include research on savannah chimpanzee diet (e.g. McGrew et al. 1988, Schoeninger et al. 1999, Piel et al. 2017), tool use (e.g. Bogart and Pruetz 2008, Stewart and Piel 2014), energy balance and thermoregulation (Wessling et al. 2018a), and the functions and site selections for nest building (e.g. Hernandez-Aguilar et al. 2013, Stewart and Pruetz 2013, Samson and Hunt 2014). As savannah chimpanzees live on the edge of their species' niche in challenging environments, unique behavioural adaptations and innovations for surviving under these extreme circumstances are observed at various study sites, including hunting with spears (Pruetz and Bertolani 2007), digging holes for drinking water (Hunt and McGrew 2002), and using caves to avoid heat stress during the hottest time of day (Pruetz 2007). Savannah chimpanzees have furthermore been shown to range over larger areas and to live at lower population densities than forest chimpanzees (e.g. Tutin et al. 1983, Hunt and McGrew 2002, Piel et al. 2015). Savannah chimpanzees thus seem to adapt their behavioural patterns flexibly to survive in their marginal landscapes. Due to limited data, however, exact interpretations of chimpanzee landscape use, adaptability and flexibility in savannahs remain difficult.

This study therefore explores current chimpanzee landscape use at a savannah field site in Issa Valley, Tanzania, using an individual-based modelling approach based on field-collected data. Specifically, it focuses on identifying the daily activity budgets, path lengths, vegetation type usage, and site selection for chimpanzees in marginal landscapes at Issa. Thereby, this study creates a realistic picture of the present-day situation and challenges faced by chimpanzees in savannah environments. To establish how accurately the individual-based model of Chapter 4 based on generic chimpanzee literature alone is able to predict chimpanzee landscape use at specific chimpanzee study sites, and to evaluate how the inclusion of site-specific details of particular study sites influences model output on chimpanzee landscape use, this study compares the savannah chimpanzee model findings of Chapter 4 to the new findings of the Issa model. It is expected that both models differ in their results due to the inclusion of site-specific detail for the Issa model, i.e. site-specific data on the behaviour, characteristics and habitat of the Issa chimpanzees. Only the Issa model is expected to enclose a sufficient amount of detail to present a realistic picture of chimpanzee landscape use at this site. Two individual-based models are thus created for this purpose, and both models follow specific rules on chimpanzee behaviour and habitat. The generic model investigated savannah chimpanzee landscape use in randomised savannah environments based on general chimpanzee literature (Chapter 4). The Issa model is adapted from the generic model to suit the behaviour, characteristics and habitats of chimpanzees at Issa Valley. Issa model rules are based on published literature and field-collected data specific to Issa when available. As such, the Issa model presents a case study for current savannah chimpanzee landscape use at a realistic, present-day savannah chimpanzee field study site. Model findings can be used to identify savannah chimpanzee adaptations and challenges, and to predict savannah chimpanzee critical habitat, priority areas for conservation and the effects of future landscape change scenarios. In comparison to the generic chimpanzee landscape use model, model findings can verify the findings of Chapter 4, and can be used to develop guidelines on how much detail is enough to create reliable predictive models of chimpanzee landscape use at particular study sites. This information will support future conservation efforts of measuring chimpanzee behaviour and habitat in the most effective and time-efficient way, and to develop appropriate mitigation strategies for savannah chimpanzee protection.

Methods

Study site and species

The Issa study area, 05°23.34S 30°35.04E, is located in western Tanzania and is situated approximately 81km east of Lake Tanganyika (Stewart 2011; Figure 5.1). The site was established by Dr. R.A. Hernandez-Aguilar in 2001, and has been permanently studied since 2008 through the Greater Mahale Ecosystem Research and Conservation (GMERC) project (e.g. Stewart 2011, Wondra et al. 2016). GMERC is directed by Dr. A.K. Piel and Dr. F.A. Stewart. The vegetation at the study area is mainly characterised by woodland (i.e. 90.5%) and other open vegetation types (e.g. swamp and grassland, 8.0%), and only a small proportion of the area is classified as forest (i.e. 1.5%; Hernandez-Aguilar 2009, Stewart 2011). Recent papers suggest ~7% forest cover due to a slight shift in location and enlargement of the study area (Piel et al. 2017, Thoemmes et al. 2018). Daily temperatures range between 11°C and 35°C, and annual rainfall equals 900 – 1400mm (Stewart et al. 2011, Wondra et al. 2016, Thoemmes et al. 2018). There is one dry season that lasts from May to October. Issa is inhabited by a community of semi-habituated chimpanzees of the eastern chimpanzee subspecies, *Pan troglodytes schweinfurthii* (Stewart 2011). Based on genetic analyses from faecal samples, community size is estimated to be at least 67 individuals (Rudicell et al. 2011). The exact home-range size of the community remains unknown, but the GMERC study area focuses on a core range of 85km^2 (e.g. Piel et al. 2017). Based on chimpanzee evidence (GMERC *unpublished data*) collected within and outside this core area, this research focused on a total study area of 110 km^2.

Figure 5.1. Map of the Issa study site (black box) in western Tanzania. Figure reprinted with permission of Elsevier, from Piel et al. (2017, p. 60); permission conveyed through Copyright Clearance Center, Inc. Credit: L. Pintea, The Jane Goodall Institute, USA.

Published Issa literature outlined *where* Issa chimpanzees performed their daily activities. For example, it was specified that most permanent water sources needed for drinking could be found in forest (Russak 2014). Feeding, resting, nesting and travel activities were observed in forest and woodland habitats (Hernandez-Aguilar 2009, Stewart 2011, Stewart and Pruetz 2013, Russak 2014), but forest was preferred for nesting (Stewart 2011, Stewart and Pruetz 2013). Issa chimpanzees furthermore used specific tree species for feeding (e.g. *Ficus exasperata*, *Brachystegia spiciformis*, *Saba comorensis*) and nesting (e.g. *Brachystegia puberula*/ *stipulate*/ *utilis*, *Julbernardia unijugata*), and nested in trees with a height between 2 – 53m, a diameter at breast height (DBH) between 3.0 – 199.5cm, a lowest branch height (LBH) between 0 – 20m, a crown width between 2 – 30m, a crown height between 1 – 37m, a leaf cover between 20 – 95%, a canopy cover between 5 – 100%, and a canopy connectivity between 0 – 100% (Stewart 2011, Hernandez-Aguilar et al. 2013, Russak 2013). Nesting locations were preferably on slopes (as compared to flat terrain) and in close proximity to food sources (Hernandez-Aguilar 2009, Stewart 2011).

Pre-existing GMERC data and analyses

GMERC has long-term data available on Issa chimpanzee behaviour and habitat gathered through chimpanzee follows, reconnaissance walks and fauna transects (*pers. comm.* A.K. Piel, 24/02/2017). GMERC furthermore created a Geographical Information System (GIS) database of the Issa study area and its surroundings, which comprises information on all long-term data, land cover (created by C. Johnson; hereafter referred to as the GMERC GIS vegetation map), and regional landmarks (*pers. comm.* A.K. Piel, 13/06/2018), and has access to a HOBO weather station for climatic measurements.

Phenology trails (Mar – Dec 2016): Data from seven phenology transects were used to assess fruit availability across the Issa environment. Phenology trails were set up in different vegetation types along the Issa trail system. Transects were monitored every month for the abundance and distribution of fruit. Only chimpanzee feeding tree species (DBH > 10cm) were measured. The presence of ripe and unripe fruit was measured in percentage of canopy covered.

Chimpanzee follows (Jan 2014 – Oct 2016): Chimpanzee follows were conducted 15 – 20 days per month with the goal of fully habituating the Issa chimpanzees. Research teams collected various data on chimpanzee behavioural ecology, including behaviour and habitat.

Fauna transects (Jan 2014 – Dec 2016): Data from seven fauna transects were used to evaluate the presence and distribution of chimpanzees and other mammals across the Issa landscape. Fauna transects traversed the study area across different vegetation types, were measured every two months, and differed from the transects used for phenology. Whenever direct or indirect evidence of chimpanzees was observed (e.g. encounters, nests, faeces, footprints, feeding remains), various details were recorded, including behaviour and habitat.

Reconnaissance walks (Jan 2014 – Dec 2016): Evidence on the presence of chimpanzees and other mammals was additionally collected during reconnaissance walks. Walks were conducted on a regular basis and spanned the entire GMERC study area. For all direct and indirect evidence of chimpanzees, a variety of data (e.g. habitat, behaviour) were recorded.

HOBO weather station (May – Jul 2017): A HOBO weather station, located 1.5km from the Issa camp, was installed in April 2017. Various climate data were measured, including temperature (^{o}C) and rainfall (mm) at one-hour intervals.

For analyses (by K.L. van Leeuwen), data from chimpanzee follows, fauna transects and reconnaissance walks were taken together to present the frequency of chimpanzee encounters and observed behaviours in each vegetation type. To ensure independence of data points following GMERC data collection protocols, behaviours were scored once for each (direct or indirect) chimpanzee encounter; i.e. when a behaviour was observed multiple times during the same encounter, it was only scored once. Multiple different behaviours could, however, be observed within the same encounter. Only one vegetation type was specified for each encounter; the chimpanzees remained only semi-habituated and encounters often did not last long. Overall and behavioural preferences for specific vegetation types were assessed using the chi-square goodness of fit test with α set at 0.05 (IBM SPPS Statistics, version 22). As chi-square tests cannot be performed when the observed total frequency of a specified category equals 0, observed frequencies for all categories (i.e. vegetation types) were given a value of 1 when total frequency equalled 0 to produce reliable output. Phenology data were used to calculate fruit availability of different vegetation types using the Fruit Availability Index (FAI; *sensu* Takemoto 2004, Hockings et al. 2010, Koops 2011):

$$\mathrm{FAI} = [\ \sum (P_i \times F_i) / \sum (P_i \times 4)\ ] \times 100$$

Where FAI is the fruit availability index (%), P_i is the basal area of the tree trunk (cm^2) and F_i is the ripe fruit availability score of the tree (0 – 4); Categories 0 – 4 indicate 0%, 1 – 25%, 26 – 50%, 51 – 75%, 76 – 100% of the tree canopy containing ripe fruit, respectively. Data from the HOBO weather station were taken together and summarised to present average daily (8am – 7pm) and nightly (8pm – 7am) temperatures (^{o}C) and rainfall (mm). The GMERC GIS vegetation map was converted to a grid with 50m x 50m cells adopting the majority vegetation type in each cell. For the individual-based model, this grid was imported as a layer of 50m x 50m patches within NetLogo (Willensky 1999) to determine the percentage of cover for each vegetation type.

Field data collection and analyses

Data on the structural vegetation and micro-climatic aspects of the Issa landscape were gathered from May to July 2017 using vegetation plots and micro-climate data loggers by K.L. van Leeuwen with the help of local field guides and research assistants.

Vegetation plots: Twenty-four 25m x 25m vegetation plots were set up randomly (i.e. using a stratified random sampling design) throughout the Issa study area for the assessment of the three-dimensional vegetation structure of different vegetation types (i.e. forest, woodland, swamp and grassland). Six plots were set up in each type of vegetation. For each plot, measurements were taken on total number of trees (DBH ≥ 10cm, and DBH < 10cm), total number of lianas (diameter ≥ 10cm), total number of (chimpanzee) feeding trees (DBH ≥ 10cm), percentage of (chimpanzee) feeding trees (%, DBH > 10cm), percentage of (chimpanzee) feeding trees (DBH > 10cm) bearing fruit (%), altitude (m), slope, canopy cover (%), canopy connectivity (%), presence of understory (%), presence of bare land (%), presence of grass (%), presence of terrestrial herbaceous vegetation (THV; %), presence of water (%), presence of ants/ ant nests, presence of termites/ termite mounds, and evidence of chimpanzee activity. The canopy cover of a plot was additionally measured with hemispherical photographs (analysed with CanopyDigi). For each tree (DBH ≥ 10cm) or liana (diameter ≥ 10cm) within a plot, measurements were taken on the species, height (m), DBH (cm), LBH (m), crown width (m), crown height (m), crown shape (Figure 5.2), crown connectivity (%), crown cover (%), and the percentage of the tree/liana bearing ripe chimpanzee food (%). Measurement details are outlined in Appendix 5.1.

Micro-climate data loggers: Thirty-six micro-climate data loggers were set up within the vegetation plots to investigate the differences in micro-climates between different vegetation types. Data loggers were set up in trees at the centre of three randomly selected vegetation plots per vegetation type. Three data loggers were installed per tree at various heights, i.e. at ground level (1m), at the bottom of the crown, and within the crown canopy. All loggers collected data for 50 subsequent days. Data loggers were equipped with HOBO software and measured the local temperature (°C) and luminosity (Lux) at every hour.

For analyses, measurements of the structural aspects of different vegetation types were taken together and summarised to produce an overview of the mean and ranges of vegetation features present in each type of land cover. Also the average percentage of food trees and the average percentage of food trees bearing fruit at any one time were assessed for each vegetation type. Micro-climate data logger data were used to highlight the mean and range of average daily (8am – 7pm) and nightly (8pm – 7am) temperatures (^{o}C) and light intensities (Lux) within each vegetation type. Statistical differences and correlations between vegetation features and micro-climates of different vegetation types were assessed using Kruskal-Wallis tests (α = 0.05), *post-hoc* Mann-Whitney U tests (Bonferroni correction, α = 0.05 / 6 = 0.008), and Spearman's correlation coefficients (α = 0.05).

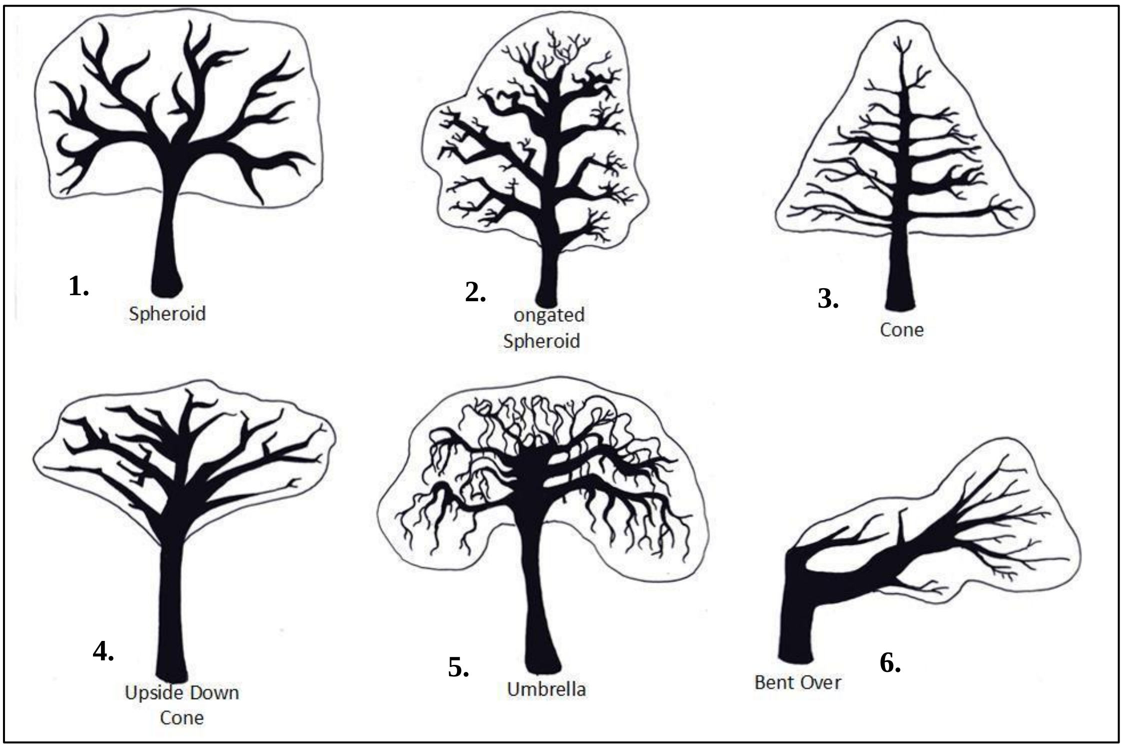

Figure 5.2. The six crown shape categories used in this study. Figure reprinted with permission from H. Slater (credited; Bournemouth University, UK), from Slater (2015, p. 40).

Model building

The individual-based models on chimpanzee landscape use were developed using NetLogo software (version 5.2.1; Willensky 1999). Details on the data collection, data analyses, model building, model testing, model calibration and sensitivity analysis for the generic chimpanzee landscape use model were outlined in Chapter 4. Descriptions of the Issa chimpanzee landscape use model below follow the ODD protocol for communicating individual-based models (Grimm et al. 2006, Grimm et al. 2010: Appendix 4.1). As the Issa model was adapted from the generic model based on site-specific (field) data from Issa Valley, Tanzania, the ODD protocols of the two models show many similarities. Issa model parameters are outlined in Appendix 5.2, the final model code is presented in Appendix 5.3, and an overview of the Issa model's interface is highlighted in Appendix 5.4. Specific model adaptations to create the Issa model from the generic model are presented in Appendix 5.5. The rationale behind Issa model rules, decisions and design is outlined in Appendix 5.6.

Purpose

The purpose of the Issa chimpanzee landscape use model developed in this study was to create a realistic picture of the present-day situation faced by chimpanzees inhabiting marginal savannahs. Specifically, it aimed to assess the daily activity budgets, path lengths, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, overall preferred vegetation, behaviourally preferred vegetation, and site selection of Issa chimpanzees (Figure 5.3). This information was used to highlight the current challenges encountered by chimpanzees in savannahs, and to evaluate how well the generic model of Chapter 4 was able to accurately predict these savannah chimpanzee landscape use patterns.

Entities, state variables and scales

The Issa model is comprised of two entities: the landscape and the chimpanzees (Figure 5.3 and Appendix 5.6). The landscape was simulated as 110km^2, i.e. the minimum Issa chimpanzee home-range size based on GMERC data, and is represented by 44,000 patches of 50m x 50m. Vegetation cover, spatial vegetation arrangement, fragmentation, overall temperature and rainfall mirrored the present-day conditions at Issa. Five types of land cover were simulated, i.e. forest, woodland, (savannah) grassland, swamp and rocky outcrops, and each vegetation type was assigned a specific range of vegetation features and micro-climates following the important landscape-scale micro-habitat characteristics outlined in Chapter 2 (Table 2.3). Similar to the generic model, values for number of fruits and amount of water were updated throughout the model run after consumption by the chimpanzees; all other vegetation features and micro-climates remained stable.

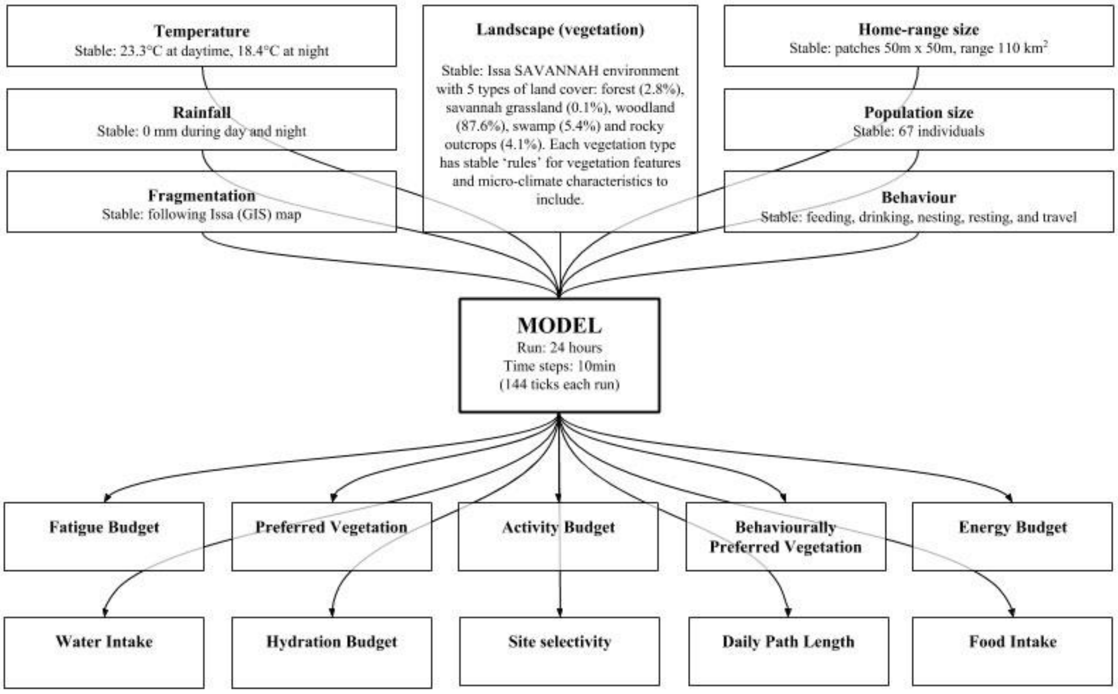

Figure 5.3. Conceptual flowchart of the Issa chimpanzee landscape use model. The Issa model aimed to assess current savannah chimpanzee behavioural patterns in a realistic, present-day savannah environment.

Within the virtual Issa environment, a population of 67 chimpanzees, i.e. the minimum chimpanzee population size at Issa (Rudicell et al. 2011), was simulated. Considering the Issa chimpanzee home-range size, this modelled a lower population density than the generic model. Each chimpanzee was placed at a randomly modelled nesting location within the model environment to simulate a realistic location to start off the day. Similar to the generic model, individuals had internal states for energy (kCal), fatigue (unitless measure), hydration (unitless measure), current activity, current vegetation type, food intake (# food items, or edible grams dry weight), water intake (hydrations), and distance travelled (m), and were simulated to perform daily feeding, drinking, nesting, resting, and travel activities guided by their main goal of maintaining homeostasis. Chimpanzees' internal states changed through time and were updated at each time step after performing a specific activity. Individuals were able to assess the vegetation features and micro-climates of all patches within a radius of 100m of their current location. Global variables were set for time of day, each time step in the model equalled 10 minutes, and a total model run simulated a 24-hour day (7am to 7am).

Process overview and scheduling

The process overview and scheduling element of the ODD protocol for the Issa model followed the generic model and is outlined in Chapter 4 (p. 97). Figure 5.4 presents the model flowchart of the Issa model, and specifies details on the decision-making process and its consequences for individuals throughout the model run (Appendix 5.6).

Design concepts

Based on published savannah chimpanzee literature and findings of the generic model, the basic principle that underlies the development and design of the Issa model is the concept that savannah chimpanzees inhabit harsh environments and face particular challenges, and therefore have to adapt their behavioural patterns to survive. All other design concepts, i.e. emergence, adaptation, objectives, sensing, interaction, stochasticity and observation, followed the rationale presented for the generic model and are outlined in Chapter 4 (p. 98, see also Appendix 5.6).

Initialisation

The GMERC GIS vegetation map and the HOBO weather station climate data (see results section below) were used to create a virtual Issa landscape in NetLogo that paralleled the present-day circumstances at Issa Valley, Tanzania (Appendix 5.6). With regards to the land cover of the Issa study area, patches were assigned a vegetation type and accordingly, a set of landscape-scale vegetation features and micro-climate characteristics (Appendix 5.6). Vegetation features and micro-climates were selected randomly within a specified range for each type of land cover based on data from the vegetation plots and micro-climate data loggers (see results section below).

Sixty-seven virtual Issa chimpanzees (Rudicell et al. 2011) were simulated within the model with initial energy, hydration and fatigue levels randomly assigned between 0 – 10, in line with the generic model (Appendix 5.6). Similarly following the generic model, initial internal state variables for daily path length, food intake and water intake were set at 0, current activity was set to ‘none’, and current vegetation type was set with respect to individuals’ initial location. Simulated Issa chimpanzees lost two energies, lost one hydration and gained one fatigue at each time step to model metabolic processes, as was also the case for the generic model (Appendix 5.6). Detailed model rules were set out on *where* and *when* to perform feeding, drinking, nesting, resting and travel activities, and on *how much* energy, hydration and fatigue was gained and lost, for Issa chimpanzees (Appendix 5.6). Behavioural rules highlighted that these activities could only be performed at suitable times of day (i.e. day/ night) and at locations with suitable vegetation features and micro-climate characteristics. Whereas rules on *where* to perform each behaviour were based on a combination of literature, GMERC and field-collected data from Issa and are outlined in the results section below, rules on *when* to perform each activity and *how much* energy, hydration and fatigue was gained and lost followed the generic model of Chapter 4 and are outlined in Table 5.1. Similar to the generic model, behavioural rules and initial levels of energy, hydration and fatigue meant that individuals started off their day with feeding and drinking activities, which is in agreement with field observations for chimpanzees at various sites (Chapter 2). Multiple individuals could be present on the same patch as long as this patch abided to the criteria outlined for the specific behaviour performed by each individual.

Submodels

Following the generic model, the Issa model consisted of four submodels: feeding, drinking, resting and nesting. Travel was included in all four submodels.

Model testing and understanding

The testing and understanding phase of the Issa model followed the same processes as those outlined for the generic model (presented in Chapter 4, p. 102).

Model calibration and verification

A model is said to be verified when its outputs match real-world observations (e.g. Railsback and Grimm 2012). Therefore, when model parameters could not be quantified empirically, the modelling cycle could be finalised by the process of calibration, in which a few especially important input parameters are calibrated to make the model output match empirical observations (e.g. Railsback and Grimm 2012). For the Issa model, however, no empirical data existed to calibrate the model, as data on Issa chimpanzee activity budgets, daily path lengths, energy budgets, fatigue budgets, hydration budgets, food intake and water intake remain limited. Calibrating the Issa model to match empirical observations was therefore not possible. The Issa model was, however, adapted from the generic model of Chapter 4, which was fully calibrated to correctly predict forest chimpanzee activity budgets within 3% of their observed range. Model results of Chapter 4 showed that the generic chimpanzee landscape use model was validated to correctly predict savannah chimpanzee landscape use patterns within 25% of their observed range where data were available. Based upon this calibrated model, the Issa model therefore presented a first attempt to quantify patterns of savannah chimpanzee landscape use in Issa Valley, Tanzania in the absence of available field data for calibration.

Model sensitivity analysis

For the Issa model, 22 parameters were selected for a local sensitivity analysis in order to investigate the effect of minor changes in input parameters on model output (e.g. Railsback and Grimm 2012, Muko et al. 2014; Appendix 5.2). Sensitivity analysis followed the generic model and is described in Chapter 4 (p. 104).

Model output and statistical analyses

Following the generic model, the Issa model was run 30 times (e.g. Crawley 2005). Data for each simulated individual on activities, vegetation types, energy, hydration, fatigue, food intake, water intake, site selections and distance travelled were averaged per run and across 30 model runs to detail mean activity budgets, daily path lengths, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, and vegetation type usage and site selections for Issa chimpanzees. Averages across 30 model runs were used for further analyses and are presented as means ± standard deviations. All data presented for the generic model are a replicate of the model output on savannah chimpanzees in Chapter 4. Differences in model output for the Issa model and the generic model were explored visually using graphs and data range tables, and statistically using Mann-Whitney U tests. Spearman's rank correlation coefficients were used for correlations. Tests were performed two-tailed with α set at 0.05. Vegetation type preferences were assessed using chi-square goodness of fit tests ($\alpha = 0.05$). In line with the generic model, chi-square tests were based on the number of time steps in each vegetation type for individuals across 30 model runs (i.e. 67 individuals x 144 time steps x 30 model runs)[6]. Total frequencies of '0' were replaced with '1' in order to produce reliable output.

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[6] As expected values within the chi-square goodness of fit test can never fall below 5 for each category (i.e. vegetation type), savannah grassland and rocky outcrops land cover types were grouped together for analyses of chimpanzee drinking behaviour.

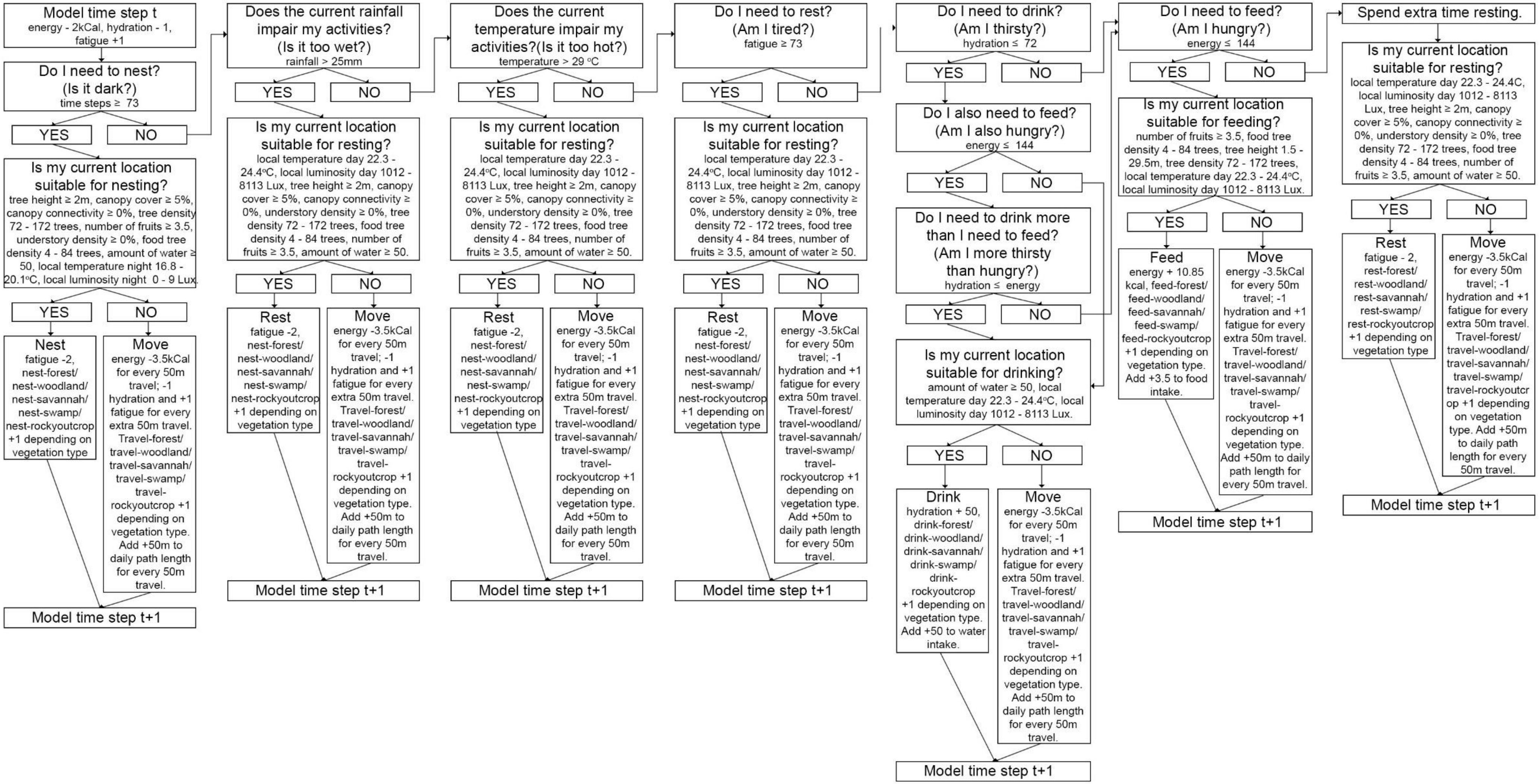

Figure 5.4. Model flowchart of the Issa model. The flowchart specifies the decisions that had to be made by each individual at each time step, and its consequences.

Table 5.1. Model rules of the Issa model on *when* to perform daily feeding, drinking, nesting, resting and travel activities, and *how much* energy to gain and lose at each time step. This table is a partial replica of Table 4.2 which specified the model rules for the generic chimpanzee landscape use model. For rationale behind Issa model rules, see Appendix 5.6. Differences between the Issa and generic models are presented in Appendix 5.5.

Behaviour	**When to perform an activity**	**How much to gain/ lose per time step**
Feeding	Energy ≤ 144 kCal (i.e. when an individual is hungry) and energy < hydration (i.e. when an individual is more hungry than thirsty).	Gain 3.1 kCal per fruit eaten (i.e. per edible gram dry weight) and eat 3.5 fruits per time step. Patches lose 3.5 fruits per time step when an individual has fed on that patch. Each feeding tree contains 7 fruits, i.e. twice the number of fruits eaten per time step.
Drinking	Hydration ≤ 72 (i.e. when an individual is thirsty) and hydration < energy (i.e. when an individual is more thirsty than hungry).	Gain 50 hydrations. Patches lose 50 hydrations per time step when an individual has drunk on that patch.
Nesting	Time steps > 72 (i.e. the second half of the 24-hour day, and thus when it is night).	Lose 2 fatigues.
Resting	Fatigue ≥ 73 (i.e. when an individual is too tired), or rainfall ≥ 25mm (i.e. when it is too wet)*, or overall temperature ≥ 29°C (i.e. when it is too hot)*, or energy > 144 and hydration > 73 (i.e. 'free' resting).	Lose 2 fatigues.
Travel	No specific rules, but travel when a current patch is not suitable for the chosen activity. In this case, first assess the suitability of neighbouring patches within 50m, then assess the patches within 100m, and if a suitable location is then still not found, jump at random between 3 – 6 patches (i.e. 150 – 300m).	Lose 3.5 kCal for every 50m of travel (i.e. one patch), and lose 1 additional hydration and gain 1 additional fatigue for every extra 50m of travel (i.e. when travelling more than 50m in one time step).

*Within the current Issa model, rainfall and overall temperature never reached above 25mm and 29°C, these model rules are, however, included for the sake of completeness (and potential future model applications). Note that overall temperature is different from local micro-climate temperature for each vegetation type.

Results

Field-collected data

Vegetation features and micro-climates differed between forest, swamp, grassland and woodland vegetation types (Table 5.2). Because it was not the main focus of this chapter, the statistical analyses of these differences are presented in Appendix 5.7.

GMERC data

Monthly FAI showed that, on average, most chimpanzee food (i.e. ripe fruit) at Issa was found in woodland (N = 633 trees), followed by forest (N = 191 trees); Neither of the two monitored swamp trees carried ripe fruit in 2016, and no transects were monitored in grassland due to the overall lack of trees in this vegetation type (Figure 5.5).

A total of 8,686 behaviours were observed in the Issa core study area during 2,320 direct and 2,815 indirect chimpanzee encounters between 2014 and 2016. Of these encounters, 3,766 were observed in forest, 4,724 in woodland, 9 in swamp, and 0 in savannah grassland. For 187 behaviours, no vegetation type was recorded. Additionally, 1,014 of the encounters were attributed to feeding, 3,806 to resting (including social time), 2,651 to nesting, and 1,028 to travel. Without controlling for survey effort and relative to the vegetation cover of the Issa core study area, forest was preferred overall (χ^2 = 105,652.0, df = 2, $p < 0.001$), and for each behaviour separately (feeding: χ^2 = 17,965.3, df = 2, $p < 0.001$; resting: χ^2 = 59,762.1, df = 2, $p < 0.001$; nesting: χ^2 = 18,597.2, df = 2, $p < 0.001$; travel: χ^2 = 12,575.5, df = 2, $p < 0.001$).

HOBO weather station data showed that Issa daytime temperatures ranged from 17.9°C to 28.8°C and had a mean of 23.3±2.3°C between May 5th and July 2nd, 2017 (i.e. the study period of the micro-climate data loggers). Nightime temperatures for this period ranged between 15.3 – 23.2°C and averaged at 18.4±1.2°C. As May – July encompasses part of the dry season at Issa, no rain fell within this time period in 2017. The GMERC GIS vegetation map imported into NetLogo showed that the total study area at Issa (110km^2) consisted of 2.8% forest, 87.6% woodland, 0.1% savannah grassland, 5.4% swamp, and 4.1% rocky outcrops (Figure 5.6). As the GMERC GIS vegetation map had to be converted to a grid with 50m x 50m cells adopting the majority vegetation type in each cell when imported into NetLogo, the resulting generalised NetLogo map may present slight overestimations of the dominant vegetation type at Issa.

Table 5.2. Mean and range of vegetation features and micro-climate characteristics of forest, woodland, swamp, and grassland vegetation types at Issa measured through vegetation plots (25m x 25m) and micro-climate data loggers. A '*' indicates whether these features are included in the model on Issa chimpanzee landscape use.

	Forest			**Woodland**			**Swamp**			**Grassland**		
	Mean	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*
Plot data												
# trees (DBH ≥10cm)*,^{1}	32	18	43	15.2	12	19	6.2	0	25	7.8	1	21
# vines (diameter ≥10cm)	1.2	0	4	0	0	0	0	0	0	0	0	0
# feeding trees (DBH ≥10cm)^{1}	11.5	1	21	7.2	5	11	3.8	0	20	0.5	0	2
% feeding trees (DBH ≥10cm)*	36	5.6	75	47	35.7	69.2	62	0	100	6	0	40
% feeding trees (DBH ≥10cm) bearing fruit*	4.0	0	23.8	27.9	0	54.5	4.2	0	25	8.3	0	50
# trees (DBH < 10cm)	89	36	142	61	8	198	28	0	76	15.5	0	25
Altitude (m)	1,516	1,364	1,619	1,488	1,249	1,635	1,641	1,603	1,690	1,216	1,150	1,255
Slope^{2}	-	-	-	-	-	-	-	-	-	-	-	-

	Forest			Woodland			Swamp			Grassland		
	Mean	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*
Canopy cover (%)*,[3]	-	51	100	-	1	75	-	0	50	-	1	50
Canopy cover (%, Canopy Digi)[4]	68.8	55.4	78.3	44.0	19.4	57.1	14.2	0.0	35.7	19.0	2.4	42.3
Canopy connectivity (%)*,[3]	-	26	100	-	1	75	-	0	50	-	0	25
Understory (%)*,[3]	-	51	100	-	1	75	-	0	50	-	1	25
Grass (%)*,[3]	-	0	0	-	26	75	-	26	100	-	75	100
Bare land (%)[3]	-	76	100	-	26	50	-	0	50	-	0	25
THV (%)[3]	-	0	0	-	0	0	-	0	25	-	0	0
Water (%)*	2.5	0	5	0	0	0	0	0	0	0	0	0
Ant nests (#)	0.5	0	2	0	0	0	0	0	0	0	0	0
Termite mounts (#)	0	0	0	0.5	0	3	0	0	0	0	0	0
Chimp evidence (#)	0	0	0	0	0	0	0	0	0	0	0	0
Plot tree data (trees/vines > 10cm DBH)												
Species[5]	-	-	-	-	-	-	-	-	-	-	-	-
Tree DBH (cm)	21.5	10	81	21,2	10.1	69.7	23.1	10.5	71.9	28.1	10	163.3
Tree LBH (m)	4.2	0	18.5	2.8	0	8.3	1.3	0	3.2	1.4	0	5.8
Tree height (m)*	11.8	1.5	29.5	8.8	2.6	18.5	5.8	2.3	11.6	7.5	1.7	24.6
Crown width N (m)	2.2	0	13.6	2.2	0	7.9	1.9	0	5.3	2.9	0	12.4
Crown width S (m)	2.8	0	13.5	2.1	0	7	1.9	0	5.5	3.2	0	9.8
Crown width E (m)	2.1	0	7.7	1.7	0	7.2	1.9	0	5.5	2.7	0	8.5
Crown width W (m)	2.5	0	16.9	2.2	0	12.6	1.8	0	6.2	2.8	0	10.2
Crown height (m)	7.6	0.5	22.7	5.9	0	14.5	4.5	1.3	9.3	6.2	0.9	19.3
Crown shape[6]	-	-	-	-	-	-	-	-	-	-	-	-
Crown connectivity (%)[3]	-	0	100	-	0	100	-	0	100	-	0	75
Crown cover (%)[3]	-	0	100	-	0	100	-	1	100	-	0	100
Tree ripe chimpanzee food coverage (%)*,[3]	-	0	25	-	0	50	-	0	25	-	0	25
Micro-climates												
Local temperature day (average, °C)*	23.3	22.3	24.4	26.6	23.9	29	25.8	23.8	28.9	29.8	28.5	31.7
Local temperature night (average, °C)*	18.5	16.8	20.1	18.6	16.7	20.4	15.7	14.8	16.2	21.1	20.7	21.8
Local luminosity day (average, Lux)*	3,767	1,012	8,113	14,440	6,854	39,578	19,454	13,059	29,192	21,968	10,092	44,272
Local luminosity night (average, Lux)*	3	0	9	8	3	18	30	11	76	23	10	50

[1]Number of (feeding) trees is equal to (feeding) tree density per plot; [2]Slope cannot be explained with a mean, minimum or maximum, as slope was visually assessed as flat, mild, medium or steep. For forest, slopes were either flat or steep, for woodland slopes ranged from flat to steep, for swamp slopes were flat, and for grassland slopes ranged from flat to mild; [3]For canopy cover, canopy connectivity, understory, grass, bare land, THV, crown connectivity, crown cover, and tree ripe chimpanzee food coverage, no mean can be presented as these variables were measured in categories (0 = 0%, 1: 1 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, 4 = 76 – 100%). Only minima and maxima are presented based on these categories; [4]Canopy cover measures are based on photograph analyses through CanopyDigi; [5]Various tree species are observed, including *Cola microcarpa* and *Brachystegia boehmii* for forest, *Brachystegia speciformis* and *Parinari curatelllifolia* for woodland, *Uapaca kirkiana* and *Erythrina excelsa* for swamp, and *Acacia polyacantha* and *Diplorhynchus condylocarpon* for grassland; [6]Crown shape cannot be explained with maxima, minima and means. All crown shapes were observed for trees in forest(Figure 5.2), and trees in woodland, grassland and swamp had crown shapes 1, 2, 4 and 6.

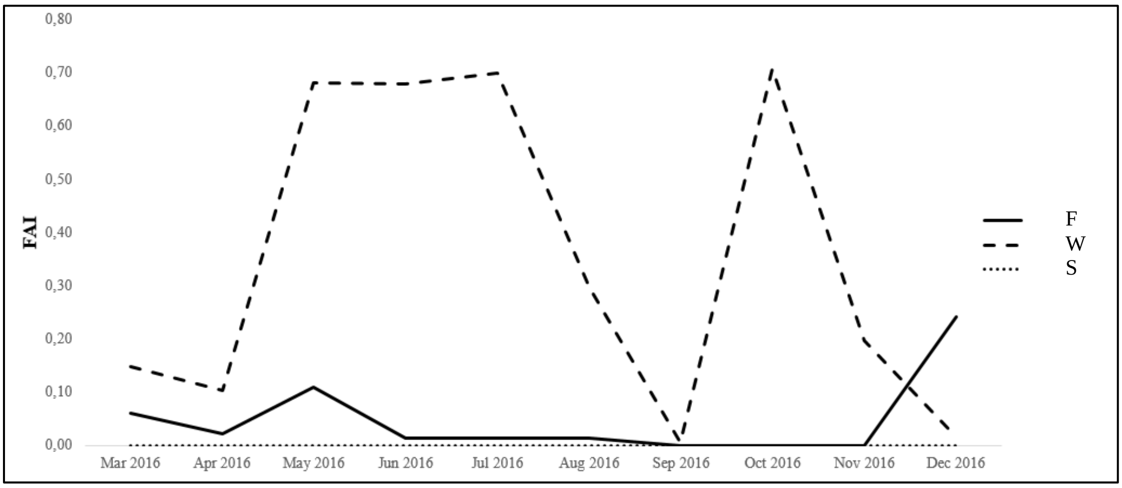

Figure 5.5. Fruit availability indices (FAI) for woodland (W), forest (F) and swamp (S) vegetation types. Data were collected on phenology transects along the Issa trail system and were measured between Mar - Dec 2016. No transects were monitored in savannah grassland vegetation types.

Model rules based on results from literature, GMERC and field-collected data

Results from literature, GMERC and field-collected data were used to set out specific rules for the Issa model on savannah chimpanzee landscape use. Based on findings from Chapter 2, the Issa model included a specific set of vegetation features and micro-climates for each vegetation type (i.e. landscape-scale vegetation features and micro-climates; Table 2.3) and in setting out model rules on *where* to perform each activity (i.e. expert-based reviews: K. Koops, A. Pascual-Garrido, and V. Reynolds; Table 2.2). The virtual Issa environment was simulated to represent the exact vegetation cover, spatial vegetation arrangement and climate of the Issa landscape as highlighted by the GMERC GIS vegetation map and the HOBO weather station data. Values for vegetation features and micro-climates per model patch (50m x 50m) were selected randomly within the specified range of Table 5.2 with regards to the respective vegetation type and patch size. No field measurements were taken to assess the vegetation features and micro-climates of rocky outcrops, but this land cover type was included within the Issa model. Based on personal observations (K.L. van Leeuwen, May – July 2017), however, rocky outcrops were assumed to contain no vegetation and to have similar micro-climates to grassland. Model rules on *where* Issa chimpanzees should perform their daily feeding, drinking, nesting, resting, and travel activities were either based on empirical data and/or based on the finding that forest was the preferred vegetation type for Issa chimpanzees. When no empirical data were presented on the range of important vegetation features and micro-climates for a behaviour, it was assumed that the range of these micro-habitat characteristics should fall within the range observed in forest. Although this initially seems to restrict individuals to only use forest vegetation types, the selected ranges of vegetation features and micro-climates also exist in other vegetation types such as woodland (Table 5.2). Detailed model rules are outlined in Table 5.3.

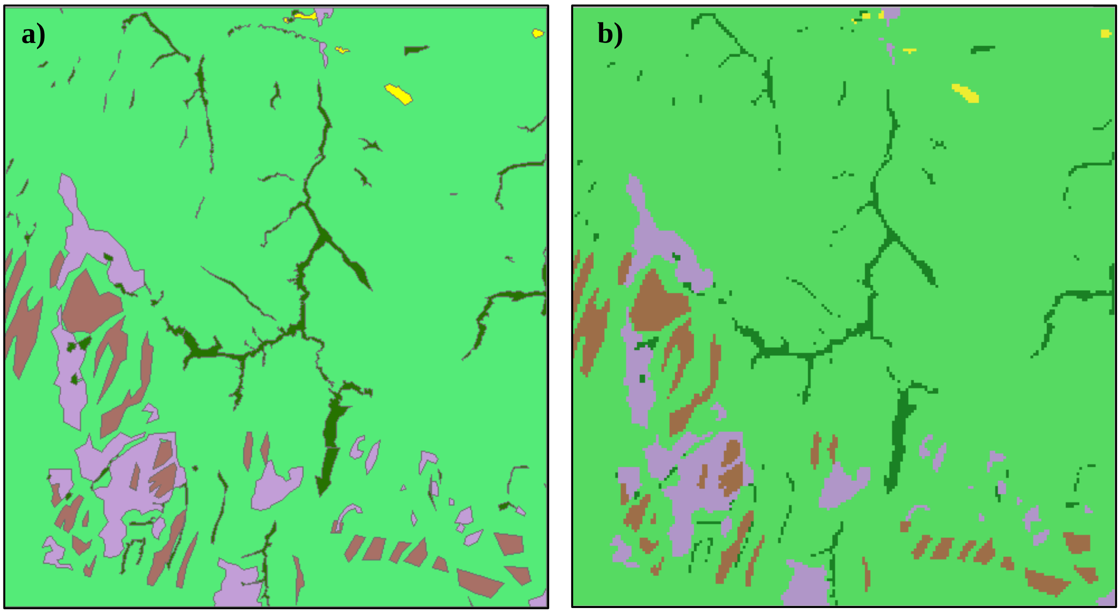

Figure 5.6. Present-day vegetation coverage and spatial arrangement of the total study area at Issa for this study (110km^2): **a)** the GMERC GIS vegetation map (created by C. Johnson); **b)** the conversion of the GMERC GIS vegetation map to a grid of 50m x 50m cells adopting the majority vegetation type of each cell imported into the NetLogo modelling environment. Due to the adaptations to the GMERC GIS vegetation map, the NetLogo map presents a slightly more generalised vegetation map of Issa. This map forms the base of the individual-based model on Issa chimpanzee landscape use.

Table 5.3. Model rules for the Issa chimpanzee landscape use model on *where* to perform each behaviour. Rules are based upon findings from literature, GMERC and field-collected data. Rationale presented in Appendix 5.6.

Behaviour	Where to perform an activity
Feeding	Patches with number fruit ≥ 3.5 fruits (i.e. number of fruits eaten, equals 3.5 grams of edible dry weight), food tree density between 4 – 84 food trees/patch, tree height between 1.5 – 29.5m, tree density between 72 – 172 trees/patch, local temperature (day) between 22.3 – 24.4°C, and local luminosity (day) between 1,012 – 8,113 Lux.
Drinking	Patches with amount water ≥ 50 hydrations (i.e. amount water drunk), local temperature (day) between 22.3 – 24.4°C, and local luminosity (day) between 1,012 – 8,113 Lux.
Nesting	Patches with tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, tree density between 72 – 172 trees/patch, number fruit ≥ 3.5 fruits, understory density > 0%, food tree density between 4 – 84 trees/patch, amount water ≥ 50 hydrations, local temperature (night) between 16.8 – 20.1°C, and luminosity (night) between 0 – 9 Lux.
Resting	Patches with local temperature (day) between 22.3 – 24.4°C, local luminosity (day) between 1,012 – 8,113 Lux, tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, understory density > 0%, tree density between 72 – 172 trees/patch, food tree density between 4 – 84 trees/patch, number fruit ≥ 3.5 fruits, and amount water ≥ 50 hydrations.
Travel	No rules set out on where to travel; travel is directed towards a suitable location for the selected activity.

Model output

Sensitivity analysis

Local sensitivity analysis of 22 input parameters showed that the Issa model output was robust to small changes in parameter settings (Table 5.4). With 10% changes in input parameters, the Issa model output was never more than 17% different from the baseline output (i.e. S^+ or $S^- \leq 1.7$; Table 5.4). Sensitivities for the Issa model were slightly higher than those presented for the generic model of Chapter 4, but were still within acceptable limits, as time spent on different behaviours still remained within 5% of the baseline activity budgets. As the Issa model was adapted from the generic model, it is assumed that the low sensitivity of the Issa model did not indicate model overfitting: large changes in parameter settings (> 50%) had a significant effect on the model output during the calibration process in Chapter 4.

Activity budgets, food intake, water intake and daily path lengths

Model output on activity budgets, food intake, water intake and daily path lengths differed significantly for the Issa model and the generic model (Table 5.5, Figure 5.7 – 5.9). Chimpanzees simulated in the Issa model spent significantly more time travelling and nesting, and had significantly longer daily path lengths than chimpanzees simulated in the generic model (Table 5.6). Simulated Issa chimpanzees furthermore spent significantly less time feeding and drinking, and had significantly lower food and water intake than chimpanzees simulated in the generic model (Table 5.6). Time spent resting was not significantly different between the two models.

Table 5.4. Sensitivity (S^+ and S^-) in the Issa model output to small changes (i.e. +/- 10%) to input parameters. 22 parameters were selected for sensitivity analysis. Sensitivities were calculated by dividing the percentage of change in the output by the percentage of change in the input; Low values for S indicated low sensitivities. The rationale behind the baseline values for all parameters is outlined in Appendix 5.6 Within the table, 'random' indicates that a value was randomly assigned within the model between 0 and 'number'.

Parameter	Base value	+10% value	S+	-10% value	S-
amount of water forest	random 100	random 110	1.6	random 90	1.7
amount of water woodland	random 75	random 82.5	0.9	random 67.5	1.0
amount of water savannah	random 50	random 55	0.4	random 45	0.7
amount of water swamp	random 75	random 82.5	1.3	random 67.5	0.4
where - number of fruits	3.5	3.85	0.4	3.15	0.5
where - amount water	50	55	0.6	45	0.4
when - feeding criterion	≤ 144	≤ 158.4	0.7	≤ 129.6	1.1
when - drinking criterion	≤ 72	≤ 79.2	1.4	≤ 64.8	0.5
when - resting criterion	≥ 73	≥ 80.3	0.6	≥ 65.7	1.0
Initial - energy	random 10	random 11	1.0	random 9	1.2
Initial - hydration	random 10	random 11	1.1	random 9	0.4
Initial - fatigue	random 10	random 11	0.4	random 9	1.2
Step - energy	-2	-2.2	1.0	-1.8	1.1
Step - hydration	-1	-1.1	0.4	-0.9	0.3
Step - fatigue	+1	1.1	0.3	0.9	0.9
Feeding - number fruits eaten	3.5	3.85	1.4	3.15	0.8
Drinking - amount water drunk	50	55	0.6	45	0.6
Resting - fatigue	-2	-2.2	0.5	-1.8	0.8
Nesting - fatigue	-2	-2.2	1.2	-1.8	1.5
Travel - hydration	-1 per extra 50m	-1.1	0.2	-0.9	0.2
Travel - fatigue	+1 per extra 50m	1.1	0.5	0,9	0.7

Table 5.5. Model output (i.e. mean ± standard deviation) on the daily activity budgets, path lengths, food intake and water intake (24 hours) for chimpanzees simulated in the Issa and generic chimpanzee landscape use models.

	Generic (savannah) model	Issa model
Time spent feeding	19.3±5.1%	12.8±9.3%
Time spent drinking	1.8±0.7%	1.2±1.0%
Time spent nesting	47.9±5.3%	48.9±2.1%
Time spent resting	11.3±5.3%	11.2±8.9%
Time spent travelling	19.7±8.8%	25.9±15.1%
Daily path length	4,142.3±2,901.4m	7,060.9±5,578.4m
Food intake	97.3±25.6 fruits	64.6±46.7 fruits
Water intake	134.7±50.7 hydrations	87.6±72.5 hydrations

Energy, hydration and fatigue budgets

Model output on energy, hydration and fatigue budgets from the Issa model differed significantly from the generic model (Table 5.7, Figure 5.10). Chimpanzees simulated in the Issa model had significantly lower (i.e. more negative) energy and hydration budgets, and significantly higher (i.e. more positive) fatigue budgets than chimpanzees simulated in the generic model (Table 5.6).

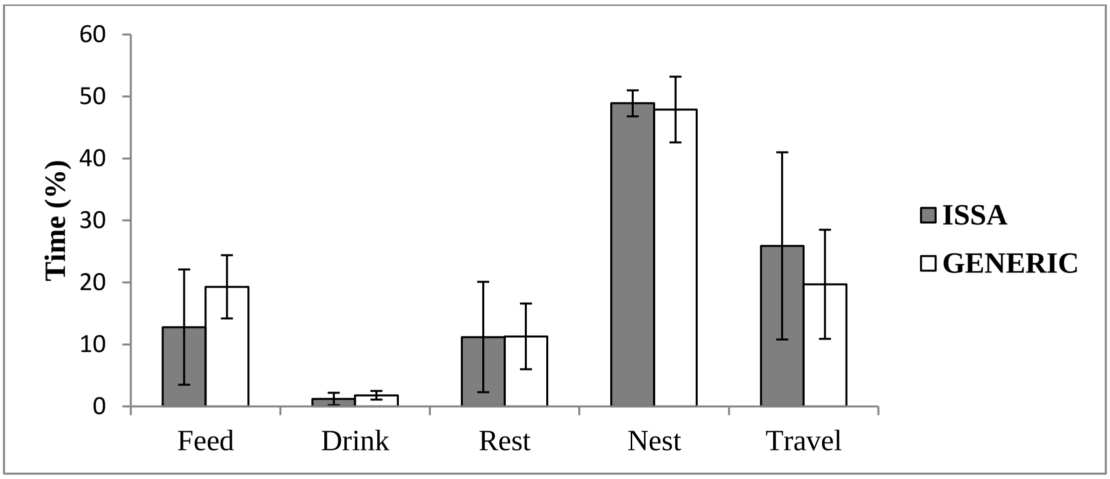

Figure 5.7. Model output on the daily activity budgets (24 hours) for chimpanzees simulated in the Issa and generic models.

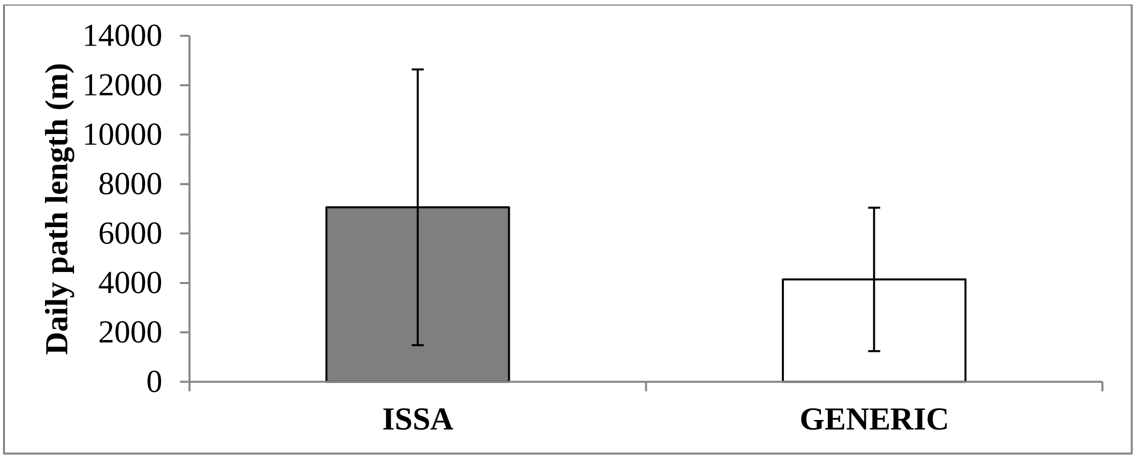

Figure 5.8. Model output on the daily path lengths of chimpanzees simulated in the Issa and generic models.

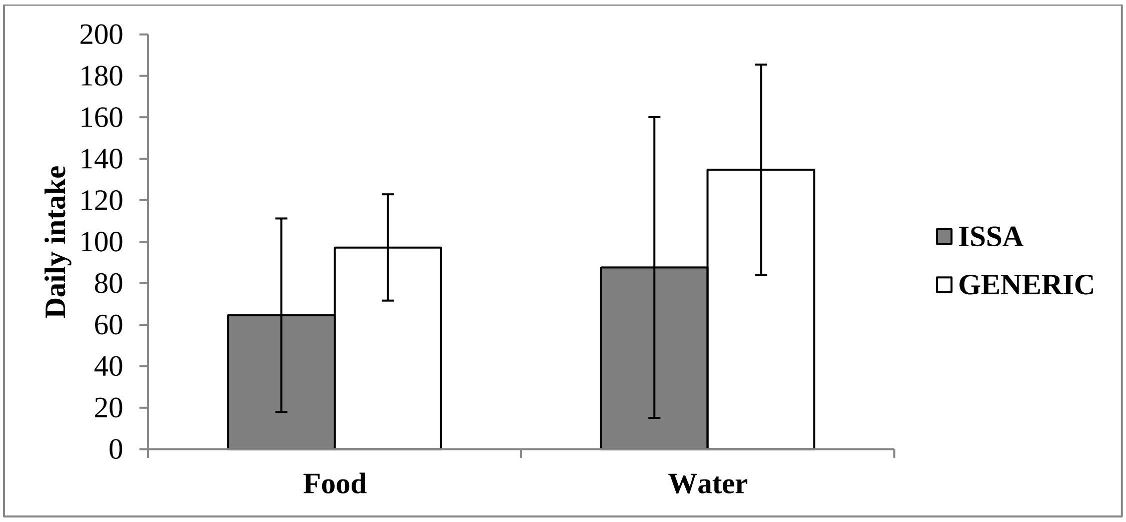

Figure 5.9. Model output on the daily food and water intake (24 hours) for chimpanzees simulated in the Issa and generic models.

Table 5.6. Mann-Whitney U test statistics for the comparisons of activity budgets, daily path lengths, food and water intake, and energy, hydration and fatigue budgets for chimpanzees simulated in the Issa model and in the generic model. An '*' denotes a significant difference. In all cases, N = 30.

	Direction of difference	**Mann-Whitney U tests statistics** ($N_{1,2}$ = 30 in all cases)
Time spent feeding	Generic model > Issa model	Z = - 6.7, p < 0.001*
Time spent drinking	Generic model > Issa model	Z = - 6.6, p < 0.001*
Time spent nesting	Issa model > Generic model	Z = - 4.1, p < 0.001*
Time spent resting	Issa model = Generic model	Z = - 0.3, p = 0.761
Time spent travelling	Issa model > Generic model	Z = - 6.7, p < 0.001*
Daily path length	Issa model > Generic model	Z = - 6.7, p < 0.001*
Energy budget	Generic model > Issa model	Z = - 6.6, p < 0.001*
Hydration budget	Generic model > Issa model	Z = - 6.7, p < 0.001*
Fatigue budget	Issa model > Generic model	Z = - 6.7, p < 0.001*
Food intake	Generic model > Issa model	Z = - 6.7, p < 0.001*
Water intake	Generic model > Issa model	Z = - 6.6, p < 0.001*

Table 5.7. Model output (i.e. mean ± standard deviation) on the daily energy, hydration and fatigue budgets (24 hours) for chimpanzees simulated in the Issa and generic chimpanzee landscape use models.

	Generic (savannah) model	**Issa model**
Energy budget	-271.4±252.2kCal	-577.0±516.4kCal
Fatigue budget	33.1±64.2 fatigues	79.9±110.6 fatigues
Hydration budget	-60.4±80.7 hydrations	155.2±152.1 hydrations

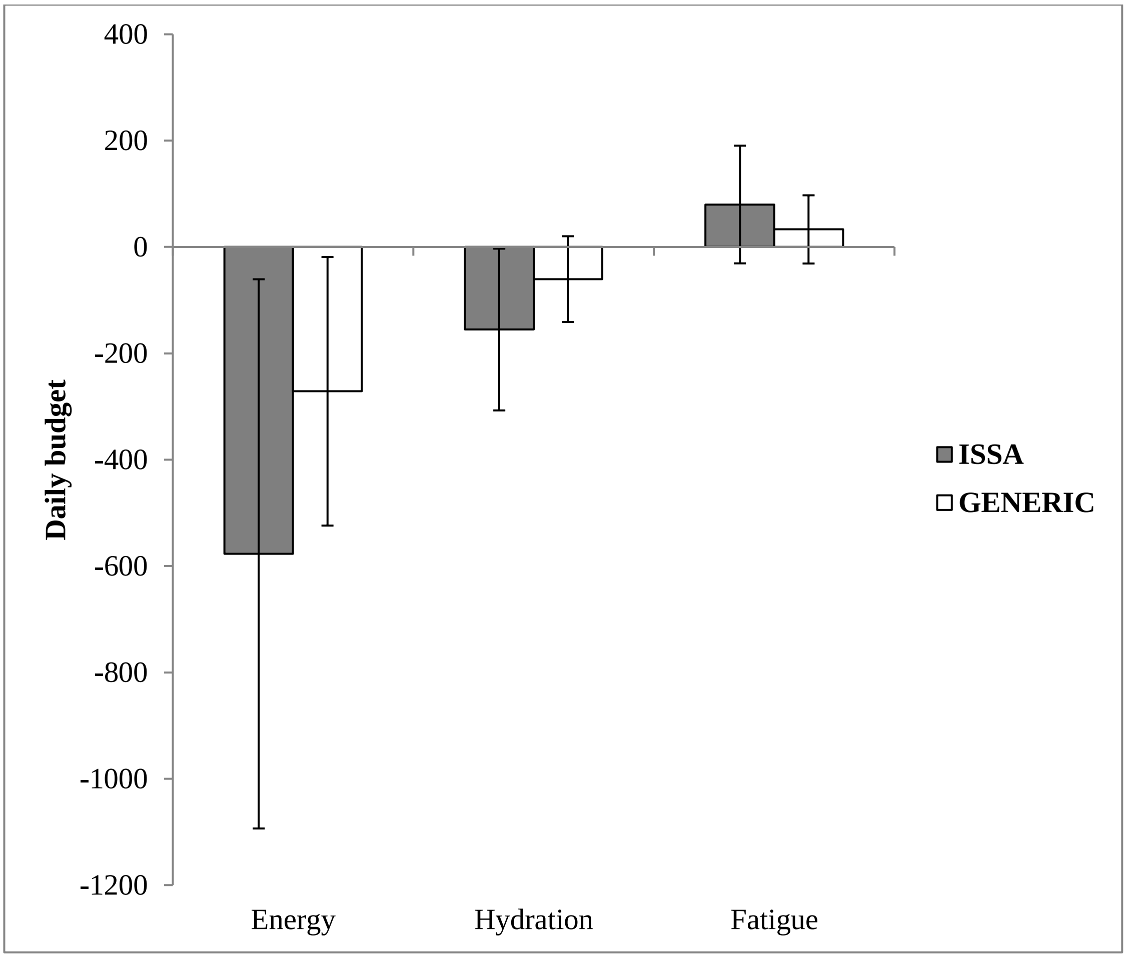

Figure 5.10. Model output on the daily energy, hydration and fatigue budgets (24 hours) for chimpanzees simulated in the Issa and generic models.

Preferred vegetation

Vegetation type usage differed significantly for the Issa model and the generic model (Table 5.8, Figure 5.11), with Issa chimpanzees spending significantly more time in woodland, and significantly less time in forest and grassland, than savannah chimpanzees simulated in the generic model (Table 5.8). As swamp and rocky outcrops were only included in the Issa model, these could not be compared. For chimpanzees simulated in the Issa model and in the generic model, forest was the preferred vegetation type and more open vegetation types were avoided (Issa model: χ^2 = 3,362,745.5, df = 4, $p < 0.001$; generic model: χ^2 =1,224,101.3, df = 2, $p < 0.001$; Figure 5.12 – 5.13).

Behaviourally preferred vegetation

Time spent on different activities within forest, woodland and grassland patches was significantly different between the Issa model and the generic model (Table 5.8, Figure 5.14). Similar to the generic model, chimpanzees simulated in the Issa model preferred forest vegetation types for their daily feeding, drinking, nesting and resting activities, and other more open vegetation types were avoided (Issa model: feeding: χ^2 = 1,181,995.8, df = 4, $p < 0.001$; drinking: χ^2 = 117,910.0, df = 3, $p < 0.001$; nesting: χ^2 =1,728,467.6, df = 4, $p < 0.001$; resting: χ^2 = 994,341.1, df = 4, $p < 0.001$). In contrast, simulated Issa chimpanzees used both forest and grassland more often than expected for travel (χ^2 = 91,579.4, df = 4, $p < 0.001$).

Site selectivity

Although site selections for chimpanzees simulated in the Issa and generic models were difficult to compare due to differences in model input parameters, general patterns of site choice seemed similar for both models. For feeding, drinking, nesting and resting activities, simulated Issa and generic savannah chimpanzees used a wide range of vegetation features and micro-climates observed across a wide range of different vegetation types. Medians and interquartile ranges, however, showed that simulated chimpanzees in both models primarily used the vegetation features or micro-climates observed in forest, or micro-habitat characteristics that were largely similar to those observed in forest (Table 5.9). Simulated Issa chimpanzees, however, seemed to include a slightly wider range of vegetation features and micro-climates for nesting behaviour as compared to chimpanzees simulated in the generic model (Table 5.9). Travel activities occurred across a wide range of micro-habitat characteristics in both models, although medians and interquartile ranges highlighted that the range of vegetation features and micro-climates observed in woodland was used predominantly (Table 5.9).

Table 5.8. Model output (i.e. mean ± standard deviation) for, and comparisons (Mann-Whitney U tests) between, the Issa and generic (savannah) models for time spent in different vegetation types, and time spent on different behaviours in different vegetation types (24 hours) for chimpanzees. Greater (>) and smaller (<) values for the generic model as compared to the Issa model are highlighted. An '*' denotes a significant difference. For all comparisons, N = 30. Within the table, 'n/a' stands for not applicable, '-' stands for not observed within the model.

	Generic model (savannah)	**Direction** of difference	**Issa model**	**Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)
Time spent in forest	75.1±23.4%	>	59.0±37.8%	Z = -6.6 p < 0.001*
Time spent in woodland	20.9±22.3%	<	39.2±36.8%	Z = -6.7 p < 0.001*
Time spent in grassland	4.0±4.2%	>	0.0±0.2%	Z = -6.8 p < 0.001*
Time spent in swamp	n/a	n/a	1.0±2.6%	n/a
Time spent in rocky outcrops	n/a	n/a	0.8±2.6%	n/a
Time spent feeding in forest	16.0±6.1%	>	12.3±9.5%	Z = -6.3 p < 0.001*
Time spent feeding in woodland	3.3±2.8%	>	0.5±1.9%	Z = -6.7 p < 0.001*
Time spent feeding in grassland	-	n/a	-	n/a
Time spent feeding in swamp	n/a	n/a	-	n/a
Time spent feeding in rocky outcrops	n/a	n/a	-	n/a
Time spent drinking in forest	1.5±0.8%	>	1.2±1.0%	Z = -5.1 p < 0.001*
Time spent drinking in woodland	0.4±0.4%	>	0.0±0.1%	Z = -7.2 p < 0.001*
Time spent drinking in grassland	-	n/a	-	n/a
Time spent drinking in swamp	n/a	n/a	-	n/a
Time spent drinking in rocky outcrops	n/a	n/a	-	n/a
Time spent nesting in forest	40.3±18.1%	>	29.5±24.4%	Z = -6.6 p < 0.001*
Time spent nesting in woodland	7.6±17.4%	<	19.4±23.4%	Z = -6.7 p < 0.001*
Time spent nesting in grassland	-	n/a	-	n/a
Time spent nesting in swamp	n/a	n/a	-	n/a
Time spent nesting in rocky outcrops	n/a	n/a	-	n/a
Time spent resting in forest	9.8±5.8%	<	10.5±8.9%	Z = -2.9 p = 0.004*
Time spent resting in woodland	1.5±3.8%	>	0.7±3.1%	Z = -4.9 p < 0.001*
Time spent resting in grassland	-	n/a	-	n/a
Time spent resting in swamp	n/a	n/a	-	n/a
Time spent resting in rocky outcrops	n/a	n/a	-	n/a
Time spent travelling in forest	7.6±3.0%	>	5.4±4.2%	Z = -6.2 p < 0.001*
Time spent travelling in woodland	8.1±6.2%	<	18.7±17.0%	Z = -6.7 p < 0.001*
Time spent travelling in grassland	4.0±4.2%	>	0.0±0.2%	Z = -6.8 p < 0.001*
Time spent travelling in swamp	n/a	n/a	1.0±2.6%	n/a
Time spent travelling in rocky outcrops	n/a	n/a	0.8±2.6%	n/a

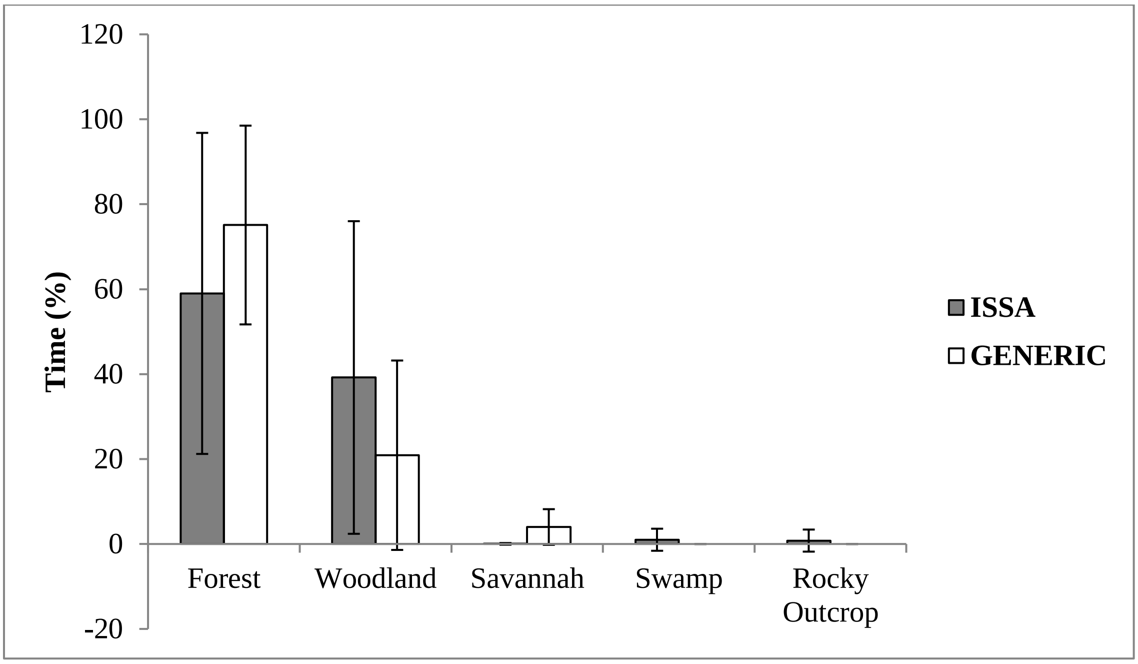

Figure 5.11. Model output on daily vegetation type usage (24 hours) for chimpanzees simulated in the Issa and generic models.

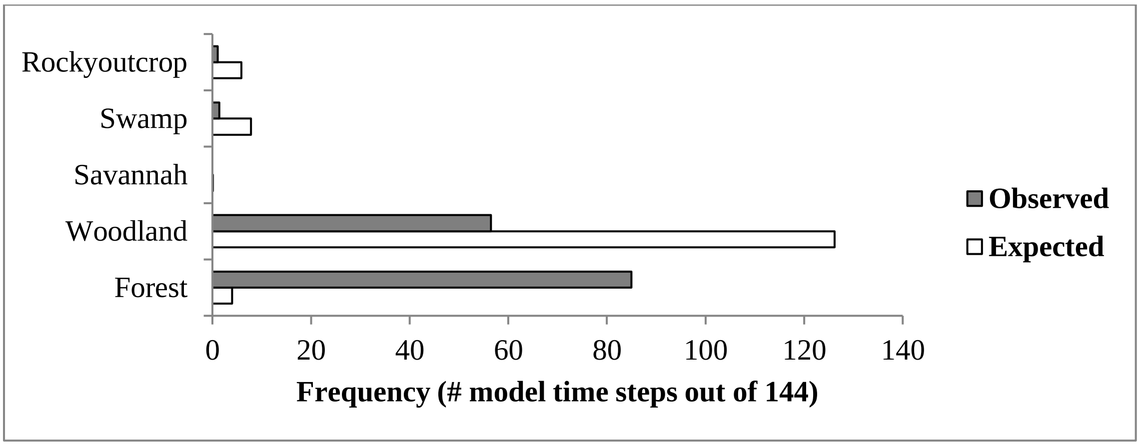

Figure 5.12. Observed versus expected vegetation type usage for chimpanzees simulated in the Issa model.

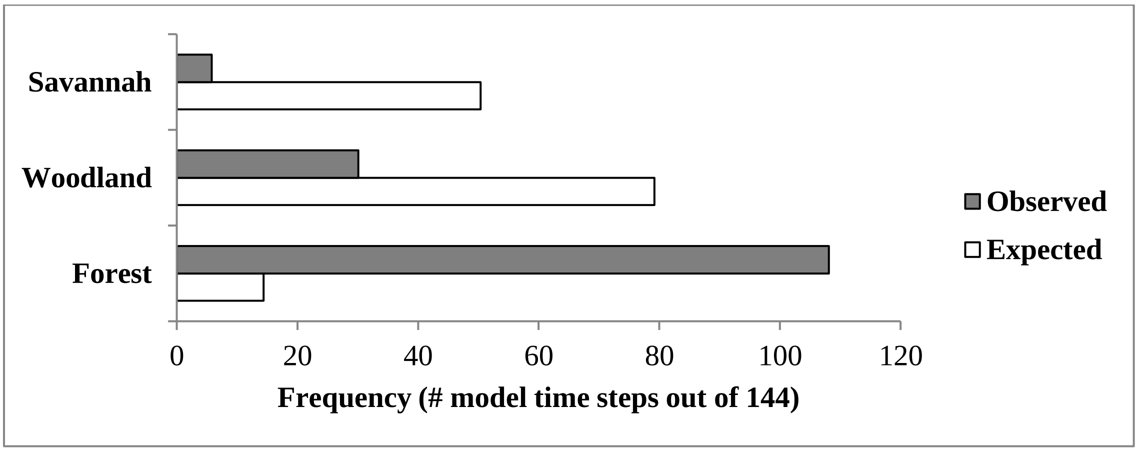

Figure 5.13. Observed versus expected vegetation type usage for chimpanzees simulated in the generic model.

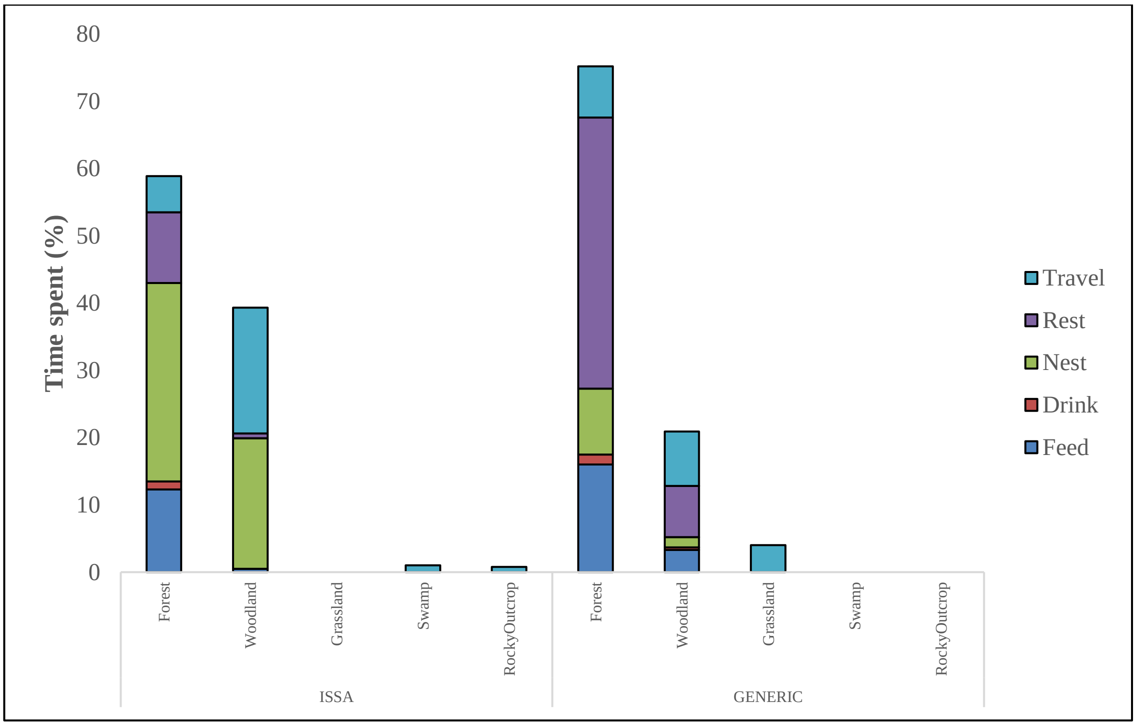

Figure 5.14. Model output for the daily activities performed in each vegetation type for chimpanzees simulated in the Issa model and in the generic model.

Inter-individual variability

Across individuals and model runs of the generic model, energy budgets ranged between -1,661.4 – 10.8 kCal (13.8% positive and 86.2% negative energy budgets across individuals; Figure 5.15), hydration budgets ranged between -420 – 50 hydrations (28.8% positive and 71.2% negative hydration budgets across individuals), and fatigue budgets ranged between -63 – 459 fatigues (74.9% positive and 25.1% negative fatigue budgets across individuals). In the Issa model, energy budgets ranged between -1,827 – 10.9 kCal, with 20.4% of simulated individuals having positive energy budgets and 79.6% having negative energy budgets (Figure 5.15). Hydration budgets ranged between -483 – 50 hydrations, with 27.6% positive and 72.4% negative hydration budgets across individuals. Fatigue budgets ranged between -64 – 402 fatigues across individuals, with 72.2% of individuals having positive and 27.8% of individuals having negative fatigue budgets. More individuals were able to maintain homeostasis in the Issa model as compared to the generic model. Inter-individual variability was also observed for other model output within the Issa model, and similar to the generic model, a significant negative correlation was observed between daily path length and time spent in forest vegetation for Issa chimpanzees (daily path length range: 400 – 2,2000m; forest use range: 0 – 100% of the 24 hour day; N = 30, $r_s = -0.735$, $p < 0.001$; Figure 5.16).

Table 5.9. Medians and interquartile ranges of the vegetation features and micro-climates most frequently used by chimpanzees simulated in the Issa and generic models in performing their daily feeding, drinking, nesting, resting and travel activities: **a**) ranges for tree height, canopy cover, canopy connectivity and understory density, **b**) ranges for tree density, food tree density, number of fruit and amount of water, and **c**) ranges for temperature and luminosity during night and day. Input values for vegetation features and micro-climates differ between models. For the Issa model, ranges of vegetation features and micro-climates are based on field data collection. For the generic model, ranges of vegetation features and micro-climates are based on literature review, with scaled values for micro-climates (i.e. put on a scale from 0 – 100) as no quantitative data have been presented (Chapter 4, Appendix 4.5). Tree density and food tree density for the Issa model is measured in number of trees, whereas it is measured in percentages for the generic model. Similarly, temperature in the Issa model is measured in degrees Celsius and luminosity in Lux, whereas it is scaled for the generic model. Q_1 stands for the lower quartile of the range used, i.e. 25%, and Q_3 stands for the upper quartile of the range used, i.e. 75%.

a)		**Tree height (m)**			**Canopy cover (%)**			**Canopy connectivity (%)**			**Understory density (%)**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Issa	Feed	8.4	15.3	22.5	62	75	87	43	62	81	24	49	74
	Drink	8.3	15.4	22.3	62	75	88	43	62	81	26	51	76
	Nest	7.9	13	18.3	51	64	80	34	53	72	21	44	66
	Rest	8.7	15.2	22.2	61	74	87	44	60	82	23	48	73
	Travel	6.3	10.7	15.4	22	46	65	22	42	61	18	39	60
Generic	Feed	16	26	38	77	85	93	77	85	93	7	15	23
	Drink	16	25	38	76	84	93	76	84	92	7	16	24
	Nest	17	26	38	78	85	93	77	85	93	7	15	23
	Rest	17	26	38	78	85	92	78	85	93	7	15	22
	Travel	11	15	24	30	61	84	30	61	84	16	39	70

b)		**Tree density (# / %)**			**Food tree density (# / %)**			**Number fruit**			**Amount water**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Issa	Feed	103	130	152	37.1	46.8	54.7	6.5	9.2	12.5	24	49	74
	Drink	98	126	150	35.6	45.4	54	4.2	8.2	11.7	62	74	87
	Nest	74	92	135	34.3	35.7	48.6	9.5	14.3	67	59	67	78
	Rest	98	127	152	35.7	45.7	54.7	7.6	10.2	13.6	62	73	86
	Travel	56	66	75	26.3	30.5	34.8	8.7	52.3	61.5	17	37	58
Generic	Feed	77	85	93	77	85	93	6	9	13	21	44	69
	Drink	76	82	92	76	82	92	2.5	6.5	11.5	60	71	84
	Nest	77	85	93	77	85	93	7	10.5	14.5	61	72	86
	Rest	78	85	93	78	85	93	6.5	10	14	62	72	86
	Travel	32	64	84	32	63	84	1	3	6	16	34	52

c)		**Temperature night (°C / scaled)**			**Temperature day (°C / scaled)**			**Luminosity night (Lux / scaled)**			**Luminosity day (Lux / scaled)**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Issa	Feed	17.7	18.5	19.3	22.8	23.4	23.9	2	5	7	2,943	4,783.5	6,597
	Drink	17.7	18.5	19.3	22.8	23.4	23.9	2	5	7	2,892	4,716	6,563
	Nest	17.5	18.4	19.2	23.1	24	25.6	3	5	7	4,004	6,768	19,152
	Rest	17.6	18.5	19.3	22.9	23.4	24	2	5	7	2,877	4,612	6,571
	Travel	17.5	18.5	19.5	24.2	25.8	27.5	5	9	14	8,552	19,034	28,900
Generic	Feed	77	85	93	7	15	23	6	12	19	7	15	23
	Drink	76	84	92	8	16	24	6	12	19	7	16	24
	Nest	78	85	93	8	15	23	6	13	19	7	14	22
	Rest	78	86	93	7	14	22	6	13	19	8	15	22
	Travel	30	61	84	16	36	68	6	13	19	16	36	67

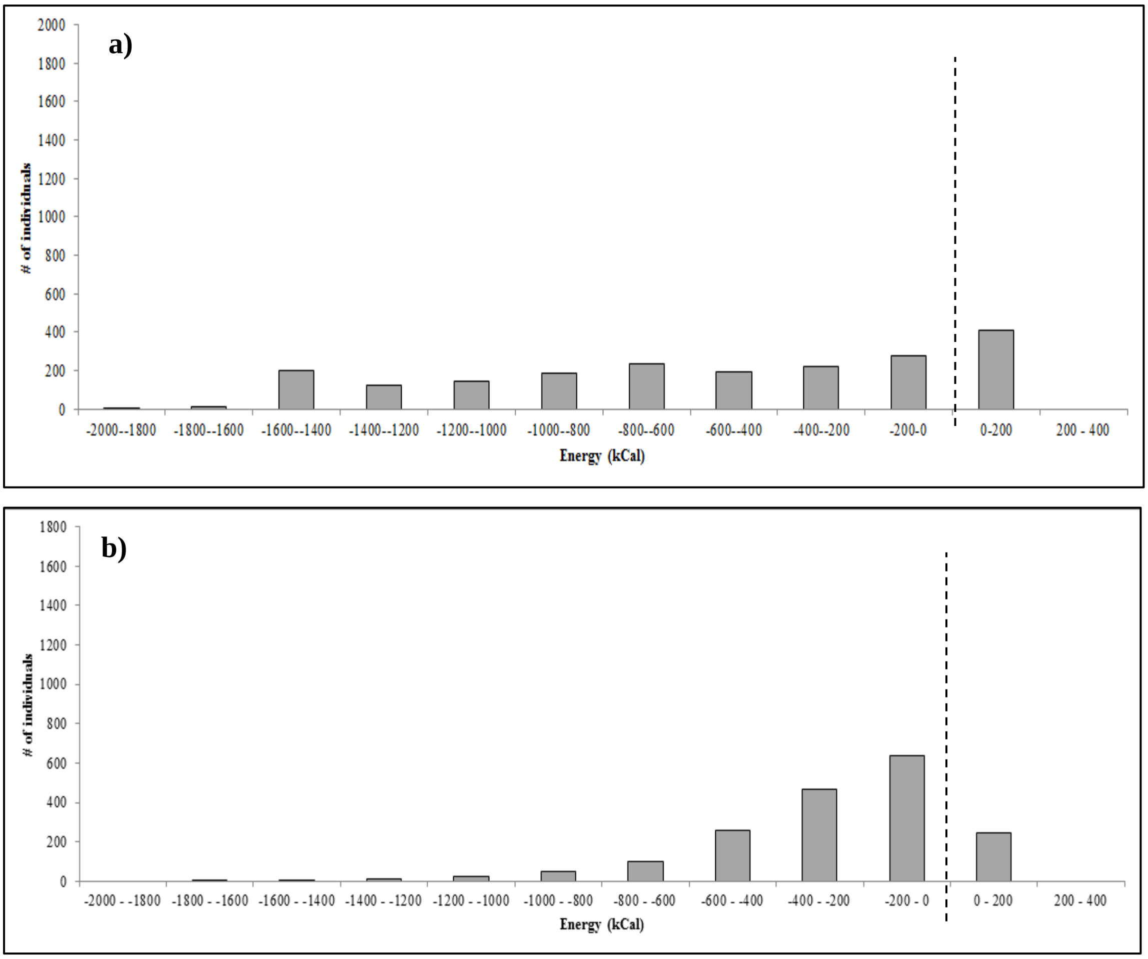

Figure 5.15. Frequency distribution of energy budgets for chimpanzees simulated in **a)** the Issa model, and **b)** the generic model. The total number of individuals equals 2,010 for the Issa model (i.e. 67 individuals per model run, and 30 model runs in total), and 1,800 for the generic model (i.e. 60 individuals per model run, 30 model runs in total). The dotted line indicates the cut-off between positive and negative energy budgets.

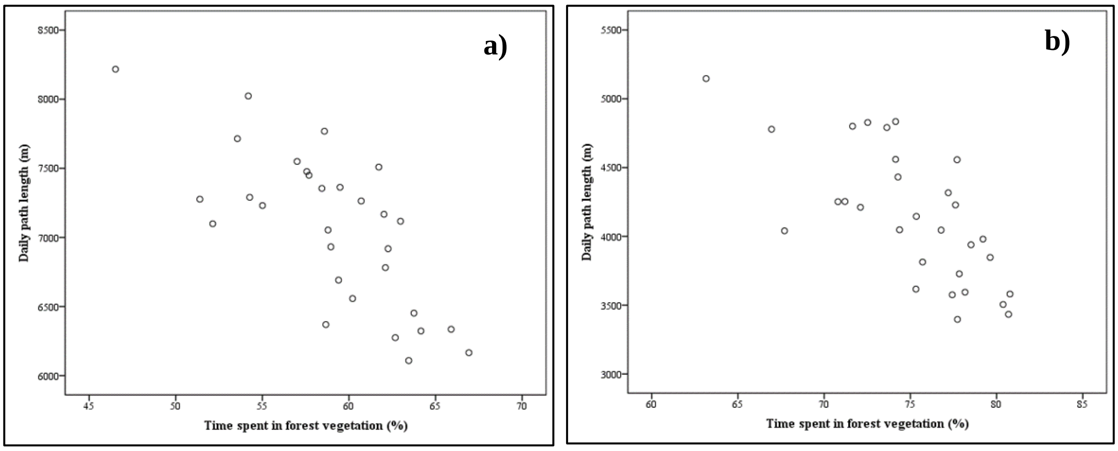

Figure 5.16. Time spent in forest (% 24 hours) and daily path length for chimpanzees simulated in **a)** the Issa model, and **b)** the generic model. A significant negative correlation is observed for both models (Issa model: N = 30, $r_s = -0.735$, $p < 0.001$; generic model: N = 30, $r_s = -0.732$, $p < 0.001$).

Discussion

This study identified patterns of savannah chimpanzee landscape use at Issa Valley, Tanzania, in order to create a realistic picture of the present-day situation and challenges faced by chimpanzees in marginal savannahs and to explore how well the generic chimpanzee landscape use model of Chapter 4 was able to accurately assess these circumstances. Using an individual-based modelling approach based on literature and field-collected data from Issa, simulated Issa chimpanzees travelled long distances, spent relatively large amounts of time on travel and small amounts on feeding, drinking, nesting and resting, were reliant on forest vegetation and selective in their site choice for different activities, had negative energy and hydration budgets, low food and water intake, and positive fatigue budgets. Whereas the generic model also highlighted these general trends for savannah chimpanzees, the Issa model showed more detailed, site-specific landscape use patterns for chimpanzees at this site. As the Issa landscape is more marginal than the savannah landscape simulated in the generic model, this accurately resulted in greater difficulties for Issa chimpanzees in managing their time and energy budgets.

Chimpanzee landscape use in savannahs

Compared to the wealth of information that is available on chimpanzees in forested environments (i.e. dense forests and forest mosaics), knowledge on the behaviour and ecology of chimpanzees in marginal savannahs remains limited (e.g. Hunt and McGrew 2002, Pruetz et al. 2002, Russak 2013). Consequently, relatively little is known about the landscape-scale patterns of habitat use for savannah chimpanzees living at the edge of their ecological niche, even though they may form the key to understanding how chimpanzees will cope with increasing habitat fragmentation and climate change throughout their range (Pruetz 2018). As shown in Chapter 4 (p. 120), primates generally cope with more marginal landscapes by increasing their travel times, feeding times and travel distances, and decreasing their resting times (e.g. Clarke et al. 2002, Asensio et al. 2007, Sha and Hanya 2013). Longer travel times and distances are related to scarcer resource abundance and distribution, and frugivorous diets generally require longer travel times and distances than more folivorous diets (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005). Increased travel times and distances are compensated for by increased feeding and drinking times necessary to maintain homeostasis, and decreased resting times (Chapter 4). Ultimately, however, as shown by the time budget models of Lehmann et al. (2008, 2010), travelling and resting times (i.e.

enforced resting; Korstjens et al. 2010) will limit chimpanzee distribution as a consequence of climate change. The increased amount of travel and the minimally required resting time may not allow for feeding and drinking time compensations (Chapter 4). This study presented a first attempt to characterise savannah chimpanzee daily landscape use using an individual-based modelling approach based on detailed data from Issa, a savannah chimpanzee field study site in Tanzania (e.g. Piel et al. 2017, Stewart et al. 2018). Simulated Issa chimpanzees spent substantial amounts of their daytime on travel, and only minimal amounts on feeding, resting, nesting and drinking. Consequently, travel distances were large, and food and water intake were low. At the end of a model run, Issa chimpanzees had highly negative energy and hydration budgets, and positive fatigue budgets, indicating that maintaining homeostasis in savannah landscapes was difficult. Issa chimpanzees used a wide range of vegetation features and micro-climates in selecting a site for a specific activity, but forest vegetation types were preferred, and the micro-habitat characteristics observed in forest patches were used wherever possible. Inter-individual variability between chimpanzees in the Issa model was large, indicating that some individuals were more successful in maintaining homeostasis and adapting to marginal savannah environments than others. Similar to the generic model, this inter-individual variation could only partly be attributed to model stochasticity (Chapter 4, p. 124), and highlighted that chimpanzees in marginal savannahs faced particular challenges. This leads to the assumption that additional adaptations and behavioural flexibility are necessary to safeguard savannah chimpanzee survival.

Even though published data on savannah chimpanzees are few, it is possible to put the model findings into perspective by comparing them to available data of other savannah chimpanzee field study sites. At Fongoli, Senegal, Pruetz and Bertolani (2009) showed that savannah chimpanzees spent 62% of their active day resting, 25% feeding, and 11% travelling (Table 4.11, Chapter 4). In a later study, Pruetz and Herzog (2017) showed that Fongoli chimpanzees spent on average 14% on travel, 40% on feeding and 46% on resting across burned, unburned and partially burned habitat conditions (Table 4.11, Chapter 4). When including only the active day range for Issa (i.e. the entire day minus the time spent nesting), simulated chimpanzees in the Issa model generally spent similar amounts of time on feeding (i.e. 25.6%), but remarkably more time on travelling (i.e. 51.8%) and less time on resting (i.e. 22.4%). This finding could potentially be attributed to the ‘extreme’ climatic conditions at Fongoli, which are more harsh (i.e. hotter, drier) than those modelled for Issa, forcing the Fongoli chimpanzees to rest more and travel less (Pruetz and Bertolani 2009). Fongoli chimpanzees also included a wider range of food items in their diets, such as unripe fruit (Wessling et al. 2018a), which may allow them to travel less and rest more. Differences may also be a result of the circular movement patterns observed for chimpanzees simulated in the Issa model; Shorter travel times for Fongoli chimpanzees may indicate more goal-directed travel and knowledge of the environment, and thus more effective travel routes. Higher cognitive abilities for memory and knowledge of the environment are not currently included in the Issa model, and simulated chimpanzees could not see more than 100m ahead at any one time.

The Issa model presented new insights into food intake, water intake, fatigue budgets and daily path lengths for savannah chimpanzees in a realistic savannah environment. It is generally assumed that chimpanzees in savannah environments have to travel longer distances in order to acquire their necessary resources due to the great resource seasonality and distribution in savannah environments (e.g. Moore 1996, Hunt and McGrew 2002). The long daily path lengths reported for the chimpanzees simulated in the Issa model are, therefore, within expectations.

Water limitations are likely a strong selective pressure for (savannah) chimpanzee survival (Wessling et al. 2018a, Wessling et al. 2018b). Wessling et al. (2018a, 2018b) showed that Fongoli chimpanzees experienced extensive periods of dehydration stress (as measured in urinary creatinine and cortisol levels) due to constraints in water availability. This finding supports the negative hydration budgets presented for the modelled savannah chimpanzees at Issa. Fongoli chimpanzees showed variable dehydration stress throughout the year, with increasing stress and dehydration levels during the dry season (Wessling et al. 2018a, Wessling et al. 2018b). As the Issa model simulates savannah chimpanzees in dry season conditions, this finding additionally supports Issa chimpanzees' negative hydration budgets. This suggests that hydration budgets may be less negative for Issa chimpanzees in other seasons, and future models could explore this prediction in more detail.

Wessling et al. (2018a, 2018b) also assessed Fongoli chimpanzees' energy budgets. Energy balance, as measured by the urinary c-peptide by-product of insulin, varied with food availability, and lower food availability resulted in lower energy balances (Wessling et al. 2018a, Wessling et al. 2018b). Nonetheless, Fongoli chimpanzees did not exhibit extensive periods of nutritional stress (Wessling et al. 2018a, Wessling et al. 2018b), which likely indicates overall positive energy budgets. This contrasts with the results for the Issa model, where Issa chimpanzees on average had highly negative energy budgets and only ~20% of individuals were able to maintain a positive energy balance. A three-fold of reasons could potentially explain this incongruency. First, this difference may indicate that Fongoli chimpanzees resort to unique behavioural adaptations such as using additional dietary items (e.g. unripe fruit items, prosimian prey), and/or including other high-quality food sources (e.g. pith, cambium, termites), which are not currently included in the Issa model (e.g. Pruetz and Bertolani 2007, Bogart and Pruetz 2008, Wessling et al. 2018a). On the other hand, differences may result from modelling assumptions and scaling of energy loss and gains due to lack of quantitative data for the units of these budgets. More detailed insights into the actual energy gained and lost over specific time periods and by performing different behavioural activities might update the observed energy budgets for Issa, indicating that the Issa environment is not as unsustainable and/or unfavourable as it currently seems in the model. Nevertheless, chimpanzees are able to cope with negative energy balance days, and studies at the dense forest site Taï, Ivory Coast, showed that even though energy balances are generally positive, days with negative energy balances are also common and strongly linked to fruit availability (N'guessan et al. 2009. Wessling et al. 2018b). The Issa model only simulates average energy budgets over a single day (i.e. 24 hours) in the dry season; future models should assess how Issa chimpanzee energy budgets vary across multiple days and under different seasonal conditions.

Modelled Issa chimpanzees used a wide range of vegetation types, but preferred forest vegetation types overall and for each behaviour. The most commonly selected vegetation patches had vegetation features and micro-climate characteristics typical of forest vegetation types. This did not indicate that simulated Issa chimpanzees only used forest vegetation types, as these micro-habitat characteristics were also observed in other vegetation types such as woodland. Rather, modelled individuals preferentially selected locations in forest vegetation types wherever possible, or otherwise locations that closely resembled these forest sites. Following Stewart (2011), these findings could presumably be attributed to predator avoidance and thermoregulation. Although these results may follow in part from model rules based on Issa field data and literature (e.g. Hernandez-Aguilar 2009, Stewart 2011, Russak 2014, GMERC *unpublished data*), wide range use and forest preferences are also observed for other savannah chimpanzee field study sites. For example, across various savannah field study sites, chimpanzees used forest, woodland and more open vegetation types for feeding (e.g. Schoeninger et al. 1999) and nesting (e.g. Baldwin et al. 1981; Stewart 2011), but chimpanzees preferred forest vegetation types for nesting (e.g. Pruetz et al. 2008, Stewart 2011). At Fongoli, chimpanzees used a wide range of vegetation features for nesting, and site selection was attributed to the antivector hypothesis, the thermoregulation hypothesis, and the anti-predation hypothesis (Stewart 2011). The finding that simulated Issa chimpanzees preferred savannah grassland for travel could potentially be attributed to the minimal amount of grassland present at Issa (i.e. 0.1%).

The Issa model thus presents a realistic picture of chimpanzee landscape use in marginal savannahs, and highlights new insights into various aspects of savannah chimpanzee behavioural ecology. As landscape use patterns of savannah chimpanzees were substantially different from observed patterns of landscape use for chimpanzees in forested environments which are thought to be more stable and less challenging (Chapter 4; but see Wessling et al. 2018b for a debate), model findings argue in favour of remarkable chimpanzee behavioural adaptability. Savannah chimpanzees are able to adjust their activity budgets, daily path lengths and vegetation type usage to suit their current landscape, with energy budgets, hydration budgets, fatigue budgets, food and water intake following accordingly, even when their environments are scarce and seasonal. Patterns of adaptation shown by savannah chimpanzees are largely similar to other primates' responses to habitat fragmentation (Chapter 4, p. 120; e.g. Clarke et al. 2002, Ganas and Robbins 2005; Asensio et al. 2007). Regardless of their ability to adjust their landscape use patterns to marginal savannahs, the Issa model showed that savannah chimpanzees faced particular survival challenges, e.g. highly negative energy and hydration budgets, positive fatigue budget and large inter-individual variability are probably not sustainable over prolonged periods of time. Observed behavioural flexibility at savannah chimpanzee field study sites may partly overcome these challenges, e.g. hunting with spears to gain access to prosimian prey (Fongoli: Pruetz and Bertolani 2007), using caves or soaking in pools of water at the hottest times of day for thermoregulation (Fongoli: Pruetz 2007, Pruetz and Bertolani 2009), including additional items into their diet (Fongoli: Wessling et al. 2018a, Issa: Hernandez-Aguilar et al. 2007), using moonlit nights for additional feeding and travel activities, social behaviour and long-distance vocal communications (Fongoli: Pruetz 2018), and digging wells for drinking water (Semliki: Hunt and McGrew 2002). The inclusion of these behaviours into the Issa model would explore their effects in more detail. In their already marginal habitat, savannah chimpanzees are especially susceptible to the impending habitat degradations and climate change. Appropriate and efficiently focused mitigation plans and strategies should therefore be developed to safeguard savannah chimpanzees from reaching critically low densities. As simulated Issa chimpanzees were reliant on forest vegetation, the Issa model showed that forest could be regarded as critical habitat for savannah chimpanzees. Protecting forest vegetation types within savannah chimpanzee habitats should therefore present a priority area for savannah chimpanzee conservation. However, as forest vegetation types within savannah landscapes are often already scarce, conservationists should furthermore focus on protecting those parts of the environment that include micro-habitats comparable to forest, and thus those with optimal availability of resources. The Issa model could additionally aid in the development of effective protection strategies by facilitating predictions on the effects of future landscape change scenarios.

Developing realistic models of (savannah) chimpanzee landscape use

To evaluate how well the generic chimpanzee landscape use model of Chapter 4 was able to accurately predict savannah chimpanzee landscape use patterns at a realistic, present-day chimpanzee environment based on general chimpanzee literature only, and thus to establish how the inclusion of site-specific details of particular study sites influences model output on chimpanzee landscape use, savannah chimpanzee findings from the generic model were compared with findings of the Issa model. Significant differences were observed in model output for both models, and using the model output of the generic model as a baseline, the Issa model showed a 34% decrease in time spent feeding and drinking, a 1% decrease in time spent resting, a 2% increase in time spent nesting, a 31% increase in time spent travelling, a 70% increase in daily path lengths, a 110% decrease in energy budgets, a 157% decrease in hydration budgets, a 141% increase in fatigue budgets, a 34% decrease in food intake, a 35% decrease in water intake, a 22% decrease in time spent in forest, an 88% increase in time spent in woodland, and a 100% decrease in time spent in grassland. Slightly more individuals (i.e. ~20% as compared to ~14%) were able to maintain homeostasis within the Issa model. Site selection was largely similar for the two models: forest vegetation types were preferred, and more open vegetation types were generally avoided, and simulated chimpanzees predominantly restricted their activities to locations with vegetation features and micro-climates similar to those encountered in forest. Issa chimpanzees used a wider range of micro-habitat characteristics for nesting. Because the Issa model was based on literature and field-collected data from Issa, Tanzania, this model presented more detailed insights into savannah chimpanzee daily habitat use than the generic model. Differences between the two models could be attributed to the greater extremity of the Issa environment as compared to the simulated environments of the generic model (i.e. less forest vegetation available), the increased stochasticity in model environments for the generic model (i.e. stochasticity in spatial vegetation arrangement), and/ or the usage of site-specific data in outlining the model environment (i.e. home-range size, climate, vegetation cover, spatial vegetation arrangement, and micro-habitats) and model rules (i.e. where to feed, drink, nest and rest) for the Issa model as compared to the generic model based on averaged data across multiple chimpanzee study sites. Similarly, greater variation (i.e. standard deviations) between Issa model individuals as compared to savannah chimpanzees simulated in the generic model is likely due to variations in model environments (i.e. home-range size, climate, vegetation, presence of preferred resources, micro-habitats) and behavioural model rules between the generic and Issa models.

Even though the differences in model output for the Issa model and the generic model are substantial, when compared to findings for chimpanzees in forested environments (Chapter 4), the models show similar trends. Both the Issa model and the generic model showed that savannah chimpanzees spent less time feeding, drinking, resting and nesting, spent more time travelling, travelled longer distances, had lower energy budgets, hydration budgets, food intake and water intake, had higher levels of fatigue, and were more reliant on forest vegetation as compared to chimpanzees in dense forests and forest mosaics. Both models implied that savannah chimpanzees faced particular survival challenges. These findings indicate that the generic chimpanzee landscape use model could be verified and was able to accurately predict the general trends and present-day challenges faced by savannah chimpanzees. When one aims to assess how flexibly chimpanzees are generally able to adapt their behavioural patterns to changing environments and how susceptible they are to change, the generic chimpanzee landscape use model provides a sufficiently detailed option. However, when the aim is to explore the effects of site-specific habitat alterations on an existing chimpanzee population, site-specific chimpanzee landscape use models based on field-collected data for a particular site (such as the Issa model) present a more reliable alternative. This result confirms the expectation that only the Issa model includes a sufficient amount of detail to present a realistic picture of chimpanzee landscape use at this site. This argues that site-specific data on the spatial arrangement, coverage and structural characteristics of different vegetation types, and chimpanzee preferences for specific vegetation features and micro-climates in selecting a site for a specific behaviour are important variables in the development of site-specific chimpanzee landscape use models. Hence, even though similar in general trends, the generic model did not encompass sufficient detail to reflect ‘real-life’ situations at specific study sites. Nonetheless, both models provide important assets for scenario testing of future climate and landscape changes on general and site-specific scales (see below). The Issa and generic model findings outline how much detail is enough for a specific chimpanzee study site to develop a reliable predictive model of chimpanzee landscape use, which can be used as a guideline for the design of future site-specific models. This information can be applied to support future conservation efforts of measuring chimpanzee behaviour and landscapes in the most effective and time-efficient way, which allows rapid assessments of the effects of future landscape change scenarios on chimpanzee behaviour and survival, and the development of appropriate mitigation strategies for chimpanzee protection.

Model limitations, implications, and future perspectives

As models are always simplifications of reality (e.g. van der Vaart et al. 2016), the Issa and generic models were subject to certain limitations. For the Issa model specifically, for example, updates in hourly temperatures, rainfall, local temperature and local luminosity based on HOBO weather station and micro-climate data logger data could be used to present more detailed insights on the effects of climatic change on Issa chimpanzee activity budgets, energy budgets and survival. Temperature, rainfall and micro-climates in the Issa model were not currently varied per hour due to comparison reasons with the generic model of Chapter 4. Additionally, the inclusion of behavioural innovations, as well as more detailed data on the exact home-range size, home-range location and population size of the Issa chimpanzees could provide a more in-depth understanding of savannah chimpanzee landscape use patterns. Due to lack of quantitative data, this information was not currently included within the Issa model. Other model improvements include updating model codes for movement, chimpanzee foresight and model run time, and/or adding model codes on grouping, seasonality and varying food quality to reduce the circularity in movement patterns observed for simulated chimpanzees, as well as energy, hydration and fatigue additions, behavioural *where* and *when* additions, updates on number of fruits and amount water per vegetation type, and free and enforced resting time separations. Model improvements were not currently included within the model due to time constraints and/or data shortages, and are outlined in detail for the generic model in Chapter 4 (p. 127).

As outlined in Chapter 4 for the generic model (p. 129), individual-based models on chimpanzee landscape use have important future applications in facilitating predictions on the effects of future climate and landscape change scenarios on chimpanzee behaviour and survival, providing a referential model for hominin landscape use, and presenting a framework for understanding the underlying reasons of behavioural adaptation and innovation to specific environments in hominid evolution through scenario testing. The Issa model could add to this by presenting a realistic, present-day environment in which the predictions of the generic model on the (extent of the) effects of future landscape changes on chimpanzees can be tested. Additionally, as the savannah landscape at Issa is assumed to present a similar environment to those encountered by many Plio-Pleistocene hominins (e.g. Reed 1997, Cerling et al. 2011), findings from the Issa model and published data from other savannah chimpanzee field study sites on how extant chimpanzees currently adapt to marginal savannahs (e.g. Pruetz and Bertolani 2009, Hernandez-Aguilar 2009, Wessling et al. 2018a), provide insights into which behavioural innovations could aid in coping with these otherwise unfavourable environments. With the Issa model, it could be simulated how differently or similarly hominins would have used an existing extant chimpanzee environment. The Issa model could therefore provide an important contribution to chimpanzee conservation in aiding the development of efficient mitigation strategies to safeguard (savannah) chimpanzee survival, as well as to studies on human evolution and origins.

Conclusion

This study aimed to identify the present-day situation and challenges faced by savannah chimpanzees and to explore how well the generic chimpanzee landscape use model of Chapter 4 was able to accurately assess these circumstances by using an individual-based modelling approach based on field-collected data from Issa, a savannah chimpanzee field study site in Tanzania. Due to the inclusion of site-specific data for the Issa model, only the Issa model was predicted to contain a sufficient amount of detail to present a realistic picture on chimpanzee landscape use at this site. In their marginal environments, simulated Issa chimpanzees travelled for long periods of time and over long distances, spent relatively small amounts of time on feeding, drinking, nesting and resting, were reliant on forest vegetation and selective in their site choice for their behaviours, and subsequently had negative energy and hydration budgets, low food and water intake, and positive levels of fatigue. Due to the scarce and seasonal distribution of resources in savannah landscapes, patterns of landscape use differed remarkably from those observed for chimpanzees in forested environments. Whereas the generic model was able to accurately explore these general trends, the Issa model was showed more detailed, site-specific landscape use patterns for chimpanzees at Issa Valley. As the Issa landscape is more marginal than the savannah landscape simulated in the generic model, this accurately resulted in greater difficulties for Issa chimpanzees in managing their time and energy budgets. Findings highlight remarkable chimpanzee behavioural adaptability, i.e. chimpanzees are capable of adapting their activity budgets, vegetation type usage and daily path lengths to suit their current environments even if these environments are marginal, but the low hydration and energy budgets, and the high levels of fatigue indicate that savannah chimpanzees still faced particular survival challenges. Behavioural innovations observed at various chimpanzee study sites may cope with these pressures. As savannah chimpanzees inhabit already marginal landscapes, they are especially susceptible to future landscape change due to continued deforestation, habitat degradation, fragmentation and climate change throughout their range. Similar to the generic model, the Issa model highlighted forest vegetation types as savannah chimpanzee critical habitat, which could aid in the development of effective mitigation strategies for (savannah) chimpanzee protection. Through scenario testing, future model applications for the Issa model include presenting a realistic, present-day environment for assessments of the effects of future environmental changes on chimpanzee behaviour and survival, and for exploring the adaptations of hominins to marginal savannahs.

PART II

EARLY HOMININ LANDSCAPE USE

CHAPTER 6

Individual-based and referential modelling of hominid landscape use: *Ardipithecus*, *Australopithecus* and extant chimpanzees

Abstract

Reconstructing early hominin behaviour remains a daunting challenge for human evolution studies. Using chimpanzee referential modelling, this study investigated how early hominin landscape use changed when their paleoenvironments varied from forest to more open environments, how this differed among early hominins, and between early hominins and chimpanzees. Individual-based models (NetLogo) parameterised based on early hominin evidence combined with findings from chimpanzees (Chapters 2 – 5) identified the activity budgets, path lengths and vegetation type usage for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* across forests, mosaics and savannahs. Models differed from the chimpanzee model (Chapter 4) by including more food items (i.e. USOs for *Ardipithecus*, and USOs and meat for *Australopithecus*, in addition to fruit) and less costly travel patterns for hominins. Model results showed that *Ardipithecus* and *Australopithecus* flexibly altered their landscape use to suit the resource availability of their environments. Similar to chimpanzees, early hominins increased their feeding time, travel time and travel distance, and decreased their nesting and resting time in more open environments. Travel time and distances were far greater in savannahs than in forests and mosaics for all species. However, whilst increased travel times resulted in decreased feeding and drinking times, and highly negative energy and hydration budgets for chimpanzees in savannahs, early hominins were better able to compensate for their increased travel due to their wider dietary breadth and increased locomotor efficiency. All species preferred forest vegetation, but early hominins were able to use open vegetation types more optimally. Species differed in their ability to successfully exploit more open landscapes, which was most evident for *Australopithecus*. Findings emphasise insights into early hominin behaviour and origins, adaptability to change, landscape use variability across species and environments, and chimpanzee referential modelling. Potential future model applications include predicting the impacts of landscape and behavioural changes on hominin survival, and providing a framework for understanding the role of landscapes in hominin evolution.

Keywords: hominins, *Ardipithecus ramidus*, *Australopithecus anamensis*, *Australopithecus afarensis*, agent-based models, referential modelling, habitat selection.

Introduction

One of the most daunting challenges in the study of human origins is the reconstruction of early hominin behaviour (e.g. Mitani 2013, Plavcan 2013, Carlson and Kingston 2014). Unlike skeletal remains, behavioural patterns do not preserve in the fossil record, rendering it difficult to understand the context and evolution of early hominin daily activities and landscape use (e.g. Mitani 2013, Plavcan 2013). Chimpanzees (*Pan troglodytes*) have often been recognised as potential (referential) models for reconstructing early hominin behaviour (e.g. Moore 1996, Stanford 2012, Mitani 2013). Chimpanzees not only show close phylogenetic relatedness to hominins, they also display many morphological similarities and are observed to inhabit a similar variety of environments including challenging habitat mosaics and marginal savannahs (e.g. Moore 1996, Mitani 2013). Comparisons with chimpanzee landscape use can provide new insights into how early hominins would have used their landscape differently or similarly to extant chimpanzees, how they would have responded to environmental changes in their habitats, and how they would have been able to adapt and survive in even more open areas.

Hominins are all members of the human lineage, including both modern humans today (*Homo sapiens*) as well as their extinct fossil relatives (e.g. Coward 2014, Boyd and Silk 2012, Su 2013). Hominin fossils date back to about 7 million years ago (Ma) and include a variety of species within the genera *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Australopithecus*, *Kenyanthropus*, *Paranthropus*, and *Homo* (e.g. Boyd and Silk 2012, Fleagle 2013, see Smithsonian Institution (2018) for an up-to-date overview; Table 6.1). Hominin fossil localities include a variety of sites in Eastern Africa (i.e. in Tanzania, Kenya and Ethiopia), Central Africa (i.e. in Chad), and Southern Africa (i.e. in South Africa), as well as in Europe and Asia (e.g. Boyd and Silk 2012, Fleagle 2013, Smithsonian Institution 2018; Figure 6.1). When referring to 'early' hominins, often the earliest (African) members of the human lineage are considered, such as *Sahelanthropus*, *Orrorin*, *Ardipithecus* and early *Australopithecus* (e.g. Simpson 2013, Hammond and Ward 2013).

Environmental reconstructions of hominin fossil localities have been presented to explore the paleoenvironments inhabited by early hominins. For this purpose, a variety of methods have been used and most are based on comparisons with present-day environments (Andrews and Bamford 2008). Methods include reconstructions based on: stable carbon and oxygen isotope analyses from paleosols (e.g. Wynn 2000, Aronson et al. 2008, Cerling et al. 2011); buccal dental microwear analyses of early hominin teeth (e.g. Estebaranz et al. 2012); adaptations of faunal assemblages associated with early hominins (e.g. Reed 1997, WoldeGabriel et al. 2009); tectonic processes (Bailey et al. 2011, Reynolds et al. 2011); the fossil record of presence/ absence and relative abundance of pollen and phytoliths (e.g. Bonnefille et al. 2004, WoldeGabriel et al. 2009); and fossil geological surroundings (e.g. WoldeGabriel et al. 2009). Generally, paleoenvironmental reconstructions have considered early hominins to have inhabited mosaic woodland-grassland landscapes, although temporal and spatial differences in exact environments exist between sites, species and reconstruction methods, and interpretations range from forests to open savannah grassland environments (e.g. Reed 1997, Aronson et al. 2008, Cerling et al. 2011). Changing landscapes in the past are expected to have played a vital role in human evolution (e.g. Bobe et al. 2002, Potts 2007).

Table 6.1. Hominin genera, species and timeline (Ma = million years ago, ka = thousand years ago) based on reviews presented by Boyd and Silk (2012), Fleagle (2013), and the Smithsonian Institution (2018). It should be noted that the presented timeline outlines the current dating of the various hominin fossils. Other published literature may present a slightly different timeline, which can be attributed to differing reconstruction approaches and/or the continuous update of the fossil record when new evidence becomes available.

Genus	**Species**	**Timeline**
Sahelanthropus	*tchadensis*	7 – 6 Ma
Orrorin	*tugenensis*	6.2 – 5.8 Ma
Ardipithecus	*kadabba*	5.8 – 5.2 Ma
	ramidus	4.4 Ma
Australopithecus	*anamensis*	4.2 – 3.9 Ma
	afarensis	3.8 – 2.9 Ma
	bahrelghazali	3.5 – 3.0 Ma
	africanus	3.3 – 2.1 Ma
	garhi	2.5 Ma
	sediba	2 Ma
Kenyanthropus	*platyops*	3.5 – 3.2 Ma
Paranthropus	*aethiopicus*	2.7 – 2.3 Ma
	boisei	2.3 – 1.2 Ma
	robustus	1.8 – 1.2 Ma
Homo	*habilis*	2.4 – 1.4 Ma
	rudolfensis	1.9 – 1.8 Ma
	ergaster	1.9 – 1.4 Ma
	erectus	9.9 Ma – 143 ka
	heidelbergensis	700 – 200 ka
	floresiensis	100 – 50 ka
	neanderthalensis	400 – 40 ka

Fossil remains of early hominins have been used to reconstruct as much detail as possible on the many aspects of early hominin behavioural ecology. Skeletal remains have been studied intensively to investigate the early hominin way of life, including locomotion (e.g. Lovejoy et al. 2009, Ruff et al. 2016), diet (e.g. Ungar 2004, Sponheimer et al. 2013), social behaviour and social systems (e.g. Shultz et al. 2014, White et al. 2015), tool use (e.g. Domínguez-Rodrigo et al. 2005, McPherron et al. 2010), brain size (e.g. Boyd and Silk 2012, White et al. 2015), activity budgets (e.g. Bettridge 2010, Dunbar and Gowlett 2014), and reproductive behaviour (e.g. Boyd and Silk 2012, White et al. 2015). Early hominin morphological adaptations to bipedality have been given special attention, with studies focusing on the reduced energetic costs and increased thermoregulatory advantage of early hominin terrestrial bipedal locomotion, and the subsequent reduced thermoregulatory stress, higher tolerance to open areas, and wider access to novel, high-quality and/or isolated food items, such as underground storage organs (USOs) and scavengable meat from carcasses (e.g. Laden and Wrangham 2005, Pontzer et al. 2009, Lieberman 2015, Pobiner 2015). Within the early hominins, 'later' hominins such as *Australopithecus* are considered as being better adapted to efficient terrestrial bipedalism than the 'earlier' hominins such as *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (e.g. Simpson 2013, Kozma et al. 2018). It should be noted, however, that a more significant shift towards efficient terrestrial bipedalism only occurred later in the hominin lineage, i.e. for the genus *Homo* (e.g. Lieberman 2015).

To provide more detailed insights into early hominin behaviour, chimpanzees have often been used as referential models for the reconstruction of hominin behavioural evolution (e.g. Mitani 2013). Findings on chimpanzees have also been used to reconstruct the behaviour of the last common ancestor of living apes and humans (e.g. Moore 1996, McGrew 2010, Pilbeam and Lieberman 2017). When using a referential modelling approach in exploring behavioural evolution, the behaviour of an extinct species, i.e. the referent, is reconstructed by using indirect evidence of another, extant species, i.e. the model (e.g. Tooby and DeVore 1987). Two types of referential models are currently recognised, and these are labelled as 'true analogies' and 'best extant models' (e.g. Jolly 2013; Chapter 1). Of these two referential modelling types, best extant models focus on living species that are closely related phylogenetically to the fossil species in question (e.g. Jolly 2013). Various species have been used as referential models for early hominins, including baboons, bonobos, extant hunter-gatherers and social carnivores, but chimpanzees have been studied most extensively in this respect (e.g. Tooby and DeVore 1987, Jolly 2013, Mitani 2013).


African Homeland

Fossil trail. Many kinds of hominids lived in Africa 6 million to 2.5 million years ago, before *Homo* appeared.

Figure 6.1. Hominin fossil localities in Africa before the appearance of *Homo*. Figure republished with permission of AAAS (see https://www.sciencemag.org/help/reprints-and-permissions), from Gibbons (2002, p. 1216). Similar to the rationale outlined for Table 6.1, within the figure, some fossil species differ in name from those outlined above, and/or some fossil species are not yet included. This can be attributed to the continuous update of the fossil record when new evidence becomes available.

Criticism on this approach exists, focusing either on referential modelling per se, or on the ‘chimpocentrism’ of early hominin behavioural reconstructions (e.g. Tooby and DeVore 1987, Sayers and Lovejoy 2008). For referential modelling, in an influential chapter, Tooby and DeVore (1987) argued that referential models are inferior to conceptual models (see also Moore 1996). Whereas conceptual models are based on evolutionary theory, referential models are based on homology and analogy, and without exact guidelines on how to select a living species as a referential model for extinct hominins, the choice of such models is arbitrary (Tooby and DeVore 1987). It is therefore difficult to highlight important differences between model and referent, and referential models tend to focus on observed similarities (Tooby and DeVore 1987). This can be problematic when one aims to explore human evolution and human uniqueness (Tooby and DeVore 1987). Tooby and DeVore (1987) therefore stressed the usage of conceptual models over referential models. Referential models based on various individual taxa should be used for comparative studies to determine relationships and theories for the conceptual model, and should be regarded as ‘data’ rather than ‘models’ (Tooby and DeVore 1987). However, as argued by Stanford (2012, p. 141) “the distinction between referential and conceptual models is something of a false dichotomy”, as knowledge of one, i.e. the referential model, is needed to inform and create the other, i.e. the conceptual model. Therefore, one should not be favoured over the other and combining the two modelling approaches may be most productive in unravelling hominin behavioural evolution (Moore 1996). For chimpanzees, criticism mostly focuses around the overemphasis on behavioural similarities between chimpanzees and early hominins, rather than focusing on differences (Sayers and Lovejoy 2008, Sayers et al. 2012). Furthermore, the focus on chimpanzees may leave the applicability of other species underemphasised (e.g. Sayers and Lovejoy 2008). Although Sayers and Lovejoy’s (2008) notion that chimpanzees are not early hominins is fair, the striking similarities between chimpanzees and early hominins should not be overlooked: Chimpanzees are, amongst others, closely related phylogenetically to humans, share many morphological adaptations with hominins, inhabit similarly challenging environments, make use of both terrestrial and arboreal substrates, use tools, hunt, and share food (e.g. Moore 1996, Stanford 2012, Mitani 2013). However, contrasts are also acknowledged and include differences in, for example, locomotor efficiency, diet and morphological adaptations (e.g. Sponheimer et al. 2006, Pontzer et al. 2009, Almécija et al. 2010). These differences do not indicate that chimpanzees should not be used as referential models. Rather, chimpanzee referential models are still very useful in early hominin behavioural reconstructions, but differences between chimpanzees and hominins should also be considered, as it is these differences that might explain their divergence (e.g. Sayers and Lovejoy 2008, Mitani 2013). Similarly, data from other species, such as bonobos, could also prove useful for early hominin behavioural reconstructions (e.g. Zihlman 1996, Sayers and Lovejoy 2008). Again, a combination of approaches might be most efficient for shedding light onto human origins. As with all models, caution in interpreting results is warranted, as models are always simplifications of real-life systems (e.g. Moore 1996, van der Vaart et al. 2016).

As chimpanzee referential models are thus sensible, findings and interpretations on (savannah) chimpanzee landscape use from Chapter 4 and Chapter 5 can provide novel information for early hominin landscape use reconstructions. The individual-based modelling approach used to simulate chimpanzee landscape use along an environmental gradient from forest to more open and mosaic savannahs, showed that chimpanzees were able to adapt their activity budgets, daily path lengths and vegetation type usage to suit their landscape, although behavioural adaptations became increasingly more difficult when the environment became more open and additional, novel behaviours were necessary to safeguard their survival. By adapting the chimpanzee individual-based model of Chapter 4 to suit the behaviours, landscapes and characteristics of early hominins wherever feasible, and by using the chimpanzee findings from Chapter 5 for interpretations, it is possible to investigate how flexibly early hominins may have been able to adapt to the environmental changes of their time. This may provide insights into how early hominins would have eventually colonised and coped with inhabiting even more open areas than extant savannah chimpanzees (e.g. Sponheimer et al. 2006).

Using chimpanzees as referential models requires the outline of clear assumptions and decisions (e.g. Moore 1996, McGrew 2010). For instance, this study focuses on East African hominins only, as East Africa is the only region where hominin fossil localities and extant chimpanzee habitats overlap. Furthermore, chimpanzees are suggested to provide best referential models for *early* hominins, as these are considered most ‘chimpanzee-like’ due to their similar morphological and physiological characteristics (e.g. Moore 1996, Zihlman 1996, Stanford 2012). As such, early hominins are expected to have been subject to similar selective pressures, especially with regards to their assumed forest-to-savannah transition and the apparent link to the adaptations of forest versus savannah chimpanzees (Collins and McGrew 1988, Moore 1996). This study concentrates on early hominins that inhabited east African environments before 3 Ma, which leaves *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus kadabba*, *Ardipithecus ramidus*, *Australopithecus anamensis*, *Australopithecus afarensis*, *Australopithecus bahrelghazali* and *Kenyanthropus platyops*. Chimpanzees are considered as best referential models for *Ardipithecus ramidus*, *Australopithecus anamensis*, and *Australopithecus afarensis,* as these are the best studied early hominins (e.g. Reed 1997, Ungar 2004, Stanford 2012). Some studies argue that there is no real divergence between *Australopithecus anamensis* and *Australopithecus afarensis* (e.g. Boyd and Silk 2012, Fleagle 2013). In consideration of this debate, *Australopithecus anamensis* and *Australopithecus afarensis* evidence is combined and investigated as a single ecological species in this study.

This study aims to investigate how early hominin (i.e. *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) activity budgets, energy budgets, and daily path lengths would have changed when their habitats differed along an environmental gradient from forests to more open landscapes, and how this varied among early hominin species and between early hominins and chimpanzees, using an individual-based modelling approach based on evidence from early hominins and findings from chimpanzees (Chapter 2 – Chapter 5). For early hominins, it is hypothesised that: ***i)*** As was the case with chimpanzees (Chapter 3), differences in vegetation composition and climatic conditions at hominin localities can be used to provide a quantitatively measurable definition of the various environments used by early hominins, characterising dense forests, forest mosaics and savannahs; ***ii)*** Just like chimpanzees (Chapter 2), early hominins would have preferred specific sites for specific activities based on optimising their thermoregulation, predator avoidance, and foraging efficiency, and preferred locations for feeding, drinking, nesting, resting, and travel would therefore have contained comparable vegetation features and micro-climate characteristics as those preferred by chimpanzees; and ***iii)*** Similar to predictions for chimpanzees (Chapter 4), along an environmental gradient ranging from forest to marginal savannahs, early hominins would have increased their daily travel distance, as well as feeding, travelling and drinking times, and would have had less time available for unrestrained resting when the environment became more open and scarce. Time spent nesting would have been similar across environments, due to the inability to perform other activities at night. For the differences between early hominins and chimpanzees, it is hypothesised that: ***iv)*** Even though most preferences in site selection for specific activities would have been similar for early hominins and modern chimpanzees, early hominins would have been able to more optimally use open vegetation types (e.g. woodland, savannah grassland), due to their energetically less costly locomotor patterns (i.e. bipedality). Early hominins' decreased energy expenditure and bipedal posture reduced exogenous heat gain and thermal stress in open areas (e.g. Wheeler 1984, Lieberman 2015), and led to wider access to high-quality and/or isolated food resources. Consequently, early hominins would, just like chimpanzees (Chapter 4), have preferentially used forest vegetation types for nesting, drinking and resting, but in contrast to chimpanzees, would have used both forest and more open vegetation types for travelling and feeding; and ***v)*** As another consequence of early hominins' reduced thermoregulatory stress and wider access to open area resources, early hominins would have spent less time feeding, more time travelling, and would have travelled longer daily distances than chimpanzees in order to access high-quality and isolated food items (e.g. Coward 2014; Chapter 4). Due to assumed morphological, physiological and behavioural similarities, time spend drinking, resting and nesting would have been similar to chimpanzees (Chapter 4). Following a similar rationale, it is further hypothesised among the early hominin species that: ***vi)*** *Ardipithecus ramidus* would have been more restricted to closed vegetation types (i.e. forest, woodland) and would have used more open vegetation types less optimally than *Australopithecus anamensis*/ *afarensis* due to the latter's greater morphological commitment to terrestrial bipedal locomotion, and vegetation type usage would have differed between the two species; and ***vii)*** As a result of the 'gradient' in bipedal locomotion efficiency, *Ardipithecus ramidus* would have spent more time feeding, less time travelling, and would have travelled shorter daily distances than *Australopithecus anamensis*/ *afarensis*. Three individual-based models are developed to explore these questions, and all models follow specific rules on hominid behaviour and habitat. The first model, i.e. the generic chimpanzee landscape use model, investigates chimpanzee landscape use in dense forests, forest mosaics and savannahs based on general chimpanzee literature, and is outlined in Chapter 4. The *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* landscape use models explore early hominin habitat use across various environments and were adapted from the generic chimpanzee landscape use model to suit the behaviour, characteristics and environments of early hominins based on evidence from published hominin literature. By using chimpanzees as a referential model for early hominin behavioural reconstructions, this study is able to provide new insights into early hominin origins and landscape use. Model findings can be used to predict the impacts of landscape changes on hominin behaviour, to evaluate the outcomes of different behavioural strategies on hominin survival, and to provide a framework for understanding the underlying role of landscapes in early hominin adaptation and evolution.

Methods

Study species

This study focused on two early hominin species: *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*. *Ardipithecus ramidus* fossils have been located at a number of sites in Ethiopia (i.e. Aramis, Gona) and Kenya (i.e. Tugen Hills), and *Australopithecus anamensis/ afarensis* fossils have been found at various sites in Ethiopia (e.g. Hadar, Afar region, Awash Valley, Omo, Asa Issie), Kenya (e.g. Kanapoi, Allia Bay, Turkana, Koobi Fora) and Tanzania (i.e. Laetoli) (e.g. for review: Boyd and Silk 2012, Hammond and Ward 2013, Simpson 2013). The *Ardipithecus* and *Australopithecus* models created in this study were based upon (and compared to) the generic chimpanzee (*Pan troglodytes*) landscape use model of Chapter 4, which treated all four chimpanzee subspecies (i.e. *P. t. verus*, *P. t. ellioti, P. t. troglodytes, P. t. schweinfurthii*) equally.

Early hominin data collection and analyses

To provide insights into *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* landscapes, behaviour and characteristics, this study conducted an extensive literature review of publications on early hominin behavioural ecology and fossil localities. Reviewed publications included peer-reviewed literature, such as articles, journals, books and book chapters. Using Web of Science, relevant literature was searched using the key words '*Ardipithecus ramidus*', '*Australopithecus anamensis*', and '*Australopithecus afarensis*', in combination with search terms such as 'habitat', 'landscape', 'environment', 'climate', 'vegetation', 'behaviour', 'ecology', 'feeding', 'drinking', 'nesting', 'resting', 'travel', 'activity budget', 'energy', 'hydration', 'fatigue', 'home-range size', and 'population size'.

For each relevant publication encountered, this study noted as much detail as possible on the early hominins, starting with species name and fossil locality whenever presented. To assess *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* environments, details were recorded on the vegetation cover, spatial vegetation arrangement, vegetation features, climate and micro-climates of their habitats wherever available. Based on the chimpanzee landscape class definitions and literature-based landscape descriptions presented in Chapter 3, it was furthermore assessed whether *Ardipithecus* and *Australopithecus* environments could be categorised into hominin typical dense forest, forest mosaic and savannah landscapes. In addition, for

Ardipithecus ramidus and *Australopithecus anamensis*/ *afarensis* behaviours, wherever possible details were recorded on feeding, drinking, nesting, resting and travel patterns, as well as on *where* and *when* these behaviours were performed in relation to vegetation cover, climate, vegetation features, micro-climates, time of day and internal states (e.g. energy, hydration, fatigue). Details were also noted on other relevant early hominin characteristics whenever encountered, including data on home-range size, population size, body size, social systems, and energy, hydration and fatigue gains and losses.

As results highlighted that specific data on the behaviour, environments and characteristics of *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* were not published in as much detail as those presented for chimpanzees, similar statistical analyses to those outlined in Chapter 2 and Chapter 3 could not be performed for the early hominins at this point. As such, the data collected during the literature review were taken together and summarised to present a comprehensive overview on *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* behavioural ecology in as much detail as possible.

Model building

The generic chimpanzee landscape use model, the *Ardipithecus* model, and the *Australopithecus* model were developed using NetLogo (version 5.2.1; Willensky 1999). Chapter 4 outlined details on the data collection, data analyses, model building, model testing, model calibration and sensitivity analysis for the generic chimpanzee model. The *Ardipithecus* and *Australopithecus* models were adapted from this chimpanzee model based on evidence from literature review on early hominins, and model descriptions follow the ODD protocol for communicating individual-based models (Grimm et al. 2006, Grimm et al. 2010; Appendix 4.1). Only one ODD protocol is presented to describe both models. The ODD protocol for the hominin models showed many similarities with the ODD protocol for the chimpanzee model. Model input parameters, the final model code, an overview of the model's 'interface', the specific model adaptations from the chimpanzee model, and the rationale behind the final model code, model rules, decisions and design are presented in Appendix 6.1 – 6.5 for the *Ardipithecus* model, and in Appendix 6.6 – 6.10 for the *Australopithecus* model.

Purpose

The purpose of the *Ardipithecus* and the *Australopithecus* models was to simulate how early hominins would have adapted their patterns of landscape use to cope with changing environments. Specifically, the models aimed to explore how daily activity budgets, path lengths, food intake, water intake, energy budgets, hydration budgets, fatigue budgets, overall and behaviourally preferred vegetation, and site selection changed for *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* when their environments differed in (dense) forest, (forest) mosaic and savannah landscapes. By only changing the percentage of vegetation cover across model runs and keeping all other environmental variables equal, the net effect of changing vegetation cover on early hominin adaptation and survival was investigated (Figure 6.2). Model outputs were compared for the early hominin and chimpanzee models to assess the differences and similarities in landscape-scale habitat use between these hominid species.

Entities, state variables and scales

The *Ardipithecus* and *Australopithecus* models are comprised of two entities: the landscape and the *Ardipithecus/ Australopithecus* individuals, respectively (Figure 6.2, Appendix 6.5, and Appendix 6.10). The landscape was simulated as a realistic early hominin environment and is represented by patches of 50m x 50m. Within the model, wrapping was turned off, meaning that the boundaries are absolute. For each model, forest, mosaic and savannah landscapes were simulated, with relative proportions of different vegetation types set out according to published early hominin literature. Values for climate, home-range size, and fragmentation were kept constant across landscapes. Three vegetation types were parameterised per environment: forest, woodland and grassland. Each vegetation type was assigned a specific range of vegetation features and micro-climates based on the important landscape-scale micro-habitat characteristics presented in Chapter 2 (Table 2.3). Following the generic chimpanzee model, amount of food and water per patch changed throughout a model run as a result of consumption. All other micro-habitat characteristics remained stable.

Within each hominin environment, a population of *Ardipithecus ramidus* or *Australopithecus anamensis/ afarensis* individuals was parameterised. Individuals were represented as a point within the landscape and were randomly placed at nesting locations to simulate a realistic start of the day. Following the generic chimpanzee model, individuals were guided by a main goal of maintaining homeostasis, and had internal states for energy (kCal), hydration (unitless measure), fatigue (unitless measure), current activity, current vegetation type, food intake (# food items, or edible grams), water intake (unitless measure), and distance travelled (m). By performing five key daily activities (i.e. feeding, drinking, nesting, resting and travel), individuals' internal states changed throughout the model run. Similar to the chimpanzee model, *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* individuals had the ability to assess the vegetation features and micro-climates of their current patch and their neighbouring patches. Each model time step represented 10 minutes, and the total model ran for 24 hours (i.e. 144 time steps, from 7am to 7am).

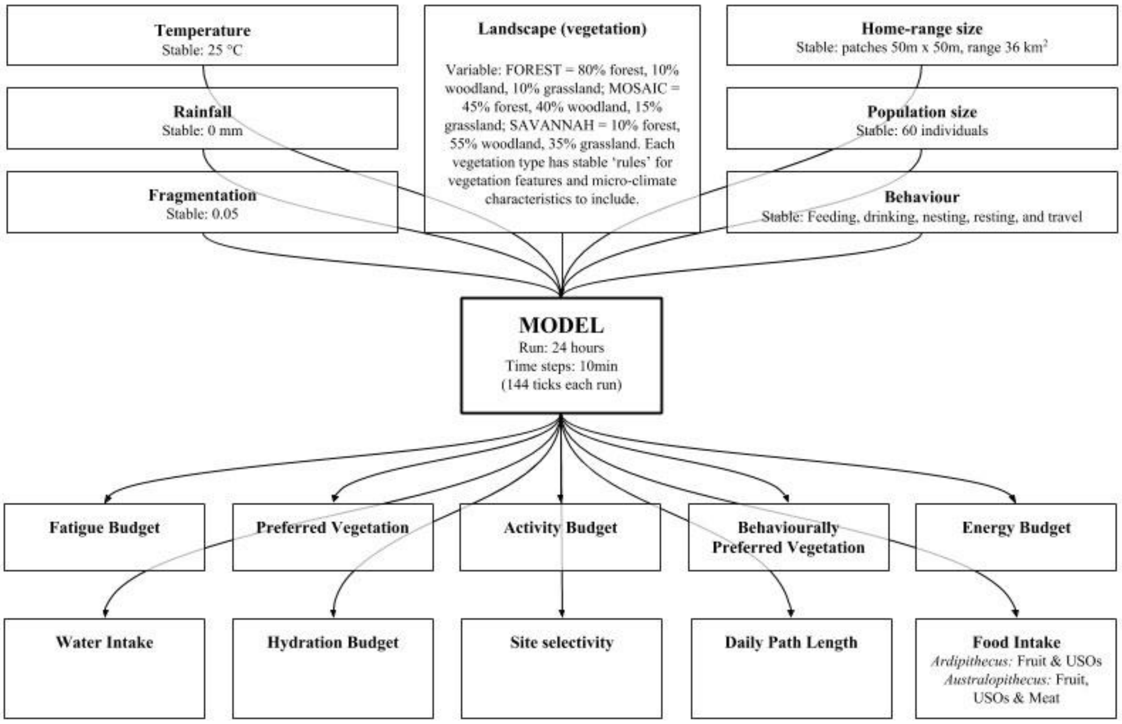

Figure 6.2. Conceptual flowchart of the *Ardipithecus* model and the *Australopithecus* model. The models aim to explore the net effect of changing vegetation cover on early hominin landscape use to assess how hominins would have coped with the environmental changes of their time. Model outputs are compared to examine the differences between species.

Process overview and scheduling

Details on the decision-making process for *Ardipithecus* and *Australopithecus* individuals throughout the model run are outlined in Figure 6.3 and Figure 6.4 (Appendix 6.5 and Appendix 6.10). The process overview and scheduling element of the ODD protocol for the *Australopithecus* and *Ardipithecus* models followed the generic chimpanzee model and is presented in Chapter 4 (p. 97).

Design concepts

The design concepts element of the ODD protocol for the two hominin models was similar to the one presented for the generic chimpanzee model (outlined in Chapter 4, p.

98), apart from the basic principle that guided the development of the early hominin models: As a consequence of morphological, behavioural and physiological similarities between early hominins and chimpanzees, early hominins and chimpanzees would have shown many similarities in their landscape use (e.g. Moore 1996, Stanford 2012, Mitani 2013). However, due to novel morphological and behavioural adaptations in early hominins as compared to chimpanzees, early hominins would have been able to inhabit more open areas more successfully and arboreal environments less efficiently, which would have altered their landscape use patterns (e.g. Ungar 2004, Lieberman 2015).

Initialisation

At the onset of a model run, initial parameter values were set to create realistic virtual early hominin environments. *Ardipithecus* and *Australopithecus* landscapes were simulated according to the vegetation cover, spatial vegetation arrangement, degree of fragmentation, climate and home-range size observed for early hominin fossil localities based on literature review. According to the vegetation cover outlined, model patches were randomly assigned a vegetation type and, accordingly, a set of landscape-scale vegetation features and a micro-climate. Vegetation features and micro-climates were selected randomly within a specified range for each type of land cover. Exact values for vegetation cover, fragmentation, climate, home range size, and ranges for structural vegetation and micro-climate characteristics are outlined within the results section below (Appendix 6. 5 and Appendix 6.10).

The *Ardipithecus* and *Australopithecus* models simulated a population of early hominin individuals according to published hominin population size estimates. Each individual was randomly assigned an initial level for energy, hydration and fatigue. Following the generic chimpanzee model, initial internal state variables for daily path length, food intake and water intake were set to 0, current activity was set to ‘none’, and current vegetation type was set with respect to the patch the individual occupied. Models outlined specific rules on *how much* energy, hydration, fatigue, food intake and water intake should be gained and/or lost at each time step and for each behaviour, as well as on *when* and *where* different activities should be performed, which differed slightly between species. Exact parameter values for these rules were based upon the early hominin literature review and are outlined within the results section below (Appendix 6.5 and Appendix 6.10).

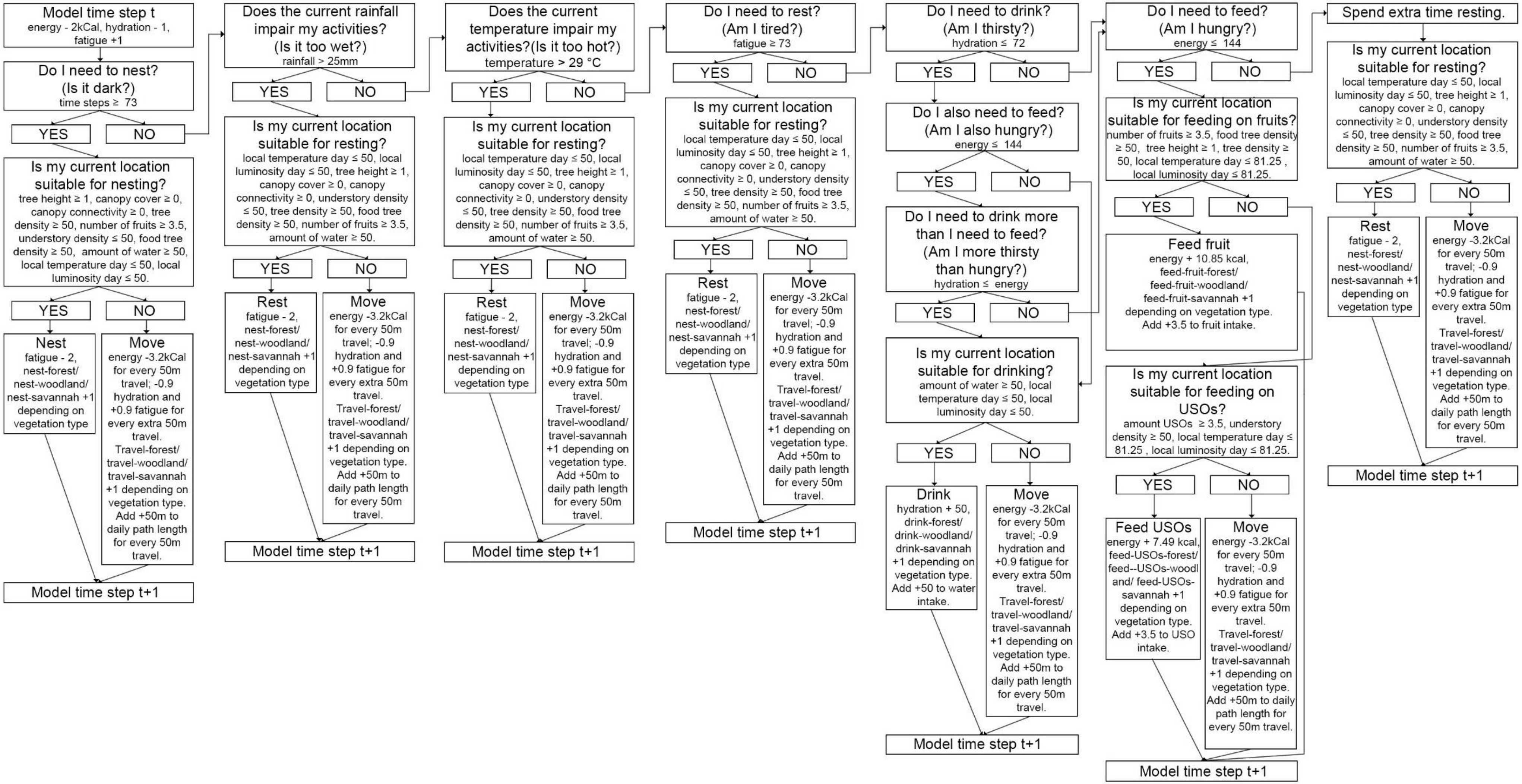

Figure 6.3. Model flowchart for the *Ardipithecus* model, which specifies the decisions that have to be made by each individual at each time step, and its consequences.

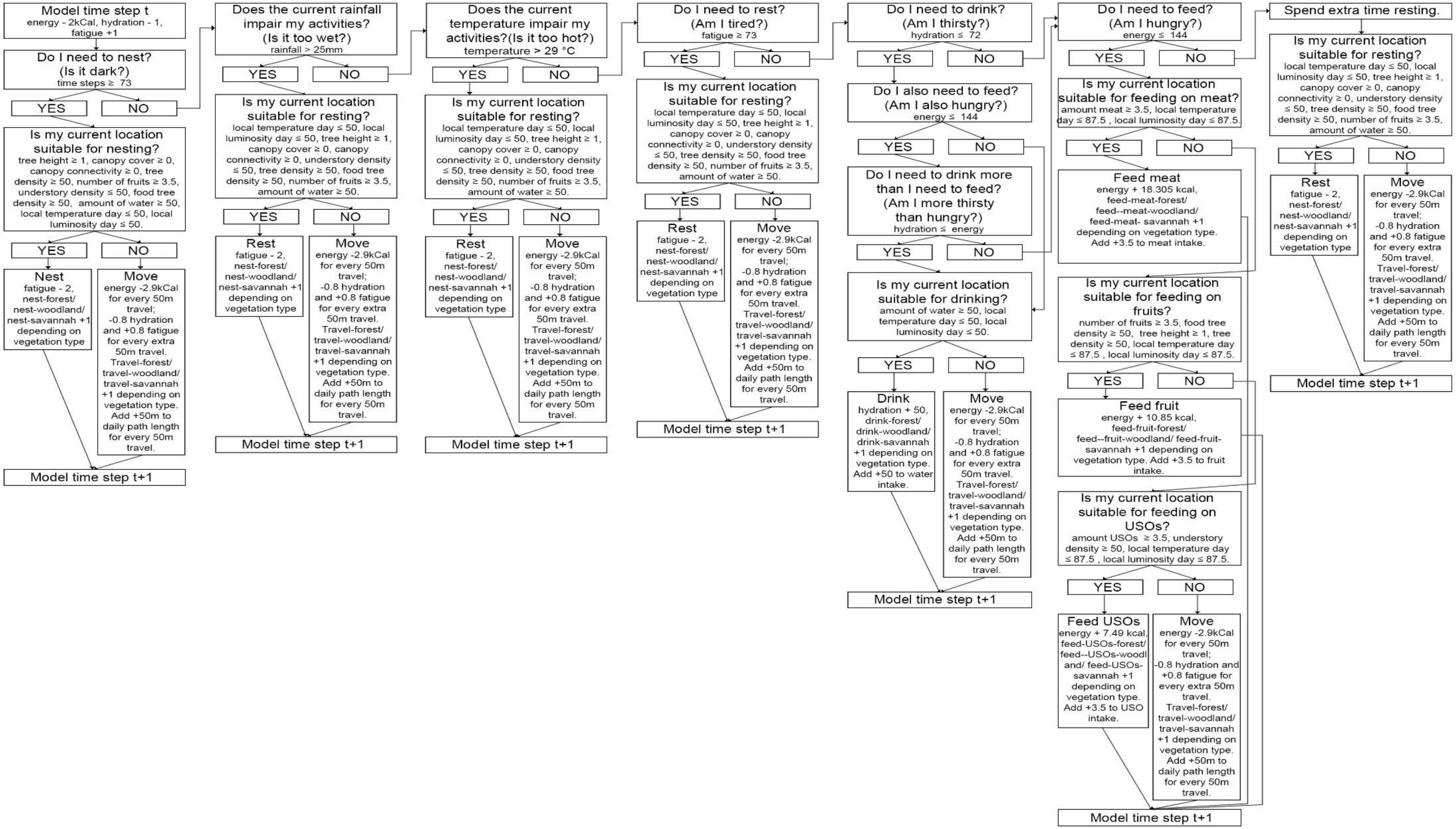

Figure 6.4. Model flowchart for the *Australopithecus* model, which specifies the decisions that have to be made by each individual at each time step, and its consequences.

Submodels

Similar to the generic chimpanzee model, the *Ardipithecus* model and the *Australopithecus* model each contained four submodels: feeding, drinking, nesting and resting. Travel was included within all four submodels.

Model testing and understanding

The *Ardipithecus* and *Australopithecus* models were thoroughly tested throughout the building phase of the models and upon model completion. The processes for testing and understanding the models followed the generic chimpanzee landscape use model (outlined in Chapter 4, p. 102).

Model calibration and verification

Verified models have outputs that match real-world observations, and model calibration is the process where (not empirically quantified) input parameters are tweaked to pair empirical data (e.g. Railsback and Grimm 2012; Chapter 5). The *Ardipithecus* and *Australopithecus* models, however, could not be calibrated to match observed patterns of early hominin landscape use, due to insufficient data on early hominin daily activity budgets, path lengths, energy budgets, fatigue budgets, hydration budgets, food intake and water intake necessary for tweaking. The *Ardipithecus* and *Australopithecus* models were, however, based upon the fully calibrated chimpanzee model of Chapter 4, which correctly predicted forest chimpanzee activity budgets within 3% of their observed range.

Model sensitivity analysis

To assess the impact of changes in input parameters on model output (e.g. Railsback and Grimm 2012, Muko et al. 2014), this study selected 33 input parameters for the *Ardipithecus* model and 35 input parameters for the *Australopithecus* model for a local sensitivity analysis. Sensitivity analysis followed those of the generic chimpanzee model (Chapter 4, p. 104)

Model output analyses and statistics

Similar to the generic chimpanzee model, to present reliable output on the landscape use patterns of *Ardipithecus* and *Australopithecus* in forest, mosaic and savannah environments, each hominin model was run 30 times per environment (e.g. Crawley 2005). Model data on activities, vegetation types, path length, energy, hydration, fatigue, food intake, water intake and site selections for each simulated *Ardipithecus*/ *Australopithecus* individual at the end of a model run were averaged to detail the mean daily path lengths, activity budgets, overall vegetation type usage, behavioural vegetation type usage, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, and site selection per model run. For each landscape, means of the 30 independent model runs were taken together and averaged to present the mean landscape use patterns per hominin environment. Averages across 30 model runs were used for further analyses and are presented in the results section below as mean ± standard deviation. Differences in landscape use patterns between species, and within species between environments, were assessed visually using data range tables and graphs, and statistically using Kruskal-Wallis tests (two-tailed, $\alpha = 0.05$). In case of significant differences, *post-hoc* Mann-Whitney U tests were performed (Bonferroni correction: $\alpha = 0.05 / 3 = 0.0167$). Spearman's rank correlation coefficients ($\alpha = 0.05$) were used to assess relationships. Vegetation type preferences were assessed using chi-square goodness of fit tests ($\alpha = 0.05$) based on counts of the number of steps spent in each vegetation type across individuals over the 30 model runs per landscape. Total frequencies per category (i.e. vegetation type) had a minimum value of 1 to present reliable output. Note that all data presented on the generic chimpanzee model are a repeat of the findings from Chapter 4.

Results

Early hominin environments

Landscape reconstructions for *Ardipithecus ramidus* environments between and within sites range from woodland-to-forest habitats to open, seasonal and grassy woodland environments, indicating that *Ardipithecus* used a wide range of landscapes (Table 6.2). Exact details on the climate, fragmentation, vegetation cover and spatial vegetation arrangement across *Ardipithecus* landscapes, however, remain largely absent, and also the presence of specific vegetation features and micro-climates has only scarcely been emphasised (Table 6.2).

A similar picture emerges for the environmental reconstructions of *Australopithecus anamensis*/ *afarensis* landscapes: Across sites, environmental reconstructions range from wooded environments with forest and permanent water sources to dry grassland habitats (Table 6.3). Data on the vegetation cover, climate, spatial vegetation layout, fragmentation, vegetation features and micro-climates for each landscape remain scarce (Table 6.3).

Table 6.2. Documented environmental reconstructions for the environments of *Ardipithecus ramidus*.

Ardipithecus ramidus		
Site	**Environmental reconstructions** *(incl. details on vegetation cover and spatial arrangement, climate and micro-habitat)*	**Reference**
Aramis Middle Awash (Ethiopia)	Ranging from closed, dense woodlands, wet woodlands with patches of forest, and cool, humid woodlands with a ground cover dominated by grass, to more open grassy woodlands, and grasslands and wooded grasslands.	Potts 1998 Cerling et al. 2011 Boyd and Silk 2012 Simpson 2013
Gona Afar region (Ethiopia)	Overall a grassy to closed woodland environment with 60 – 70% tree cover (as measured by isotopic C_3 values and the assumption that all C_3 plants were trees) that is slightly more open than Aramis. Individual reconstructions include wooded conditions, 90% coverage of trees, 60% coverage of grasses, and environments like extant bushland, grassland or thicket habitats with extensive C_4 plants (i.e. grasses).	Aronson et al. 2008 Copeland 2009 Cerling et al. 2011 Simpson 2013
Tugen Hills (Kenya)	A closed woodland landscape.	Simpson 2013
General reconstructions of *Ardipithecus ramidus* environments*	Descriptions of *Ardipithecus ramidus* environments are highly variable and range from forests, woodland-to-forest landscapes, humid and cool woodland habitats with a grassy ground cover, and closed, semi-deciduous woodland environments to more open, seasonal woodland habitats. With respect to vegetation types, based on current definitions, various studies categorise forest as a continuous stand of trees with a tree height between 10 – 40m, closed canopies, a woody cover of > 80%, and a sparse ground cover of herbs and shrubs. Woodlands have more open stands of trees with tree heights of 8 – 20m, open to closed canopies, canopy cover of > 20%, > 40% of woody cover, a ground layer dominated by grasses and herbs, sometimes also open areas with trees <3m are present in woodland. Bushlands have an open stand of trees ranging in height between 1 – 8m, a woody cover > 40%, dominated by shrubs and a tree-shrub cover of > 20%. Shrubland has an open stand of trees and shrubs < 6m tall, and a canopy cover of <20%. Savannah grasslands have scattered trees and shrubs with a height of <2m, a woody cover of < 40%, a tree-shrub cover of < 20% and a ground layer dominated by grasses and herbs. Swamps are characterised as herbaceous marshes with permanent to seasonal presence of water. These vegetation features are partly in agreement with findings from Chapter 3 (Table 3.4).	Bromage 1999 Wynn 2000 Andrews and Bamford 2008 Copeland 2009 White et al. 2009 WoldeGabriel et al. 2009 Cerling et al. 2011 Estebaranz et al. 2012 Fleagle 2013 White et al. 2015

*When no site was specified, the paper was assumed to refer to the general environment of the species.

As environmental specifics (i.e. vegetation cover, spatial vegetation arrangement, and climate) for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* were not outlined in as much detail as those presented for chimpanzees, *Ardipithecus* and *Australopithecus* landscapes could not be classified into typical hominin environments in a similar way to the landscape classifications for chimpanzees described in Chapter 3 using statistical analyses. However, early hominin fossil localities can be compared to the quantified classifications of chimpanzee dense forest,

forest mosaic and savannah landscapes presented in Chapter 3. For *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*, some reconstructions indicate forested environments and densely wooded environments with permanent water, which fit well into the chimpanzee dense forest landscape classification (Table 6.1 – 6.2). Other reconstructions imply open environments dominated by grassland, or dry grasslands and open environments, which fit well into chimpanzee savannah landscape classifications. Some reconstructions point to mosaic environments with various types of vegetation present, which fit well into chimpanzee forest mosaic landscape classifications. Lastly, again other reconstructions point to woodland environments, which fit into chimpanzee forest mosaic or savannah landscape classifications, depending on vegetation cover (Table 6.1 – 6.2).

Table 6.3. Documented environmental reconstructions for the paleoenvironments of *Australopithecus anamensis/ afarensis*.

Australopithecus anamensis – Australopithecus afarensis		
Site	**Environmental reconstructions** *(incl. details on vegetation cover and spatial arrangement, climate and micro-habitat)*	**Reference**
Afar region (Ethiopia)	A range of vegetation types was present, including closed woodlands, swamp and seasonal pans.	Reynolds et al. 2011
Laetoli (Tanzania)	Ranging between a woodland environment with some areas of grassland and forest, a closed to medium density woodland habitat, an open habitat mosaic with woodland, shrubland, grassland and seasonal ponds and streams, an environment more open than that of *Ardipithecus ramidus* at Aramis, a dry grassland with some trees, and a mosaic habitat dominated by grassland and shrubland, but with also some areas of woodland and gallery forest.	Reed 1997 Potts 1998 Su and Harrison 2007 Andrews and Bamford 2008 Su and Harrison 2008 Boyd and Silk 2012
Hadar (Ethiopia)	Ranging between grassy woodlands with 60-70% of C_3 trees and 30-40% of C_4 grasses, medium to open density woodlands with patches of forest and edaphic grasslands, open to closed woodland habitats with 800-900mm of rainfall, dry grasslands, more open environments than *Ardipithecus ramidus* at Aramis, more densely wooded environments with permanent water than *Australopithecus afarensis* habitats at Laetoli, and mosaic landscapes with woodland, scrub and grassland.	Reed 1997 Reed 1998 Potts 1998 Aronson et al. 2008 Su and Harrison 2008 Boyd and Silk 2012
Omo-Turkana Basin (Kenya)	Wooded environments.	Cerling et al. 2011
Awash Valley (Ethiopia)	Wooded environments.	Cerling et al. 2011
Koobi Fora (Kenya)	Regions of scrub woodland with flooding rivers.	Reed 1997
Omo (Ethiopia)	A mosaic wooded riverine landscape with patches of bushland, thicket, woodland, forest and grasslands.	Reed 1997
Kanapoi (Kenya)	Mosaic, open environments of grasslands and woodlands with seasonal climate regimes and annual rainfall between 350 – 600mm.	Wynn 2000
Allia Bay (Kenya)	Ranging from similar landscapes as Kanopoi with more patches of closed woodland and forest, to mosaic landscapes with dry woodland, riverine gallery forest and open grasslands.	Wynn 2000 Boyd and Silk 2012
Asa Issie	Closed to grassy woodlands which are similar to the	Boyd and Silk 2012

Australopithecus anamensis – Australopithecus afarensis		
Site	**Environmental reconstructions** *(incl. details on vegetation cover and spatial arrangement, climate and micro-habitat)*	**Reference**
(Ethiopia)	environments of *Ardipithecus ramidus*.	
General reconstructions of *Australopithecus anamensis/ afarensis* environments*	Descriptions of *Australopithecus anamensis* and *Au. afarensis* environments indicate that these species inhabited variety of landscapes. Whereas *Au. anamensis* environments included fewer areas of (C_4) grasslands (~15%) than the landscapes of *Au. afarensis*, the habitats for both species included woodland, grassland, forest, bushland, shrubland and wetlands. Whereas some reconstructions indicate wooded environments, others imply more open environments dominated by grassland and other open vegetation types. Generally, *Australopithecus* environments are considered more open than the environments of *Ardipithecus ramidus* and extant chimpanzees. Even though no preferences are observed for a single vegetation type in australopiths, it is assumed that wooded environments (such as dense woodland and forest) are more optimal. This could explain, in part, the differences in *Australopithecus* fossil densities at various sites (e.g. more fossil remains at Hadar than at Laetoli). For vegetation types, based on current definitions, various studies categorise forest as a continuous stand of trees with a tree height between 10 – 40m, closed canopies, woody cover of > 80%, and sparse ground cover of herbs and shrubs. Woodlands have more open stands of trees with a tree height of 8 – 20m, open to closed canopies, canopy cover of > 20%, > 40% of woody cover, a ground layer dominated by grasses and herbs, sometimes also open areas with trees <3m are present in woodland. Bushlands have an open stand of trees ranging in height between 1 – 8m, a woody cover > 40%, dominated by shrubs and a tree-shrub cover of > 20%. Shrubland has an open stand of trees and shrubs < 6m tall, and a canopy cover of <20%. Savannah grasslands have scattered trees and shrubs with a height of <2m, a woody cover of < 40%, a tree-shrub cover of < 20% and a ground layer dominated by grasses and herbs. Swamps are characterised as herbaceous marshes with permanent to seasonal presence of water. These vegetation features are partly in agreement with findings from Chapter 3 (Table 3.4).	Reed 1998 Wynn 2000 Bonnefille et al. 2004 Andrews and Bamford 2008 Su and Harrison 2008 Copeland 2009 Cerling et al. 2011 Boyd and Silk 2012 Estebaranz et al. 2012 Fleagle 2013 Hammond and Ward 2013 Sponheimer et al. 2013

*When no site was specified, the paper was assumed to refer to the general environment of the species.

Early hominin behaviour

Whereas early hominin feeding and travel patterns are fairly well studied, limited information is currently available on early hominin drinking, nesting and resting patterns. For *Ardipithecus ramidus*, insights on drinking behaviour are restricted to the notion that *Ardipithecus*, like all other hominins, is considered as a strongly water-dependent species, and that access to drinking water was critical for their survival (Table 6.4). For nesting, it is indicated that *Ardipithecus ramidus* almost certainly had similar sleeping patterns to those observed for extant chimpanzees, i.e. individuals likely nested in trees. No data are presented on *Ardipithecus ramidus* resting patterns. *Ardipithecus ramidus* locomotion (or travel) patterns have been reconstructed to arboreal quadrupedalism when in trees, and terrestrial bipedalism when on the ground, based on observed morphological adaptations. *Ardipithecus* bipedality has been assumed to have increased their terrestrial locomotor efficiency at a slight cost to arboreal efficiency as compared to chimpanzees. For feeding, the diet of *Ardipithecus ramidus* has been reconstructed as a generalised omnivorous diet, which includes both ripe fruits (i.e. C_3 foods, 85 – 90% of the diet) as well as more tough, hard and brittle foods (i.e. C_4 foods, 10 – 15% of the diet) such as nuts and underground storage organs (USOs). An occasional scrap of meat may also have been included. These diets differ from savannah chimpanzees which include > 90% of C_3 foods (Sponheimer et al. 2006, Suwa et al. 2009). *Ardipithecus ramidus* diets are consistent with a partially terrestrial, partially arboreal pattern of feeding in a wooded habitat (Table 6.4).

Table 6.4. Behavioural reconstructions for *Ardipithecus ramidus*.

Ardipithecus ramidus		
Behaviour	**Behavioural reconstructions and descriptions** *(incl. when and where)*	**Reference**
Feeding	Diet: A generalised omnivorous diet consisting of 85-90% of C_3 food items (i.e. fruits), which differs from extant savannah chimpanzees (>90% C_3 foods) and *Australopithecus* (> 30% C_4 foods). The remaining 10-15% of the diet consisted of C_4 foods including tough, hard and brittle food items such as nuts and tubers, and an occasional, opportunistic scrap of meat. *Ardipithecus ramidus* was not as reliant on ripe fruits, fibrous plants, and/or hard and tough foods as extant apes and later australopithecines. Diets are consistent with a partially terrestrial, partially arboreal pattern of feeding in a wooded habitat.	Bromage 1999 Suwa et al. 2009 White et al. 2009 Boyd and Silk 2012 Estebaranz et al. 2012 Stanford 2012 Daegling et al. 2013 Fleagle 2013 Sponheimer et al. 2013 White et al. 2015 Grine and Daegling 2017 Takemoto 2017
Drinking	Hominins were strongly water-dependent; access to drinking water was critical for survival.	Foley 2018
Nesting	It is indicated that *Ardipithecus ramidus* almost certainly had similar sleeping patterns to extant chimpanzees, and thus nested in trees.	Stanford 2012
Resting	-	-
Travel	Postcranial reconstructions for *Ardipithecus ramidus* show morphological adaptations to arboreal quadrupedalism when in trees, and terrestrial bipedalism when on the ground. Bipedality has been assumed to be less efficient than in australopiths or extant humans. Terrestrial locomotor patterns of *Ardipithecus ramidus* are considered more efficient than those observed for extant chimpanzees.	Bromage 1999 Lovejoy et al. 2009 White et al. 2009 Stanford 2012 Fleagle 2013 Simpson 2013 White et al. 2015 Kozma et al. 2018

Australopithecus anamensis and *Australopithecus afarensis* are considered strongly water-dependent species that slept in trees, and would potentially also have built nests, similar to chimpanzees (Table 6.5). *Australopithecus* spp. distribution and time budget models (not restricted to *Australopithecus anamensis*/ *afarensis*; Bettridge 2010) showed that *Australopithecines* spent 32.5% of their active day on (enforced) resting and 8.0% on social time. *Australopithecus anamensis*/ *afarensis* diets have been reconstructed to include a mix of C_3 and C_4 foods. Whereas C_3 foods would have included mainly fruits, hard, brittle and tough C_4 food items would have included grasses, sedges, seeds, nuts, and USOs. Also meat (likely obtained through scavenging and using tools) is considered an important item within the *Australopithecus* diet. Whereas this indicates an adaptive shift for *Australopithecus* spp. with morphological adaptations to exploit more open habitats more efficiently and include C_4 foods (> 30%) in their diet, it is likely that australopiths would still have preferred soft fruits. *Australopithecus afarensis* would have been best morphologically adapted to include hard, tough food items, whereas *Australopithecus anamensis* would have been intermediate between *Ardipithecus ramidus* and *Australopithecus afarensis*. The *Australopithecus* time budget models (Bettridge 2010) showed that Australopithecines spent 43.1% of their active day on feeding. With regards to travel patterns, *Australopithecus anamensis* and *Australopithecus afarensis* are considered as habitual terrestrial bipeds that retained the ability to move around in trees. Based on morphological adaptations, *Australopithecus* terrestrial bipedality would have been more efficient than that of *Ardipithecus ramidus,* but less efficient than that of later hominins and extant humans. According to the australopith time budget models (Bettridge 2010), *Australopithecines* spent 16.1% of their day on travel (Table 6.5).

Other early hominin characteristics

Although early hominin home range sizes remain unspecified, they would have likely increased as environments became more open due to early hominin fruit dependency (Table 6.6). On the other hand, early hominin home-range size would have likely decreased again when diets shifted towards the inclusion of more readily available resources. Australopithecine population sizes were likely comparable to those of extant chimpanzees. Body size for *Ardipithecus ramidus* has been reconstructed to 30 – 51kg in weight and about 1.2m in height. *Australopithecus anamensis* females weighed about 33kg and males about 51kg. *Australopithecus afarensis* individuals weighed between 28 – 50kg and were between 1.05 – 1.51m tall. Various mating and social systems have been suggested for *Ardipithecus ramidus* and early *Australopithecus*. Australopiths are assumed to have had similar fission-fusion social systems as chimpanzees. Griffith et al. (2010) specified within their hominin individual-based model that their hominin agents were able to assess their environment within 100m, i.e. their foresight (Table 6.6), based on a Moore neighbourhood with cell sizes of 1 ha (i.e. 100m x 100m). Allen et al. (2019) also highlighted a minimum mean detection distance of about 100m across different types of vegetation when investigating the relationship between prey detection rates and environments for ancient humans.

Table 6.5. Behavioural reconstructions for *Australopithecus anamensis* and *Australopithecus afarensis*.

Australopithecus anamensis – Australopithecus afarensis		
Behaviour	**Behavioural reconstructions and descriptions** *(incl. when and where)*	**Reference**
Feeding	Diets include a mix of C_3 (e.g. fruits) and C_4 (e.g. hard, tough food) food sources. Whereas this indicates an adaptive shift with morphological adaptations to exploit more open habitats and include C_4 foods (> 30%) in the diet, it is likely that australopiths would still have preferred soft fruits and had a highly flexible diet. Hard, tough and brittle C_4 food items included grasses, sedges, seeds, nuts, underground storage organs (USOs, such as tubers), and other fallback foods. *Australopithecus afarensis* is best morphologically adapted to include hard, tough food items, and *Au. anamensis* is intermediate between *Ardipithecus ramidus* and *Au. afarensis*. Some evidence suggests that early australopithecines still foraged (partly) in trees, and also included meat in their diet (likely obtained through hunting and/or scavenging, and using tools). Model results on australopith activity budgets indicate that australopithecines spent 43.1% of their active day (i.e. 12 hours) on feeding.	Sponheimer and Lee-Thorp 2003 Ungar 2004 Sponheimer et al. 2006 Suwa et al. 2009 Bettridge 2010 Macho and Shimizu 2010 Ungar et al. 2010 Reynolds et al. 2011 Boyd and Silk 2012 Estebaranz et al. 2012 Daegling et al. 2013 Fleagle 2013 Hammond and Ward 2013 Sponheimer et al. 2013 Dunbar and Gowlett 2014 Wynn et al. 2016 Grine and Daegling 2017
Drinking	Hominins were strongly water-dependent, and that access to drinking water was critical for survival.	Foley 2018
Nesting	It is assumed that australopithecines, including *Australopithecus afarensis*, slept in trees and potentially also build nests.	Sabater-Pi et al. 1997 Boyd and Silk 2012 Fleagle 2013
Resting	Australopithecine models on activity budgets showed that they spent 32.5% of their active day (i.e. 12 hours) on enforced resting, and 8% on social time. Larger groups may require more social time for maintaining social relationships.	Bettridge 2010 Dunbar and Gowlett 2014
Travel	Both australopithecine species were habitual bipeds that retained the ability to move around in trees. Australopith bipedalism was more efficient (in energy and speed) than that of *Ardipithecus ramidus*, but less efficient than that of later hominins and extant humans. Australopith arboreality was distinct from that of *Ardipithecus ramidus* and extant apes. Model results on australopith activity budgets indicate that they spent 16.1% of their active day (i.e. 12 hours) on travel.	Stern and Susman 1983 Potts 1998 Stern 2000 Boyd and Silk 2012 Lovejoy et al. 2009 Bettridge 2010 Reynolds et al. 2011 Fleagle 2013 Hammond and Ward 2013 Dunbar and Gowlett 2014 Ruff et al. 2016 Ibanez-Gimeno et al. 2017 Kozma et al. 2018

The total daily energy expenditure for *Australopithecus afarensis* has been reconstructed to 1662 – 2408 kCal/day based on calculations from general primate, chimpanzee and human models; these costs include those for metabolism as well as for different behavioural activities (Table 6.6). Morphological adaptations resulted in lower energy expenditure for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* while travelling terrestrially as compared to chimpanzees due to increased efficiency in terrestrial bipedalism. Energetic travel costs have been calculated to 0.08 ml O_2 kg^{-1} m^{-1}

for terrestrial bipedalism in humans and to 0.17 ml O_2 kg^{-1} m^{-1} for terrestrial quadrupedalism in chimpanzees, and have been reconstructed to 0.14 ml O_2 kg^{-1} m^{-1} for terrestrial bipedalism in *Australopithecus afarensis*; travel costs for *Ardipithecus ramidus* would likely have been intermediate between the travel cost estimates of chimpanzees and *Australopithecus afarensis*. Bipedalism offered certain thermoregulatory advantages for early hominins: Due to their erect and upright posture, hominins could forage at higher temperatures and over greater distances, while consuming less food and water than quadrupedal animals. This would also have reduced their enforced resting time, as early hominins would have been better able to cope with extreme climates. During travel, therefore, early hominins are also assumed to have experienced a decreased loss of hydration, and a decreased gain of fatigue. With regards to feeding, fruits are most commonly found in more densely wooded vegetation (i.e. forest, dense woodland), and fruits are considered high-quality foods, containing on average 3.1kCal of energy per gram dry weight. Meat is also considered a high-quality food item, with a gram of wet weight containing between 4Cal – 1.57kCal of energy and the assumption that meat contains about 70% water. Meat intake rates vary, and only small carcasses can be scavenged by single individuals. Meat and carcasses are assumed to be more prevalent in open grassland vegetation due to the higher density of herbivores. Just as is the case for chimpanzees, insects may also have been included within the hominin diet, with energy gains ranging between 48.9 – 315.4kCal/100gram depending on species and variable intake rates between 0.2 – 1.2 grams/minute. Bone marrow may also have been an important dietary item, but intake rates vary per type of bone and species consumed. USOs, such as tubers, are considered important fallback foods for hominins, and their distribution varies between vegetation types, with USOs being widely available in grassland and wetland habitats, and limited availability in forests. Nutritional value varies, both within and between species, and the amount of edible dry weight varies considerably between species. On average, USOs contain between 146 – 298 kCal/100gram of tuber dry weight. Other hard and brittle food items, such as seeds, nuts, sedges and grasses, vary in density across vegetation types, with sedges (including USOs) being most prominent in wetlands and swamp, grasses in savannah grassland, and seeds in forest and woodland. Whereas seeds are considered as high-quality foods, grasses and other fallback food items are less nutritious, requiring consumption in greater quantities (Table 6.6).

Table 6.6. Documented characteristics for *Ardipithecus ramidus*, *Australopithecus anamensis* and *Australopithecus afarensis* across environments.

Ardipithecus ramidus, Australopithecus anamensis* and *Australopithecus afarensis		
Characteristic	**Reconstructions and descriptions**	**Reference**
Home-range size	For frugivorous species, home range size is expected to increase in more open environments as fruit becomes more scarce and more dispersed. Early hominins could thus have coped with more open environments by increasing their home range, or by including other, more widely available food items in their diets. Early hominins were probably less dependent on ripe fruit than extant chimpanzees.	Ganas and Robbins 2005 Copeland 2009 Coward and Grove 2011
Population size	Australopithecines likely had group sizes similar to chimpanzees. Average group size estimates vary, and include averages of 30 individuals, 43.6 individuals, and 55 individuals.	Dunbar 2014 Dunbar et al. 2014 Dunbar and Gowlett 2014
Body size	*Ardipithecus ramidus* weighted ~30 – 51kg and were ~1.2m tall. *Australopithecus anamensis* females weighed ~33kg and males ~51kg. *Australopithecus afarensis* weighed between ~28 – 50kg and were between ~1.05 – 1.51m tall, with females weighing ~29kg and males ~45kg.	Bromage 1999 Su and Harrison 2008 Suwa et al. 2009 White et al. 2009 Boyd and Silk 2012 Fleagle 2013 Hammond and Ward 2013
Social system	Both monogamy and polygyny have been suggested for *Ardipithecus ramidus* and early *Australopithecus*. Strong competition between males is expected for *Australopithecus afarensis* based on sexual dimorphism. Male-bonded social systems are assumed for *Ardipithecus ramidus*. Australopiths (and other hominins) likely had fission-fusion social systems.	White et al. 2009 Fleagle 2013 Hammond and Ward 2013 Coward and Dunbar 2014 Dunbar et al. 2014 Dunbar and Gowlett 2014 Shultz et al. 2014
Energy – existing	Based on underlying model calculations and equations for primates, chimpanzees, and humans, daily energy expenditure for *Australopithecus afarensis* has been reconstructed to fall between 1662 – 2408 kcal/day. These costs include those for metabolism as well as for different behavioural activities.	Leonard and Robertson 1997
Energy – travel	Early hominins were efficient bipeds that surpassed extant chimpanzees (in energy and speed); *Ardipithecus ramidus* was less efficient than australopithecines, and *Australopithecus anamensis* and *Au. afarensis* were less efficient (in energy and speed) than later hominins and extant humans. Decreased energy expenditure with increased bipedal locomotion is a result of morphological adaptations to more efficient bipedality. Travel costs for *Ar. ramidus* only slightly differed from those of chimpanzees due to small morphological adaptations. Chimpanzees are best adapted to arborealism and least to bipedalism, *Australopithecus* would have been best adapted to bipedalism and least to arborealism, and *Ar. ramidus* would have been intermediate in both arboreal as well as in bipedal patterns. As *Au. anamensis* and *Au. afarensis* were more adapted to terrestrial bipedalism, energy costs for travel would have been significantly reduced. Travel costs have been calculated to 0.08 ml O_2 kg^{-1} m^{-1} for humans (terrestrial bipedalism), to 0.17 O_2 kg^{-1} m^{-1} for chimpanzees (terrestrial quadrupedalism), and reconstructed to 0.14 O_2 kg^{-1} m^{-1} for *Au. afarensis* (terrestrial bipedalism).	Stern and Susman 1983 Wheeler 1992 Lovejoy et al. 2009 Mitchells et al. 2009 Pontzer et al. 2009 Bettridge 2010 Cerling et al. 2011 Boyd and Silk 2012 Hammond and Ward 2013 Dunbar and Gowlett 2014 Pontzer et al. 2014 White et al. 2015 Ruff et al. 2016 Kozma et al. 2018
Energy – fruit	Fruits are considered as high-quality food items. Energy gains from fruits equal on average 3.1kCal of energy per gram dry weight for chimpanzees. The distribution of fruits varies between different types of vegetation, with more fruits in more densely wooded (i.e. forest, woodland) patches.	Copeland 2009 Laden and Wrangham 2005 Leonard and Robertson 1997 Emery Thompson and Wrangham 2008 McLennan and Ganzhorn 2017
Energy – meat	Meat eating and scavenging is considered an important dietary strategy for early hominins including *Ardipithecus ramidus, Australopithecus anamensis* and *Australopithecus afarensis*. Scavenging is rarely observed for chimpanzees. Meat is considered a high-quality food, with energy	Leonard and Robertson 1997 Boesch and Boesch-Achermann 2000 Laden and Wrangham 2005 Stanford 2006 Brown 2008 Watts 2008

Ardipithecus ramidus, Australopithecus anamensis **and** *Australopithecus afarensis*		
Characteristic	**Reconstructions and descriptions**	**Reference**
	intake gains ranging from about 4 Cal/gram to 1.57 kCal/gram wet weight. Meat consists of about 70% and 30% 'dry weight'. Intake rates for meat are uncertain, with suggested intake ranging from obtaining meat 'scraps' of 150 grams to about 50grams of meat (wet weight) per minute. Meat and carcasses are assumed to be more prevalent in open grassland vegetation due to the higher density of herbivores. Carcass probability rates are estimated to 18% for grassland and 6% for forest and woodland. It is assumed that only small carcasses (i.e. < 1kg of scavengable meat) can be accessed by single individuals, whereas larger carcasses needed to be approached by a group of hominins.	Griffith et al. 2010 Hammond and Ward 2013 Pobiner 2015
Energy – insects	Although little studied, insects may have also been a part of early *Homo* diets, and potentially also for earlier hominins. Insects are considered high-quality foods. Chimpanzees in Gombe (Tanzania), gain between 48.9 – 315.4 kCal/100gram insects, with an average of 110.9 kcal/100gram insects. Intake rates vary per species, but range between 0.2 – 1.2 grams/min. Similar energy gains and intake rates can be expected for hominins.	McGrew 2001 Laden and Wrangham 2005 O'Malley and Power 2012 O'Malley and Power 2014
Energy – bone (marrow)	Bone marrow is rich in energy, but exact energy gains vary per species and type of bone.	Madrigal and Blumenschine 2000
Energy – USOs	Underground storage organs (USOs), such as tubers, corms, bulbs and caudex, are considered as important fallback foods for early hominins, and their distribution varies between different types of vegetation. In general, USOs are widely available in grassland and wetland habitats, and there is only limited availability in forests. USOs are considered as low-quality foods, but, as they are widely available in certain vegetation types, they can provide important fallback foods when preferred foods are absent. Nutritional value varies widely, both within and between species. On average, USOs contain between 146 – 298 kCal/ 100gram of tuber dry weight, with a mean of 214kCal/100gram tuber dry weight. Intake rates remain unknown, but the amount of edible dry weight varies considerably between species.	Schoeninger et al. 2001 Laden and Wrangham 2005 Copeland 2009 Wrangham et al. 2009
Energy – hard foods (e.g. seeds, nuts, sedges, grass)	Hard, tough and brittle foods, such as seeds, nuts, sedges and grass, vary in density across different vegetation types. Generally, sedges (which include USOs) are assumed to be most prominent in wetlands and swamp, grasses in grassland, and seeds in forest and woodland. Whereas seeds are considered as high-quality foods, grasses and other fallback food items are less nutritious. Tough, hard and brittle food items likely have significant mechanical defences and may need dental adaptations to be exploited optimally. Such morphological adaptations are observed in hominins, including *Ardipithecus ramidus*, *Australopithecus anamensis* and *Australopithecus afarensis*.	Leonard and Robertson 1997 Sponheimer and Lee-Thorp 2003 Laden and Wrangham 2005 Copeland 2009 Grine and Daegling 2017
Hydration – existing	-	-
Hydration – travel	Bipedalism offered certain thermoregulatory advantages for early hominins over extant primates. Due to their erect and upright posture, they could forage at higher temperatures and over greater distances, while consuming less food and water than quadrupedal animals. This would indicate a decreased loss of energy and hydration while travelling.	Wheeler 1991 Wheeler 1992 Mitchells et al. 2009
Hydration – drinking	-	-
Fatigue – existing	-	-
Fatigue – resting	-	-
Fatigue – nesting	-	-
Fatigue – travel	The thermoregulatory advantage of bipedalism in early hominins would have reduced their enforced resting time, i.e. early hominins are better able to cope with extreme (i.e. hot) climates. This would	Dunbar et al. 2014

Ardipithecus ramidus, Australopithecus anamensis **and** *Australopithecus afarensis*		
Characteristic	**Reconstructions and descriptions**	**Reference**
	indicate less fatigue gains while travelling.	
Foresight	Even though early hominin foresight (i.e. the distance individuals can 'see') is not outlined in current hominin literature, within their HOMINID (i.e. Hungry Omnivores Moving, Interacting, and Nesting in Independent Decision-making Simulations) model, Griffith et al. (2010) specify that their modelled individuals can see 100m ahead.	Griffith et al. 2010

Model rules based on early hominin data and findings from chimpanzees

Literature data on the behaviour, environments and characteristics of *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* were used to set out specific rules for the *Ardipithecus* and *Australopithecus* landscape use models. Species-specific details on early hominins were used within the models wherever feasible and were combined with findings from chimpanzees (Chapter 2 – Chapter 5) whenever early hominin data remained absent (for rationale: Appendix 6.5 and Appendix 6.10). With regards to landscapes, the literature review showed that *Ardipithecus* and *Australopithecus* inhabited forest, mosaic and savannah environments, but exact data on vegetation cover, spatial vegetation arrangement, overall temperature, rainfall and fragmentation remained absent. Virtual early hominin environments were therefore parameterised similar to the generic chimpanzee model, and landscape details for each environment are outlined in Table 6.7. Similarly, in the absence of exact data, *Ardipithecus* and *Australopithecus* home-range sizes followed the generic model and were simulated as 36 km^2 (with 14400 patches of 50m x 50m), the average home-range size for chimpanzees (Chapter 4). As details on the vegetation features and micro-climates of early hominin habitats were only sporadically presented, micro-habitat characteristics for each vegetation type and patch followed the generic chimpanzee model and are outlined in Table 6.8. For each simulated hominin landscape, model runs differed slightly in the spatial arrangement of vegetation types, as well as in the random allocation of micro-habitat characteristics of each patch with respect to the assigned vegetation type.

Following the generic chimpanzee model, *Ardipithecus* and *Australopithecus* population size was set to 60 individuals, as published population size estimates of early hominins were highly variable. Following the generic chimpanzee model, individuals were parameterised to have initial levels of energy, hydration and fatigue between 0 – 10, and to gain 1 fatigue, to lose 2 kCal of energy and to lose 1 hydration per time step simply by existing (i.e. due to basic metabolic processes), as no exact data for early hominins exist. Initial geographical placement of individuals at random nesting locations within the virtual model environment differed slightly between model runs due to the random assignment of patch characteristics. Detailed model rules were set out on *where* and *when* to perform each behaviour, as well as on *how much* energy, hydration and fatigue were gained and lost. As detailed data on early hominin drinking, nesting, and resting patterns remained absent, model rules for these behaviours followed the generic chimpanzee model (Table 6.9).

Table 6.7. Vegetation cover for the three landscapes simulated for *Ardipithecus* and *Australopithecus* following the generic chimpanzee model: forests, mosaics and savannahs. For all models, overall temperature was set at 25°C, rainfall was set at 0mm, and fragmentation was set as 0.05.

Landscape	**Forest cover**	**Woodland cover**	**Grassland cover**
Dense Forest	80%	10%	10%
Forest Mosaic	45%	40%	15%
Savannah	10%	55%	35%

Table 6.8. Range of vegetation features and micro-climates simulated for each vegetation type within the *Ardipithecus* and *Australopithecus* models, following the generic chimpanzee model. Note that values for local temperature and luminosity are scaled (0 – 100) due to lack of data; local temperature values are different from overall temperature (Table 6.7). For rationale: see Appendix 6.5 and 6.10. Note that this table represents a partial replicate of Table 4.1 (Chapter 4). Fruits, USOs and meat are measured in edible grams dry weight.

	Forest	**Woodland**	**Grassland**
Tree height	10 – 50m	8 – 20m	3 – 15m
Canopy cover	75 – 100% (i.e. dense/ closed)	25 – 75% (i.e. medium)	0 – 25% (i.e. sparse/ open)
Canopy connectivity	75 – 100%	25 – 75%	0 – 25%
Understory density	0 – 25%	25 – 75%	75 – 100%
Tree density	75 – 100%	25 – 75%	0 – 25%
Food tree density	75 – 100%	25 – 75%	0 – 25%
Local temperature day	0 – 25 (i.e. cold - scaled)	25 – 75 (i.e. medium - scaled)	75 – 100 (i.e. hot - scaled)
Local temperature night	75 – 100	25 – 75	0 – 25
Local luminosity day	0 – 25 (i.e. shaded - scaled)	25 – 75 (i.e. medium - scaled)	75 – 100 (i.e. bright - scaled)
Local luminosity night	0 – 25	0 – 25	0 – 25
Number of fruits	0 – 21 fruits	0 – 14 fruits	0 – 7 fruits
Amount of USOs	0 – 7 USOs	0 – 14 USOs	0 – 21 USOs
Carcass probability	6%	6%	18%
Amount of meat	0 – 21 grams	0 – 21 grams	0 – 21 grams
Amount of water	0 – 100 hydrations	0 – 75 hydrations	0 – 50 hydrations

For feeding, model rules from the generic chimpanzee model were adapted to suit the wider dietary breadth of the early hominins. For *Ardipithecus*, fruit and USOs were included and for *Australopithecus* fruit, USOs and scavengable meat were included in the diet. Meat and USO consumption is also observed for chimpanzees, but constitute only a minor part of their diets and were therefore not included within the generic chimpanzee model (e.g. McGrew et al. 1988, Stanford 2006, Hernandez-Aguilar et al. 2007, Hernandez-Aguilar 2009, Moore et al. 2017). Furthermore, chimpanzees obtain meat through hunting rather than scavenging (e.g. Watts 2008, Stanford 2012, Wood and Gilby 2017). Hominins are expected to have exploited meat sources more habitually (e.g. Coward 2014). Model rules for feeding on fruit for *Ardipithecus* and *Australopithecus* were kept similar to the generic chimpanzee model, apart from the micro-climate criteria. As *Ardipithecus* individuals had a thermoregulatory advantage in open areas over extant chimpanzees, and *Australopithecus* had a thermal advantage over *Ardipithecus* and chimpanzees, due to their bipedal locomotor patterns, the micro-climate criteria for when model patches were suitable for feeding activities could be relaxed to also include a part of the more extreme grassland vegetation types, i.e. 81.25 (local micro-climate temperature and luminosity, scaled – Table 6.8) for *Ardipithecus* and 87.5 (local micro-climate temperature and luminosity, scaled – Table 6.8) for *Australopithecus* compared to 50 (local micro-climate temperature and luminosity, scaled – Table 6.8) for chimpanzees (Table 6.10).

Table 6.9. Model rules for the *Ardipithecus* and *Australopithecus* models on *how much* energy, hydration, fatigue and water to gain/ lose at each time step for drinking, nesting and travelling behaviour, as well as *where* and *when* these behaviours could be performed. Note that this table is a partial replica of Table 4.2 (Chapter 4). For rationale, see Appendix 6.5 and 6.10.

Behaviour	Where	When	How much to gain/ lose
Drinking	Patches with amount water ≥ 50 hydrations, local temperature day ≤ 50 (scaled), and local luminosity day ≤ 50 (scaled).	Hydration ≤ 72 (i.e. when it is thirsty) and hydration < energy (i.e. when it is more thirsty than hungry).	Gain 50 hydrations. Patches lose 50 hydrations.
Nesting	Patches with tree height ≥ 1m, canopy cover ≥ 0%, canopy connectivity ≥ 0%, tree density ≥ 50%, number fruit ≥ 3.5 fruits (or edible grams), understory density ≤ 50%, food tree density ≥ 50%, amount water ≥ 50 hydrations, local temperature (day) ≤ 50 (scaled), and local luminosity (day) ≤ 50 (scaled).	Time steps > 72 (i.e. the second half of the 24-hour day, and thus when it is night).	Lose 2 fatigues.
Resting	Patches with local temperature (day) ≤ 50 (scaled), local luminosity (day) ≤ 50 (scaled), tree height ≥ 1m, canopy cover ≥ 0%, canopy connectivity ≥ 0%, tree density ≥ 50%, number fruit ≥ 3.5 fruits (i.e. grams edible dry weight), understory density ≤ 50%, food tree density ≥ 50%, and amount water ≥ 50 hydrations.	Fatigue ≥ 73 (i.e. when it is too tired), or rainfall ≥ 25mm (i.e. when it is too wet), or overall temperature ≥ 29°C (i.e. when it is too hot), or energy > 144 and hydration > 73 (i.e. 'free' resting).	Lose 2 fatigues.

*Within the *Ardipithecus* and *Australopithecus* models, rainfall and overall temperature never reached above 25mm and 29°C; Overall temperature and rainfall are, however, included in model rules for completeness. Note that overall temperature differed from local micro-climate temperature (scaled).

For feeding on USOs, one gram of dry weight USOs contained 2.14kCal of energy (Schoeninger et al. 2001; Table 6.6). As USOs come from understory plants (e.g. Laden and Wrangham 2005), understory density, amount of USOs, local temperature at daytime and local luminosity at daytime were assumed to be important characteristics in deciding *where* to feed. The criterion for understory density in *where* to feed on USOs was set at ≥ 50%, similar to the ‘feeding-on-fruit’ criteria for tree and food tree density; Local temperature at daytime and local daytime luminosity were kept equal to the feeding-on-fruit criteria with respect to the thermoregulatory advantage of *Ardipithecus* and *Australopithecus*. It was furthermore assumed that early hominin individuals could eat the same amount of edible dry weight for USOs as for fruits. USOs were expected to be regularly available in savannah grassland, and occasionally in forest; USO availability in woodland was expected intermediate between these two types of vegetation (Laden and Wrangham 2005; Table 6.6). Detailed model rules on feeding on USOs are outlined in Table 6.10.

For feeding on meat, calculations of literature data showed carcass probabilities per patch of 6% in forest and woodland, and 18% in grassland (Leonard and Robertson 1997, Griffith et al. 2010; Table 6.6). Following the hominin individual-based model of Griffith et al. (2010), one gram of wet weight meat contained 1.57kCal (Table 6.6). This was rescaled based on the assumption that 1 gram of meat consisted of 30% dry weight (Brown 2008; Table 6.6), leading to 1.57kcal/0.3gram dry weight, and thus to 5.23kCal/gram dry weight meat. For feeding on meat, important criteria in deciding *where* to feed included daytime temperature, daytime luminosity, and amount of food, and criteria were kept equal to those for feeding on fruit and USOs. Australopithecines were assumed to gain equal amounts of dry weight per time step feeding on meat as when feeding on fruit or USOs. Model rules for feeding on meat are outlined in Table 6.10. Based on the energetic gains from the different food items, meat was preferred overall for early hominins, followed by fruit. Nonetheless, australopithecines were parameterised to focus on a location that contained enough fruit for a subsequent feeding bout whilst selecting a nesting or resting location. As meat was a highly opportunistic food source and nesting/ resting close to a carcass would not have been a safe choice due to predator attraction, the presence of meat was not considered in selecting a nesting or resting location. It should be noted that the thermoregulatory advantage for *Ardipithecus* and *Australopithecus* was not implemented into the nesting, resting, and drinking rules, as shadier, cooler areas were still assumed to be preferred for these behaviours.

For travel, model rules from the generic model were adapted to accommodate the increased terrestrial locomotor efficiency of early hominins as a consequence of their adaptations to bipedalism. The generic chimpanzee model did not distinguish between terrestrial and arboreal patterns of locomotion, and specified that individuals lost 3.5kCal of energy for every 50m of travel, and lost an additional hydration and gained an additional fatigue for every extra 50m. Literature data outlined travel costs of 0.17 ml O_2 kg^{-1} m^{-1} for chimpanzees and 0.14 ml O_2 kg^{-1} m^{-1} for *Australopithecus afarensis* (Pontzer et al. 2009; Table 6.6). Although different in units of measurement, these findings could be used for scaling. For *Australopithecus*, travel costs could be calculated to 2.9kCal of energy lost for every 50m of travel, and to 0.8 hydration lost and 0.8 fatigues gained for every extra 50m. As *Ardipithecus* was assumed intermediate between *Australopithecus* and chimpanzees, their travel costs were calculated to 3.2kCal of energy lost for every 50m of travel, and to 0.9 hydrations lost and 0.9 fatigues gained for every extra 50m. Following Griffith et al. (2010) and similar to the generic model, *Ardipithecus* and *Australopithecus* individuals were assumed to see ahead a maximum of 100m (Table 6.6). Detailed model rules on where to travel are outlined in Table 6.10.

Model output

Sensitivity analysis

The *Ardipithecus* and *Australopithecus* landscape use models were robust to small changes in input parameter settings. Sensitivity analysis of 33 input parameters for the *Ardipithecus* model and 35 input parameters for the *Australopithecus* model showed that small, i.e. 10%, changes in input parameter settings never resulted in more than 7% change in baseline model output (Table 6.11 and Table 6.12). Model output for *Ardipithecus* and *Australopithecus* activity budgets always remained within the 5% range of the baseline activity budget output. As the *Ardipithecus* and *Australopithecus* models were adapted from the generic chimpanzee model (Chapter 4), it was assumed that models were not overfitted, as large changes in input parameters (i.e. > 50%) during the calibration process (Chapter 4) had a significant effect on model output.

Table 6.10. Model rules for the *Ardipithecus* and *Australopithecus* models on *how much* energy, hydration, fatigue and food to gain/ lose at each time step for feeding and travelling behaviour, as well as *where* and *when* these activities could be performed. Note that this table is a partial replica of Table 4.2 (Chapter 4). For rationale, see Appendix 6.5 and 6.10. Local temperature and luminosity are scaled between 0 – 100 (Table 6.8). Fruits, USOs and meat are measured in edible grams dry weight.

Behaviour	**Where**	**When**	**How much to gain/ lose**
Feeding (Fruit)	*Ardipithecus*: Patches with number fruit ≥ 3.5 fruits, food tree density ≥ 50%, tree height ≥ 1m, tree density ≥ 50%, local temperature day ≤ 81.25 (scaled), and local luminosity day ≤ 81.25 (scaled). *Australopithecus*: Patches with number fruit ≥ 3.5 fruits, food tree density ≥ 50%, tree height ≥ 1m, tree density ≥ 50%, local temperature day ≤ 87.5 (scaled), and local luminosity day ≤ 87.5 (scaled).	Energy ≤ 144 kCal and energy < hydration.	Gain 3.1 kCal per fruit eaten and eat 3.5 fruits per time step. Patches lose 3.5 fruits.
Feeding (USOs)	*Ardipithecus*: Patches with amount USOs ≥ 3.5 USOs, understory density ≥ 50%, local temperature day ≤ 81.25 (scaled), and local luminosity day ≤ 81.25 (scaled). *Australopithecus*: Patches with amount USOs ≥ 3.5 USOs, understory density ≥ 50%, local temperature day ≤ 87.5 (scaled), and local luminosity day ≤ 87.5 (scaled).	Energy ≤ 144 kCal and energy < hydration.	Gain 2.14 kCal per USO eaten (and eat 3.5 USOs per time step. Patches lose 3.5 USOs.
Feed (Meat)	*Australopithecus*: Patches with amount meat ≥ 3.5 gram dry weight, local temperature day ≤ 87.5 (scaled), and local luminosity day ≤ 87.5 (scaled).	Energy ≤ 144 kCal and energy < hydration.	Gain 5.23 kCal per gram dry weight meat, and eat 3.5 grams dry weight meat per time step. Patches lose 3.5 grams of meat.
Travel	No rules set out on *where* to travel; travel is directed towards a suitable location for the selected activity.	No specific rules, but travel *when* a current patch is not suitable for the chosen activity. In this case, first assess the suitability of neighbouring patches within 50m, then assess the patches within 100m, and if a suitable location is still not found, jump at random between 3 – 6 patches (i.e. 150 – 300m).	*Ardipithecus*: Lose 3.2 kCal for every 50m of travel (i.e. one patch), and lose 0.9 additional hydrations and gain 0.9 additional fatigues for every extra 50m of travel (i.e. when travelling more than 50m in one time step). *Australopithecus*: Lose 2.9 kCal for every 50m of travel, and lose 0.8 additional hydrations and gain 0.8 additional fatigues for every additional 50m of travel.

Table 6.11. Sensitivity (S^+ and S^-) of the *Ardipithecus* model to small (i.e. +/- 10%) changes in input parameters. 33 parameters were selected for sensitivity analysis. Sensitivities were calculated by dividing the percentage of change in the output by the percentage of change in the input; Low values for S indicated low sensitivities. The rationale behind the baseline values for all parameters is outlined in Appendix 6.5. 'random' indicates that a value was randomly assigned between 0 and 'number'.

Parameter	**Base value**	**+10% value**	**S+**	**-10% value**	**S-**
number of fruit forest	random 21	random 23.1	0.20	random 18.9	0.47
number of fruit woodland	random 14	random 15.4	0.20	random 13.6	0.09
number of fruit savannah	random 7	random 7.7	0.07	random 6.3	0.24
amount USOs forest	random 7	random 7.7	0.04	random 6.3	0.25
amount USOs woodland	random 14	random 15.4	0.27	random 13.6	0.24
amount USOs savannah	random 21	random 23.1	0.24	random 18.9	0.09
amount of water forest	random 100	random 110	0.04	random 90	0.04
amount of water woodland	random 75	random 82.5	0.07	random 67.5	0.08
amount of water savannah	random 50	random 55	0.15	random 45	0.07
where - understory density criterion	< 50	< 55	0.19	< 45	0.13
where - tree density criterion	> 50	> 55	0.09	> 45	0.09
where - food tree density criterion	> 50	> 55	0.16	> 45	0.17
where - local temperature criterion	< 50	< 55	0.12	< 45	0.19
where - local luminosity criterion	< 50	< 55	0.03	< 45	0.13
where - understory feeding criterion	> 50	> 55	0.26	> 45	0.10
where - temperature feeding criterion	< 81.25	< 89.35	0.04	< 73.13	0.18
where - luminosity feeding criterion	< 81.25	< 89.35	0.12	< 73.13	0.22
when - feeding criterion	<144	< 158.4	0.20	<129,6	0.34
when - drinking criterion	<72	< 79.2	0.28	< 64.8	0.23
when - resting criterion	> 73	> 80.3	0.13	> 65.7	0.09
Initial - energy	random 10	random 11	0.26	random 9	0.08
Initial - hydration	random 10	random 11	0.11	random 9	0.16
Initial - fatigue	random 10	random 11	0.06	random 9	0.19
Step - energy	-2	-2,2	0.20	-1.8	0.42
Step - hydration	-1	-1.1	0.19	-0.9	0.12
Step - fatigue	+1	+1.1	0.05	+0.9	0.12
Feeding fruit - number fruits eaten	3,5	3.85	0.46	3.15	0.47
Feeding USOs - amount USOs eaten	3,5	3.85	0.21	3.15	0.03
Drinking - amount water drunk	50	55	0.17	45	0.66
Resting - fatigue	-2	-2.2	0.17	-1.8	0.07
Nesting - fatigue	-2	-2.2	0.33	-1.8	0.05
Travel - hydration	-0,9	-0.99	0.07	-0.81	0.09
Travel - fatigue	+0.9	+0.99	0.05	+0.81	0.11

Activity budgets and daily path lengths

Activity budgets and daily path lengths differed significantly between forest, mosaic and savannah landscapes for chimpanzees, *Ardipithecus*, and *Australopithecus* (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 15.7$, df = 2, $p < 0.001$; Table 6.13, Figure 6.5 – Figure 6.6). For all three hominid species, individuals spent significantly more time resting and nesting in forests than in mosaics and savannahs, and significantly less time nesting and resting in savannahs than in mosaics (Table 6.14). Additionally, time spent travelling and travel distances were significantly longer in savannahs than in forests and mosaics, and travel time and distance was significantly shorter in forests than in mosaics. For all species, individuals spent significantly more time feeding in mosaics as compared to forests; For *Ardipithecus* and *Australopithecus*, significantly more time was spent feeding in savannahs as compared to forests and mosaics, chimpanzees, however, spent significantly less time feeding in savannahs as compared to forests and mosaics. Chimpanzees drank for significantly less time in savannahs than in forests and mosaics, and drank for more time in mosaics as compared to forests. *Ardipithecus* and *Australopithecus* spent significantly more time drinking in savannahs than in forests and mosaics, but drinking times did not differ significantly between mosaics and forests (Table 6.14).

Table 6.12. Sensitivity (S$^+$ and S$^-$) of the *Australopithecus* model to small (i.e. +/- 10%) changes in input parameters. 35 parameters were selected for analysis. Sensitivities were calculated by dividing the percentage of change in the output by the percentage of change in the input; Low values for S indicated low sensitivities. The rationale behind the baseline values for all parameters is outlined in Appendix 6.5. Within the table, ‘random’ indicates that a value was randomly assigned between 0 and ‘number’.

Parameter	**Base value**	**+10% value**	**S+**	**-10% value**	**S-**
number of fruit forest	random 21	random 23.1	0.23	random 18.9	0.24
number of fruit woodland	random 14	random 15.4	0.05	random 12.6	0.11
number of fruit savannah	random 7	random 7.7	0.19	random 6.3	0.03
amount USOs forest	random 7	random 7.7	0.09	random 6.3	0.13
amount USOs woodland	random 14	random 15.4	0.12	random 12.6	0.17
amount USOs savannah	random 21	random 23.1	0.13	random 18.9	0.01
amount of water forest	random 100	random 110	0.16	random 90	0.05
amount of water woodland	random 75	random 82.5	0.23	random 67.5	0.03
amount of water savannah	random 50	random 55	0.01	random 45	0.13
amount meat	random 21	random 23.1	0.04	random 18.9	0.08
where - understory density criterion	< 50	< 55	0.06	< 45	0.10
where - tree density criterion	> 50	> 55	0.08	> 45	0.23
where - food tree density criterion	> 50	> 55	0.10	> 45	0.04
where - local temperature criterion	< 50	< 55	0.05	< 45	0.09
where - local luminosity criterion	< 50	< 55	0.12	< 45	0.08
where - understory feeding criterion	> 50	> 55	0.14	> 45	0.16
where - temperature feeding criterion	< 87.5	< 96.25	0.19	< 78.75	0.13
where - luminosity feeding criterion	< 87.5	< 96.25	0.01	< 78.75	0.05
when - feeding criterion	< 144	< 158.4	0.11	< 129.6	0.30
when - drinking criterion	< 72	< 79.2	0.16	< 64.8	0.09
when - resting criterion	> 73	> 80.3	0.06	> 65.7	0.10
Initial - energy	random 10	random 11	0.03	random 9	0.15
Initial - hydration	random 10	random 11	0.07	random 9	0.18
Initial - fatigue	random 10	random 11	0.05	random 9	0.17
Step - energy	-2	-2.2	0.20	-1.8	0.34
Step - hydration	-1	-1.1	0.37	-0.9	0.10
Step - fatigue	+1	+1.1	0.08	+0.9	0.28
Feeding fruit - number fruits eaten	3.5	3.85	0.29	3.15	0.32
Feeding USOs - amount USOs eaten	3.5	3.85	0.04	3.15	0.38
Feeding meat - amount meat eaten	3.5	3.85	0.09	3.15	0.13
Drinking - amount water drunk	50	55	0.15	45	0.69
Resting - fatigue	-2	-2.2	0.11	-1.8	0.04
Nesting - fatigue	-2	-2.2	0.18	-1.8	0.15
Travel - hydration	-0.8	-0.88	0.05	-0.72	0.09
Travel - fatigue	+0.8	+0.88	0.07	+0.72	0.06

In forest environments, significant differences were found in travel distances and time spent feeding, nesting, resting and travelling between the three hominid species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 9.0$, df = 2, $p \leq 0.011$). Chimpanzees spent significantly more time feeding and travelling, and had significantly longer daily path lengths than *Ardipithecus* and *Australopithecus*, and *Australopithecus* had shorter feeding times, travel times and travel distances than *Ardipithecus* (Table 6.15). *Australopithecus* spent significantly more time resting as compared to chimpanzees and *Ardipithecus*, and *Ardipithecus* spent more time resting than chimpanzees. Chimpanzees spent significantly less time nesting than *Australopithecus*, but no significant differences in nesting time were found for chimpanzees and *Ardipithecus*, and for *Ardipithecus* and *Australopithecus* (Table 6.15). Time spent drinking did not differ significantly between species within forest environments (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 0.0$, $df = 2$, $p = 1.000$).

Significant differences in activity budgets and daily path lengths between species were also observed in mosaic landscapes (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 7.9$, $df = 2$, $p \leq 0.019$). Chimpanzees travelled and fed for significantly more time and travelled significantly longer daily distances than *Ardipithecus* and *Australopithecus*, and *Ardipithecus* had longer daily path lengths, feeding times and travel times than *Australopithecus* (Table 6.15). Chimpanzees spent significantly less time resting than *Ardipithecus* and *Australopithecus*, and *Ardipithecus* spent less time resting than *Australopithecus*. *Australopithecus* nested for significantly more time than chimpanzees, but no significant differences were found in nesting time between chimpanzees and *Ardipithecus*, and between *Ardipithecus* and *Australopithecus*. Chimpanzees spent significantly more time drinking than *Ardipithecus* and *Australopithecus*, but no significant differences were found in drinking time between the two hominin species (Table 6.15).

Within savannahs, significant differences were found in travel distance and time spent feeding, drinking, resting and travelling between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 58.1$, $df = 2$, $p < 0.001$). Chimpanzees spent significantly more time travelling and had longer daily path lengths than *Ardipithecus* and *Australopithecus*; *Ardipithecus* travelled for more time than *Australopithecus*, but no significant differences were observed for daily travel distance (Table 6.15). *Ardipithecus* spent significantly more time feeding than chimpanzees and *Australopithecus*, and *Australopithecus* fed for more time than chimpanzees. *Australopithecus* spent significantly more time drinking than *Ardipithecus* and chimpanzees, and *Ardipithecus* spent more time drinking than chimpanzees. Resting time was significantly less for *Ardipithecus* as compared to chimpanzees and *Australopithecus*, and chimpanzees rested for less time than *Australopithecus* (Table

6.15). Time spent nesting was not significantly different between species in savannah landscapes (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 1.0$, $df = 2$, $p = 0.616$).

Feeding time, food intake and water intake

Feeding time, food intake and water intake differed significantly between environments for chimpanzees, *Ardipithecus*, and *Australopithecus* (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 33.9$, $df = 2$, $p < 0.001$; Table 6.13, Figure 6.7 – 6.9). Across the hominid species, fruit intake, time spent feeding on fruit and water intake were significantly less in savannahs as compared to forests and mosaics (Table 6.14). For chimpanzees and *Ardipithecus* fruit feeding time, fruit intake and water intake were significantly higher in mosaics as compared to forests, but no difference was observed in fruit feeding time and fruit intake in forests and mosaics for *Australopithecus*. *Australopithecus* water intake was significantly higher in mosaics as compared to forests. For *Ardipithecus* and *Australopithecus*, time spent feeding on USOs and USO intake were significantly higher in savannahs as compared to forests and mosaics, and in mosaics as compared to forests. For *Australopithecus*, meat intake and time spent feeding on meat was significantly higher in savannahs as compared to forests and mosaics, but no difference was observed between mosaics and forests (Table 6.14).

Within forest environments, food intake and feeding time differed significantly between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 79.2$, $df = 2$, $p < 0.001$). Chimpanzees spent significantly more time feeding on fruit and had a significantly higher fruit intake than *Ardipithecus* and *Australopithecus*, and *Ardipithecus* had significantly higher fruit intake and fruit feeding times than *Australopithecus* (Table 6.15). *Australopithecus* had significantly higher USO intake and spent more time feeding on USOs than *Ardipithecus* (Table 6.15). Water intake was not significantly different between species (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 1.7$, $df = 2$, $p = 0.466$).

Within mosaic landscapes, water intake, food intake and feeding time differed significantly between the three hominids (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 21.3$, $df = 2$, $p < 0.001$). Chimpanzees had significantly lower water intake than *Ardipithecus* and *Australopithecus*, but water intake did not differ significantly between the two hominin species (Table 6.15). *Australopithecus* fed for significantly less time on fruit and had lower fruit intake than chimpanzees and *Ardipithecus*, and *Ardipithecus* had significantly lower fruit intake and spent less time feeding on fruit than chimpanzees. Time spent feeding on USOs in mosaic environments did not differ significantly between *Ardipithecus* and *Australopithecus* (Table 6.15).

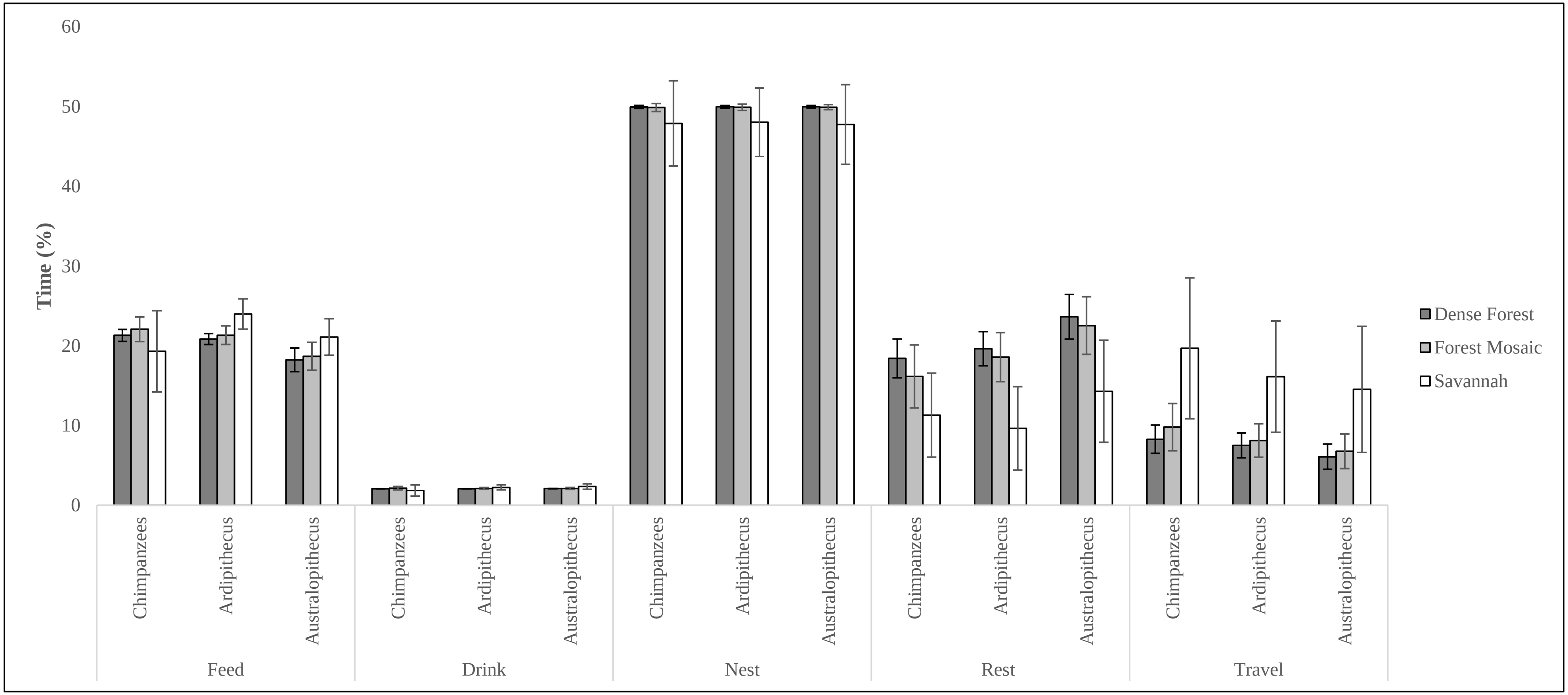

Figure 6.5. Model output for the daily activity budgets (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah landscapes.

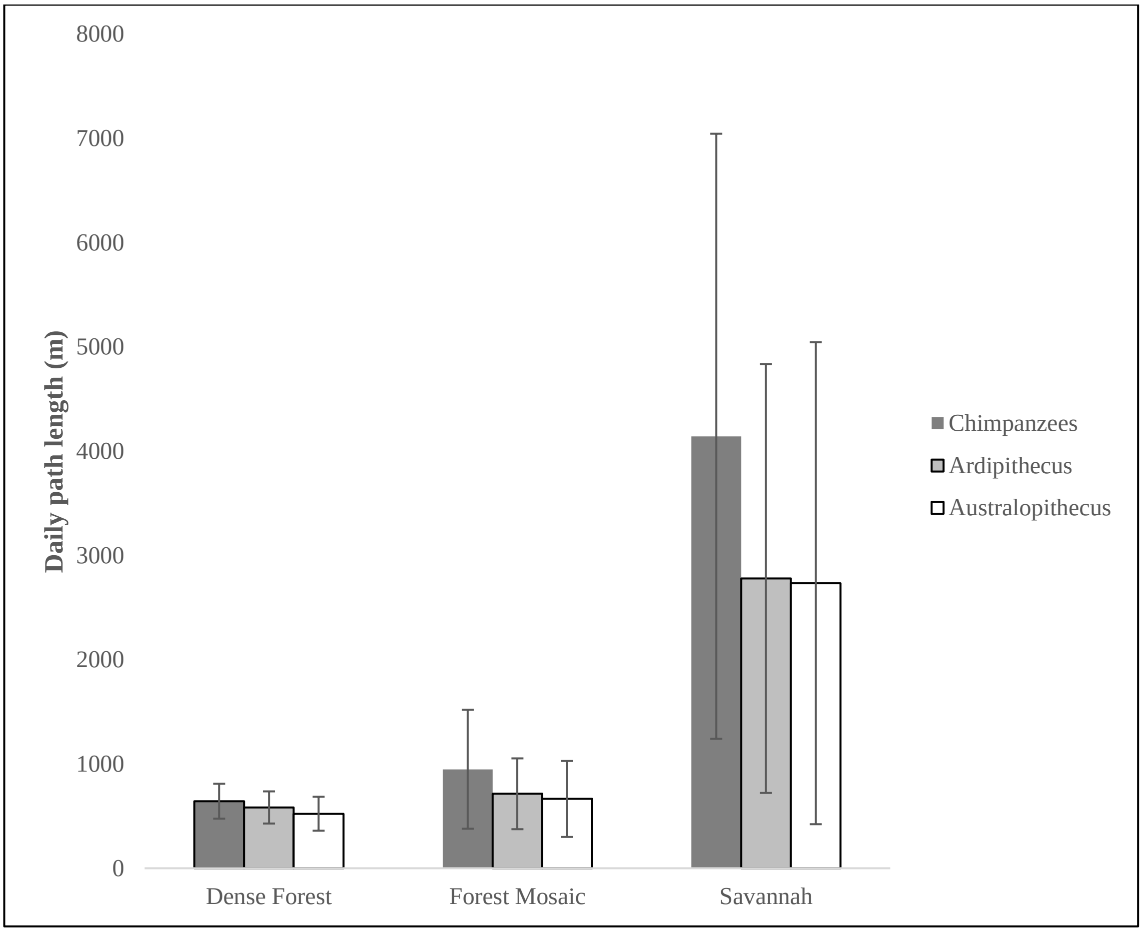

Figure 6.6. Model output for the daily path lengths of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah landscapes.

Within savannah habitats, water intake, food intake and feeding time differed significantly between the three hominid species (in all cases, Kruskal-Wallis: $N_{1,2,3}$ = 30, H ≥ 63.0, df = 2, p < 0.001). *Ardipithecus* fed for significantly more time on fruit and had significantly higher fruit intakes than chimpanzees and *Australopithecus*, and chimpanzees had higher fruit intakes and spent significantly more time feeding on fruit than *Australopithecus* (Table 6.15). *Ardipithecus* furthermore spent significantly more time feeding on USOs and had significantly higher USO intakes than *Australopithecus*. *Australopithecus* had significantly higher water intake than chimpanzees and *Ardipithecus*, and *Ardipithecus* had significantly higher water intake than chimpanzees (Table 6.15).

Energy, hydration and fatigue budgets

Energy, hydration and fatigue budgets were significantly different for chimpanzees, *Ardipithecus* and *Australopithecus* between forest, mosaic and savannah environments (in all cases, Kruskal-Wallis: $N_{1,2,3}$ = 30, H ≥ 32.7, df = 2, p < 0.001; Table 6.13, Figure

6.10 – 6.12). For all species, energy budgets were significantly higher in forests as compared to mosaics and savannahs, and for mosaics as compared to savannahs (Table 6.14). Additionally, fatigue budgets were significantly lower in forests as compared to savannahs and mosaics, and for mosaics as compared to savannahs. For all species, hydrations budgets were significantly lower in savannah habitats as compared to forest and mosaic landscapes; for *Ardipithecus* and chimpanzees no significant differences were observed in hydration budgets between forests and mosaics, but for *Australopithecus* hydration budgets in forests were significantly lower than in mosaics (Table 6.14).

In forest environments, energy, hydration and fatigue budgets differed significantly between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 9.8$, df = 2, $p \leq 0.008$). Fatigue budgets were significantly lower for *Australopithecus* than for *Ardipithecus* and chimpanzees, and for *Ardipithecus* as compared to chimpanzees (Table 6.15). Energy budgets were significantly higher for *Australopithecus* than for chimpanzees, but energy budgets did not differ significantly between *Australopithecus* and *Ardipithecus*, and between chimpanzees and *Ardipithecus*. *Australopithecus* had significantly lower hydration budgets than chimpanzees and *Ardipithecus*, and no significant differences were observed in hydration budgets between *Ardipithecus* and chimpanzees (Table 6.15).

Energy and fatigue budgets differed significantly between species in mosaic landscapes (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 47.5$, df = 2, $p < 0.001$), with energy budgets being significantly lower and fatigue budgets being significantly higher for chimpanzees than for *Ardipithecus* and *Australopithecus*, and *Ardipithecus* having significantly lower energy budgets and significantly higher fatigue budgets than *Australopithecus* (Table 6.15). Hydration budgets were not significantly different between chimpanzees, *Ardipithecus* and *Australopithecus* in mosaics (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 1.1$, df = 2, $p = 0.572$).

In savannah habitats, energy, hydration and fatigue budgets were also significantly different between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 68.8$, df = 2, $p < 0.001$). Energy budgets and hydration budgets were significantly higher for *Australopithecus* as compared to chimpanzees and *Ardipithecus*, and for *Ardipithecus* as compared to chimpanzees (Table 6.15). Fatigue budgets, on the other hand, were significantly lower for *Australopithecus* than for chimpanzees and *Ardipithecus*, and for *Ardipithecus* as compared to chimpanzees (Table 6.15).

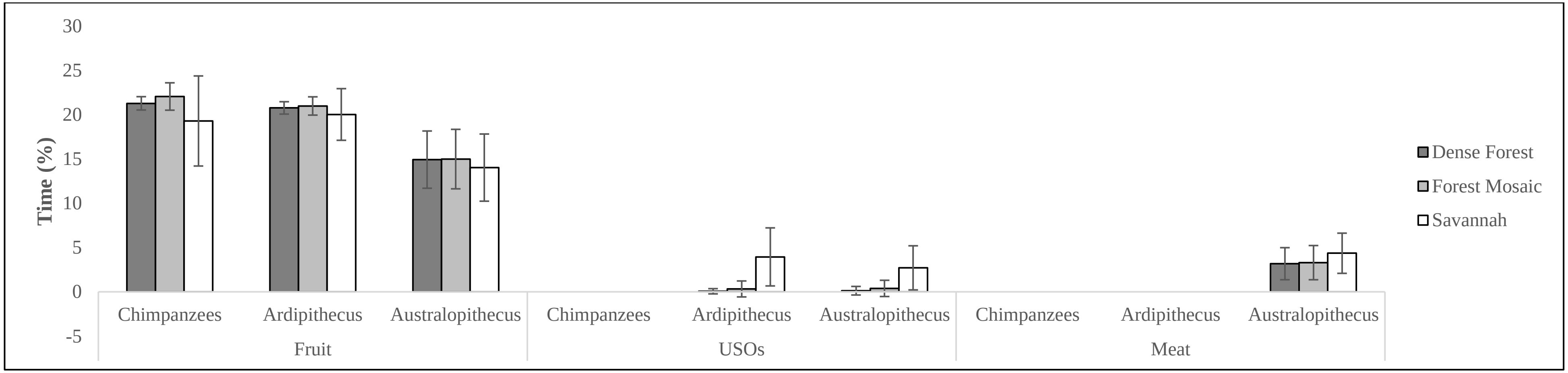

Figure 6.7. Model output for the daily feeding time (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forests, forest mosaics and savannahs. In the model, chimpanzees feed only on fruit, *Ardipithecus* on fruit and USOs, and *Australopithecus* on fruit, USOs and meat.

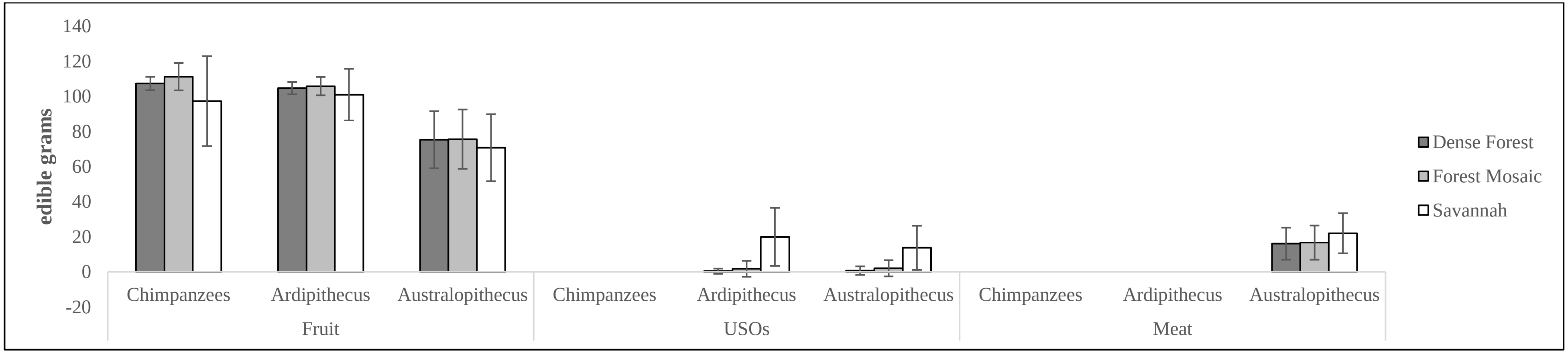

Figure 6.8. Model output for the daily food intake (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah environments. Chimpanzees feed only on fruit, *Ardipithecus* on fruit and USOs, and *Australopithecus* on fruit, USOs and meat.

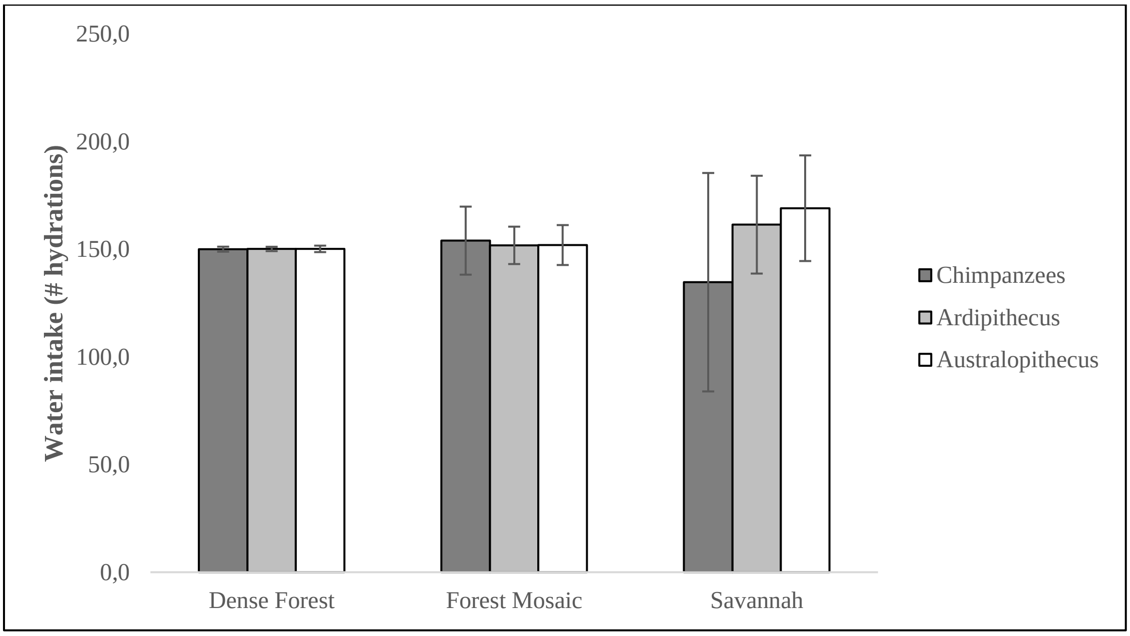

Figure 6.9. Model output for the daily water intake (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah environments.

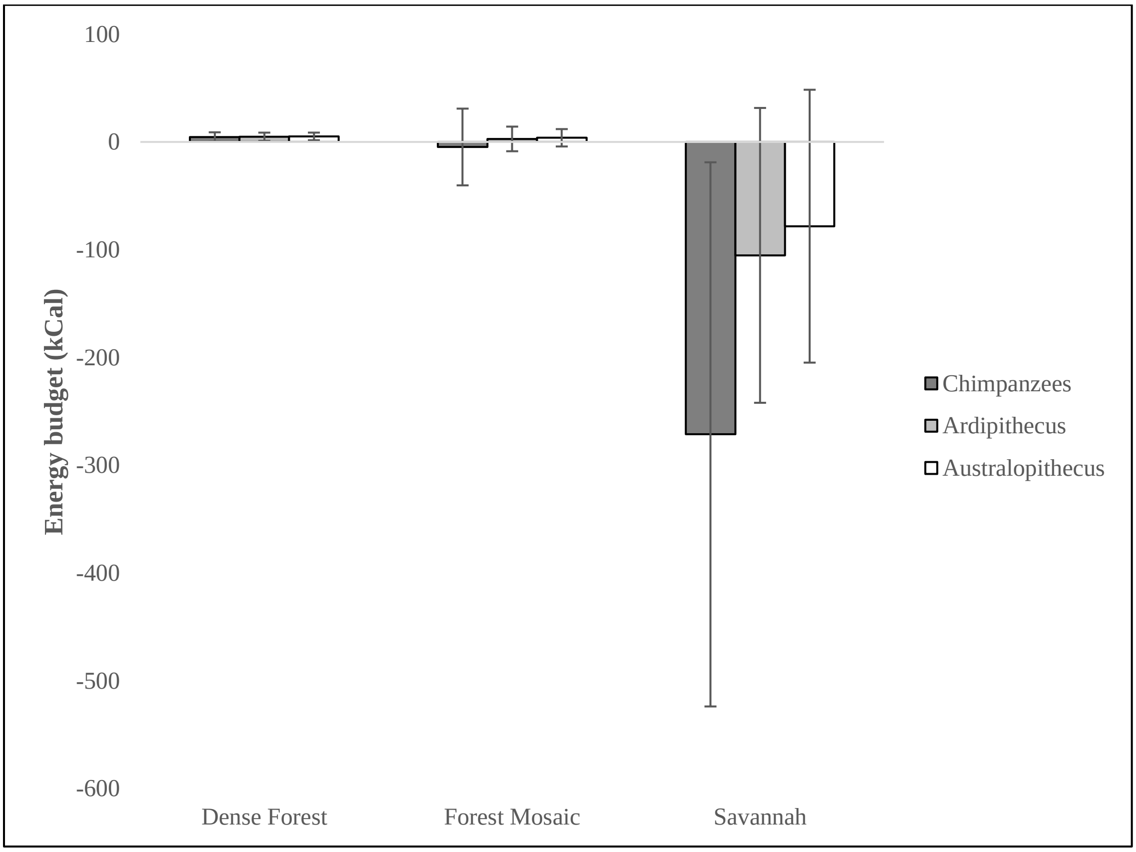

Figure 6.10. Model output for the daily energy budgets (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forests, forest mosaics and savannahs.

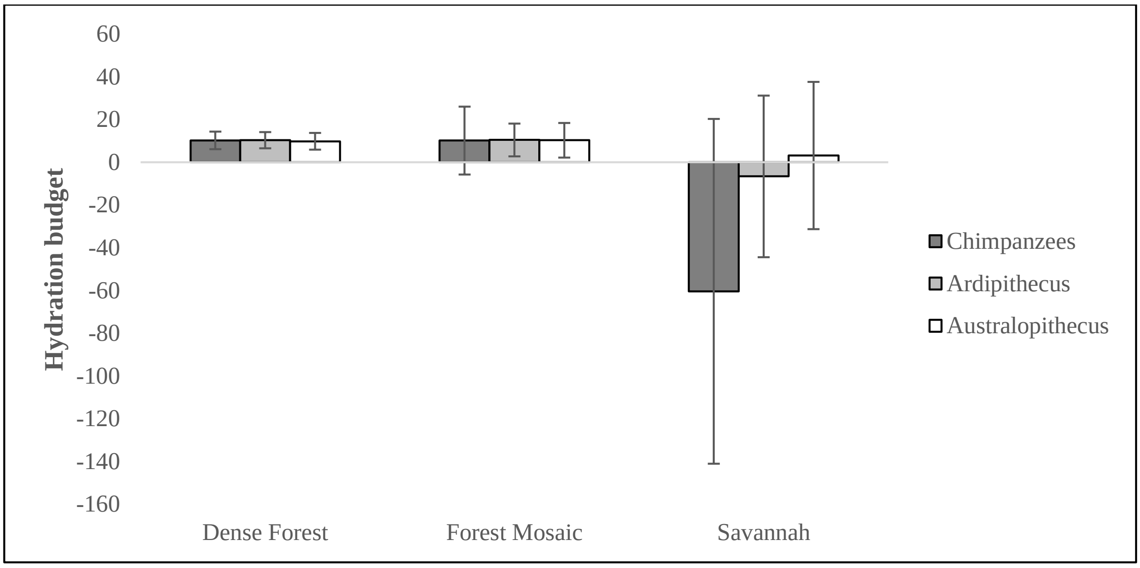

Figure 6.11. Model output for the daily hydration budgets (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forests, forest mosaics and savannahs.

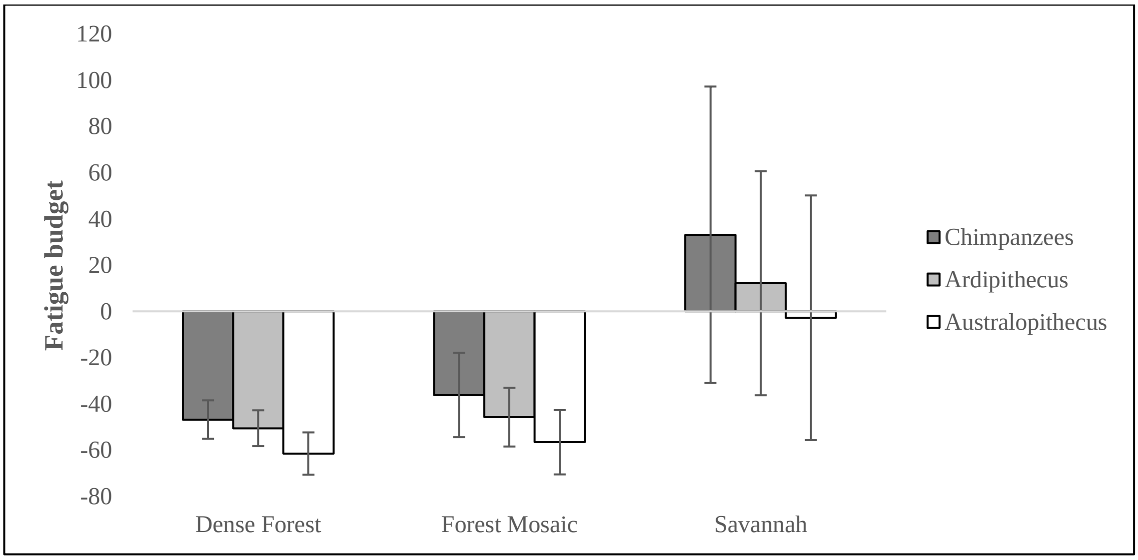

Figure 6.12. Model output for the daily fatigue budgets (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forests, forest mosaics and savannahs.

Preferred and behaviourally preferred vegetation

Vegetation type usage differed significantly between forests, mosaics and savannahs for chimpanzees, *Ardipithecus*, and *Australopithecus* (in all cases, Kruskal-Wallis: $N_{1,2,3}$ = 30, $H \geq 67.4$, df = 2, $p < 0.001$; Table 6.13, Figure 6.13). Across all species, individuals spent significantly more time in woodland and grassland in savannah environments as compared to forest and mosaic landscapes, and individuals in mosaics spent significantly more time in woodland and grassland than individuals in forests (Table 6.14). Significantly more time was spent in forest vegetation types in forest landscapes as compared to mosaics and savannahs, and for mosaics as compared to savannah habitats (Table 6.14). Across all landscapes and for each hominid species, forest was the preferred vegetation type overall and for each behaviour, and woodland and savannah grassland vegetation types were avoided (in all cases: $\chi^2 \geq 1{,}244.6$, df = 2, $p < 0.001$; Figure 6.14). For detail on behavioural vegetation type usage and preferences across the three hominid species, see Appendix 6.11.

In forest environments, vegetation type usage differed significantly between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 20.4$, df = 2, $p < 0.001$). *Australopithecus* spent significantly less time in forest vegetation types than *Ardipithecus* and chimpanzees, but time spent in forest vegetation types did not differ significantly between for chimpanzees and *Ardipithecus* (Table 6.15). Time spent in woodland was significantly more for *Australopithecus* than for chimpanzees and *Ardipithecus,* and *Ardipithecus* spent significantly more time in woodland than chimpanzees. *Australopithecus* spent significantly more time in grassland than *Ardipithecus* and chimpanzees, and chimpanzees spent significantly more time in grassland than *Ardipithecus* (Table 6.15).

Forest and grassland vegetation type usage was significantly different between species in mosaic environments (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 7.6$, df = 2, $p \leq 0.023$). *Australopithecus* spent significantly more time in grassland than chimpanzees and *Ardipithecus*, and chimpanzees spent significantly more time in grassland than *Ardipithecus* (Table 6.15). *Australopithecus* spent significantly less time in forest vegetation than *Ardipithecus*, but forest usage did not differ significantly between *Australopithecus* and chimpanzees, and between chimpanzees and *Ardipithecus* (Table 6.15). Amount of time spent in woodland vegetation was not significantly different between species within mosaics (Kruskal-Wallis: $N_{1,2,3} = 30$, $H = 2.4$, df = 2, $p = 0.306$).

Within savannah environments, vegetation type usage differed significantly between species (in all cases, Kruskal-Wallis: $N_{1,2,3} = 30$, $H \geq 8.0$, df = 2, $p \leq 0.018$). Chimpanzees spent significantly more time in forest vegetation than *Ardipithecus*, but *Australopithecus* and *Ardipithecus,* as well as chimpanzees and *Australopithecus*, did not differ significantly in this respect (Table 6.15). *Ardipithecus* spent significantly less time in grassland than *Australopithecus* and chimpanzees, but time spent in grassland did not differ significantly for chimpanzees and *Australopithecus*. *Ardipithecus* spent significantly more time in woodland than chimpanzees and *Australopithecus*, but no significant differences occurred in time spent in woodland vegetation for chimpanzees and *Australopithecus* (Table 6.15).

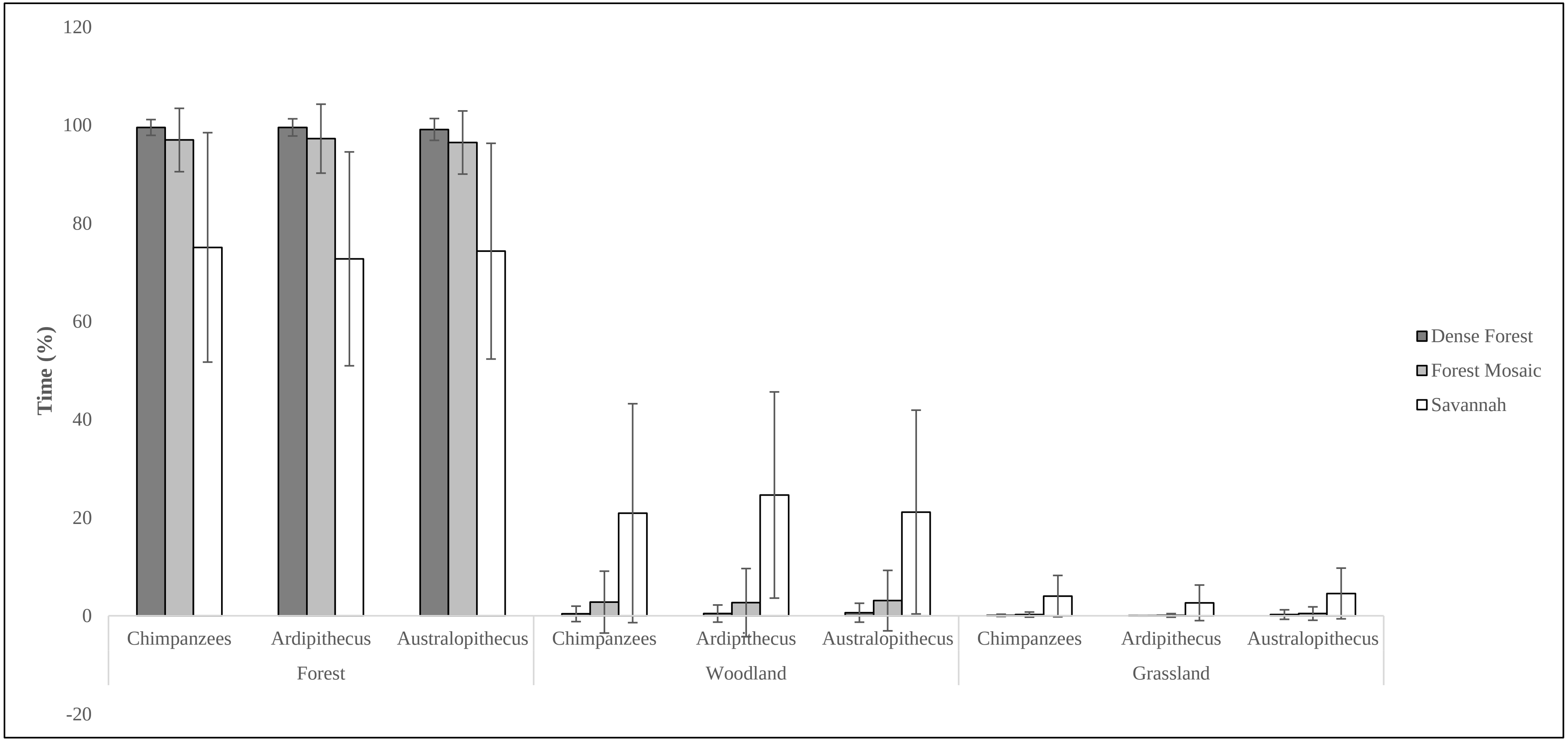

Figure 6.13. Model output for the vegetation type (i.e. forest, woodland and savannah grassland) usage (24 hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah environments.

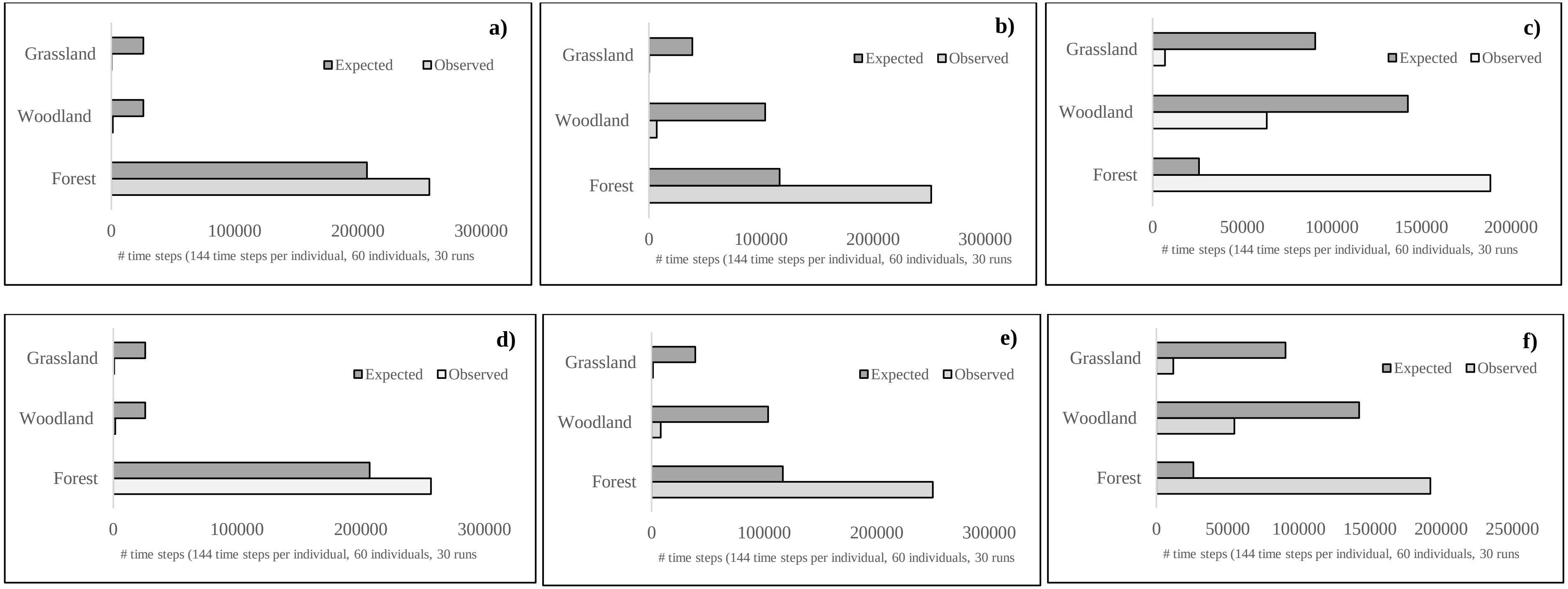

Figure 6.14. Observed vs expected vegetation type usage for *Ardipithecus ramidus* simulated in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs, and for *Australopithecus anamensis/ afarensis* simulated in **d)** dense forests, **e)** forest mosaics, and **f)** savannahs. Expected frequencies followed from the vegetation cover as outlined for the models (i.e. p. 203).

Table 6.13. Model output (i.e. mean ± standard deviation) on the daily activity budgets (% time of 24-hours), daily path lengths (m), food intake (# edible grams), water intake (hydrations), energy budgets (kCal), hydration budgets (hydrations), fatigue budgets (fatigues) and vegetation type usage (% time of 24-hours) of chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah landscapes. Chimpanzees are parameterised to only feed on fruits, *Ardipithecus* feeds on fruits and underground storage organs (USOs), and *Australopithecus* feeds on meat, fruit and USOs.

	Chimpanzees			***Ardipithecus***			***Australopithecus***		
	Forest	**Mosaic**	**Savannah**	**Forest**	**Mosaic**	**Savannah**	**Forest**	**Mosaic**	**Savannah**
Time spent feeding	21.3±0.8%	22.1±1.5%	19.3±5.1%	20.8±0.7%	21.3±1.2%	24.0±1.9%	18.2±1.5%	18.7±1.8%	21.1±2.3%
Time spent drinking	2.1±0.0%	2.1±0.2%	1.8±0.7%	2.1±0.0%	2.1±0.1%	2.2±0.3%	2.1±0.0%	2.1±0.1%	2.3±0.3%
Time spent nesting	49.9±0.2%	49.9±0.5%	47.9±5.3%	50.0±0.2%	49.9±0.4%	48.0±4.3%	50.0±0.2%	49.9±0.3%	47.7±5.0%
Time spent resting	18.4±2.4%	16.1±4.0%	11.3±5.3%	19.6±2.1%	18.6±3.1%	9.6±5.2%	23.6±2.8%	22.5±3.6%	14.3±6.4%
Time spent travelling	8.3±1.8%	9.8±3.0%	19.7±8.8%	7.5±1.6%	8.1±2.1%	16.1±7.0%	6.1±1.6%	6.8±2.2%	14.5±7.9%
Daily path length	642.6±167.4m	949.1±570.2m	4,142.3±2,901.4m	583.1±154.4m	714.0±339.6m	2,778.7±2,056.5m	522.6±162.7m	664.3±364.3m	2,733.2±2,311.0m
Time spent feeding – fruit	21.3±0.8%	22.1±1.5%	19.3±5.1%	20.8±0.7%	21.3±1.2%	24.0±1.9%	14.9±3.2%	15.0±3.4%	14.0±3.8%
Time spent feeding – USOs	-	-	-	0.1±0.3%	0.3±0.9%	4.0±3.3%	0.1±0.5%	0.4±0.9%	2.7±2.5%
Time spent feeding – meat	-	-	-	-	-	-	3.2±1.8%	3.3±1.9%	4.4±2.3%
Fruit intake	107.3±3.8	111.2±7.8	97.3±25.6	104.7±3.5	105.8±5.2	101.0±14.7	75.3±16.3	75.6±16.9	70.7±19.1
USO intake	-	-	-	0.3±1.5	1.7±5.2	19.9±16.5	0.6±2.4	2.0±4.6	13.6±12.6
Meat intake	-	-	-	-	-	-	16.0±9.1	16.6±9.7	22.0±11.4
Water intake	150.1±1.2	154.0±15.8	134.7±50.7	150.2±1.0	151.8±8.7	161.4±22.7	150.2±1.5	152.0±9.3	169.1±24.5
Energy budget	4.6±4.3kCal	-4.7±35.6kCal	-271.4±252.5kCal	4.8±3.8kCal	2.8±11.4kCal	-105.3±136.8kCal	5.1±3.5kCal	3.9±8.1kCal	-78.2±126.6kCal
Hydration budget	10.2±4.1	10.1±15.9	-60.4±80.7	10.3±3.8	10.4±7.7	-6.6±37.8	9.8±3.9	10.3±8.1	3.2±34.5
Fatigue budget	-46.8±8.3	-36.2±18.3	33.1±64.2	-50.6±7.8	-45.8±12.7	12.2±48.5	-61.5±9.2	-56.7±13.9	-2.8±52.9
Time spent in forest	99.5±1.6%	97.0±6.5%	75.1±23.4%	99.5±1.7%	97.2±7.0%	72.8±21.8%	99.1±2.2%	96.5±6.4%	74.3±22.0%
Time spent in woodland	0.4±1.6%	2.8±6.3%	20.9±22.3%	0.5±1.7%	2.7±6.9%	24.6±21.0%	0.6±1.9%	3.1±6.2%	21.1±20.8%
Time spent in grassland	0.1±0.2%	0.2±0.5%	4.0±4.2%	0.0±0.0%	0.1±0.4%	2.6±3.6%	0.2±1.0%	0.4±1.4%	4.5±5.2%

Table 6.14. *Post-hoc* Mann-Whitney U test statistics for the comparisons of landscape use for chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* between dense forest (F), forest mosaic (M) and savannah (S) environments. An ‘X’ means not included within the model. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)								
	Chimpanzees			***Ardipithecus***			***Australopithecus***		
	F vs M	**F vs S**	**M vs S**	**F vs M**	**F vs S**	**M vs S**	**F vs M**	**F vs S**	**M vs S**
Time spent feeding	M > F Z = -6.5*	F > S Z = -6.3*	M > S Z = -6.6*	M > F Z = -6.3*	S > F Z = -6.7*	S > M Z = -6.6*	M > F Z = -5.5*	S > F Z = -6.7*	S > M Z = -6.7*
Time spent drinking	M > F Z = -4.4*	F > S Z = -6.3*	M > S Z = -6.3*	F = M Z = 0.0**	S > F Z = -7.3*	S > M Z = -7.3*	F = M Z = 0.0**	S > F Z = -7.2*	S > M Z = -7.2*
Time spent nesting	F > M Z = -3.9*	F > S Z = -6.8*	M > S Z = -6.7*	F > M Z = -4.7*	F > S Z = -6.8*	M > S Z = -6.8*	F > M Z = -4.6*	F > S Z = -6.9*	M > S Z = -6.9*
Time spent resting	F > M Z = -6.7*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -5.8*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -6.1*	F > S Z = -6.7*	M > S Z = -6.7*
Time spent travelling	M > F Z = -6.6*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -5.6*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.4*	S > F Z = -6.7*	S > M Z = -6.7*
Daily path length	M > F Z = -6.7*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.3*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.3*	S > F Z = -6.7*	S > M Z = -6.7*
Time spent feeding – *fruit*	M > F Z = -6.5*	F > S Z = -6.3*	M > S Z = -6.6*	M > F Z = -5.2*	F > S Z = -6.2*	M > S Z = -6.2*	F = M Z = -0.8**	F > S Z = -5.0*	M > S Z = -5.0*
Time spent feeding – *USOs*	X	X	X	M > F Z = -6.1*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.5*	S > F Z = -6.7*	S > M Z = -6.7*
Time spent feeding – *meat*	X	X	X	X	X	X	F = M Z = -1.5**	S > F Z = -6.6*	S > M Z = -6.5*
Fruit intake	M > F Z = -6.4*	F > S Z = -6.2*	M > S Z = -6.6*	M > F Z = -5.2*	F > S Z = -6.2*	M > S Z = -6.2*	F = M Z = -0.8**	F > S Z = -6.7*	M > S Z = -5.0*
USO intake	X	X	X	M > F Z = -6.1*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.5*	S > F Z = -6.7*	S > M Z = -6.7*
Meat intake	X	X	X	X	X	X	F = M Z = -1.5**	S > F Z = -6.6*	S > M Z = -6.5*
Water intake	M > F Z = -6.9*	F > S Z = -5.8*	M > S Z = -5.8*	M > F Z = -5.6*	S > F Z = -6.9*	S > M Z = -6.7*	M > F Z = -6.2*	S > F Z = -6.9*	S > M Z = -6.7*
Energy budget	F > M Z = -6.5*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -5.5*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -4.3*	F > S Z = -6.7*	M > S Z = -6.7*
Hydration budget	F = M Z = -1.3**	F > S Z = -6.7*	M > S Z = -6.7*	F = M Z = -0.5**	F > S Z = -6.7*	M > S Z = -6.7*	M > F Z = -2.6*	F > S Z = -4.4*	M > S Z = -4.9*
Fatigue budget	M > F Z = -6.7*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.1*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.6*	S > F Z = -6.7*	S > M Z = -6.7*
Time spent in forest	F > M Z = -6.7*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -6.4*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -6.7*	F > S Z = -6.7*	M > S Z = -6.7*
Time spent in woodland	M > F Z = -6.6*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.4*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.7*	S > F Z = -6.7*	S > M Z = -6.7*
Time spent in grassland	M > F Z = -6.4*	S > F Z = -6.9*	S > M Z = -6.7*	M > F Z = -5.0*	S > F Z = -7.1*	S > M Z = -6.7*	M > F Z = -4.1*	S > F Z = -7.1*	S > M Z = -7.1*

*significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$); **no significant difference, i.e. $p > 0.0167$.

Table 6.15. *Post-hoc* Mann-Whitney U test statistics for the comparisons of landscape use for chimpanzees (Ch), *Ardipithecus* (Ar) and *Australopithecus* (Au) in dense forest, forest mosaic and savannahs. An 'X' means not included within the model, and a '-' means Kruskal-Wallis tests not significant (no *post-hoc* tests). In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)								
	Dense Forest			***Forest Mosaic***			***Savannah***		
	Ch vs Ar	**Ch vs Au**	**Ar vs Au**	**Ch vs Ar**	**Ch vs Au**	**Ar vs Au**	**Ch vs Ar**	**Ch vs Au**	**Ar vs Au**
Time spent feeding	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.4*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ar > Ch Z = -6.7*	Au > Ch Z = -6.0*	Ar > Au Z = -6.7*
Time spent drinking	-	-	-	Ch > Ar Z = -4.4*	Ch > Au Z = -4.4*	Ar = Au Z = 0.0**	Ar > Ch Z = -6.7*	Au > Ch Z = -6.8*	Au > Ar Z = -5.2*
Time spent nesting	Ch = Ar Z = -2.1**	Au > Ch Z = -2.9*	Ar = Au Z = -0.9**	Ch = Ar Z = -0.9**	Au > Ch Z = -2.7*	Ar = Au Z = -2.0**	Ch > Ar Z = -5.0*	Au > Ch Z = -6.3*	Au > Ar Z = -6.6*
Time spent resting	Ar > Ch Z = -6.6*	Au > Ch Z = -6.7*	Au > Ar Z = -6.7*	Ar > Ch Z = -6.7*	Au > Ch Z = -6.7*	Au > Ar Z = -6.7*	-	-	-
Time spent travelling	Ch > Ar Z = -6.5*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.3*	Ch > Au Z = -6.6*	Ar > Au Z = -4.2*
Daily path length	Ch > Ar Z = -5.9*	Ch > Au Z = -6.7*	Ar > Au Z = -6.3*	Ch > Ar Z = -6.5*	Ch > Au Z = -6.7*	Ar > Au Z = -3.5*	Ch > Ar Z = -6.6*	Ch > Au Z = -6.6*	Ar = Au Z = -0.8**
Time spent feeding – fruit	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ar > Ch Z = -2.9*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*
Time spent feeding – USOs	X	X	Au > Ar Z = -4.3*	X	X	Ar = Au Z = -1.8**	X	X	Ar > Au Z = -5.6*
Time spent feeding – meat	X	X	X	X	X	X	X	X	X
Fruit intake	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.6*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ar > Ch Z = -2.9*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*
USO intake	X	X	Au > Ar Z = -4.3*	X	X	Ar = Au Z = -1.8**	X	X	Ar > Au Z = -5.6*
Meat intake	X	X	X	X	X	X	X	X	X
Water intake	-	-	-	Ch > Ar Z = -4.1*	Ch > Au Z = -3.7*	Ar = Au Z = -0.8**	Ar > Ch Z = -6.2*	Au > Ch Z = -6.6*	Au > Ar Z = -5.6*
Energy budget	Ch = Ar Z = -1.0**	Au > Ch Z = -3.1*	Ar = Au Z = -2.0**	Ar > Ch Z = -5.2*	Au > Ch Z = -6.2*	Au > Ar Z = -2.5*	Ar > Ch Z = -6.7*	Au > Ch Z = -6.7*	Au > Ar Z = -3.9*
Hydration budget	Ch = Ar Z = -0.5**	Ch > Au Z = -3.0*	Ar > Au Z = -2.8*	-	-	-	Ar > Ch Z = -6.7*	Au > Ch Z = -6.7*	Au > Ar Z = -5.0*
Fatigue budget	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.1*	Ch > Au Z = -6.6*	Ar > Au Z = -5.4*
Time spent in forest	Ch = Ar Z = -0.5**	Ch > Au Z = -5.1*	Ar > Au Z = -4.9*	Ch = Ar Z = -1.0**	Ch = Au Z = -1.8**	Ar > Au Z = -2.7*	Ch > Ar Z = -2.6*	Ch = Au Z = -1.4**	Ar = Au Z = -1.9**
Time spent in woodland	Ar > Ch Z = -2.0*	Au > Ch Z = -4.4*	Au > Ar Z = -2.8*	-	-	-	Ar > Ch Z = -3.9*	Ch = Au Z = -0.8**	Ar > Au Z = -4.0*
Time spent in grassland	Ch > Ar Z = -6.5*	Au > Ch Z = -5.7*	Au > Ar Z = -7.0*	Ch > Ar Z = -6.0*	Au > Ch Z = -4.4*	Au > Ar Z = -6.5*	Ch > Ar Z = -2.6*	Ch = Au Z = -2.2**	Au > Ar Z = -6.4*

*significant difference, i.e. p < 0.0167 (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: α = 0.05 / 3 = 0.0167); **no significant difference, i.e. p > 0.0167.

Site selectivity

Following model rules, chimpanzees, *Ardipithecus* and *Australopithecus* in dense forests, forest mosaics and savannahs used the total range of vegetation features and micro-climates found in forest, woodland and grassland vegetation types for travel (Table 6.8 – 6.10). For feeding, drinking, nesting and resting, the three hominid species used the total range of vegetation features and micro-climates found in forest and a part of the micro-habitat characteristics observed in woodland (Table 6.8 – 6.10). For all species, however, the medians and interquartile ranges of vegetation features and micro-climates used showed that the micro-habitat characteristics observed in forest vegetation types were used predominantly for the daily activities, irrespective of vegetation type (Table 6.16). When environments differed along an environmental gradient from forest to savannah, the interquartile range of vegetation features and micro-climates used became wider, and medians shifted towards the range of micro-habitats found in woodland. Site selection for the three hominid species was similar in forest and mosaic environments, but differences were observed in savannahs: *Ardipithecus* used a slightly wider range of vegetation features and micro-climates for feeding than chimpanzees, and *Australopithecus* used a slightly wider range of micro-habitat characteristics for feeding and travelling than chimpanzees and *Ardipithecus*, which followed in part form model rules, but could also be observed within the interquartile ranges of vegetation features and micro-climates used (Table 6.16).

Inter-individual variability

Similar to the generic chimpanzee model (Chapter 4, p. 115) inter-individual variability was observed for *Ardipithecus* and *Australopithecus* individuals within each environment and across model runs. Inter-individual variability was especially evident for internal states (i.e. hydration, energy and fatigue; Table 6.17 and Figure 6.15), but was also observed for various other model output including time spent in forest vegetation types and daily path lengths (Table 6.18 and Figure 6.16). Significant negative correlations were observed between daily path length and time spent in forest vegetation in savannahs (*Ardipithecus*: N = 30, r_s = -0.408, p = 0.025; *Australopithecus*: N = 30, r_s = -0.389, p = 0.034). A significant negative correlation between travel distance and forest time was also observed for *Australopithecus* in mosaics (N = 30, r_s = -0.580, p = 0.001), but this was not observed for *Ardipithecus* (N = 30, r_s = -0.336, p = 0.070). No significant correlations between daily path length and time spent in forest were observed in forests (*Ardipithecus*: N = 30, $r_s = -0.168$, $p = 0.374$; *Australopithecus*: N = 30, $r_s = -0.201$, $p = 0.278$).

Discussion

To shed new light on human evolution, this study investigated how activity budgets, energy budgets and daily path lengths would have changed for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* when their environments varied along an environmental gradient from forest to more open landscapes, and how this differed between the two early hominin species and among early hominins and extant chimpanzees. Using an individual-based modelling approach based on early hominin evidence combined with findings from chimpanzees, this study presented detailed data on the daily activity budgets, energy budgets, hydration budgets, fatigue budgets, food intake, water intake, path lengths, site selections, and vegetation type usage for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* in dense forest, forest mosaic and savannah environments. Within the models, *Ardipithecus* and *Australopithecus* individuals differed from chimpanzees in the generic model (Chapter 4) by including a wider range of food items (i.e. fruit and USOs for *Ardipithecus*, and fruit, USOs and meat for *Australopithecus*, as compared to only fruit for chimpanzees), and having less costly travel patterns (in terms of energy, hydration and fatigue). Model output showed that behavioural strategies differed between species and landscapes. Similar to chimpanzees (Chapter 4), early hominins increased their feeding time, travel time and travel distance, and decreased nesting and resting time, when their environments were more open. For all species, travel time and distances were far greater in savannah environments as compared to dense forests and forest mosaics. Whereas chimpanzee increases in travel time happened at the cost of feeding and drinking time and resulted in highly negative energy and hydration budgets, early hominins were better able to compensate for their increase in travel time as a result of their wider dietary breadth and their more efficient terrestrial locomotor patterns. Species thus differed in their ability to more optimally use open landscapes, which was especially evident for *Australopithecus*. Nonetheless, all three species showed strong forest preferences across all environments. Forest patches, and locations with vegetation features and micro-climates comparable to forest, were used predominantly.

Table 6.16. Interquartile range and median vegetation features and micro-climates used by chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/*afarensis* when feeding, drinking, nesting, resting and travel in dense forest, forest mosaic and savannah landscapes: **a**) ranges for tree height, canopy cover, canopy connectivity and understory density, **b**) ranges for tree density, food tree density, food availability and water availability, and **c**) ranges for temperature and luminosity at daytime, amount USOs and amount meat. As current literature has not presented quantitative data on micro-climates, these variables are presented on a 0-100 scale, with 0 being cold/dark and 100 being hot/light. Amount meat, amount USOs and number of fruits are defined in edible grams of dry weight. Q_1 stands for the lower quartile of the range used, i.e. 25%, and Q_3 stands for the upper quartile of the range used, i.e. 75%.

a)		**Tree height (m)**			**Canopy cover (%)**			**Canopy connectivity (%)**			**Understory density (%)**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Chimpanzees **Dense Forest**	Feeding	20	30	40	81	87	94	81	88	94	6	13	19
	Drinking	20	30	40	81	87	94	81	88	94	6	12	19
	Nesting	19	30	40	80	87	94	81	88	94	5	13	19
	Resting	19	30	41	81	87	94	81	88	94	6	12	19
	Travel	19	29	40	80	87	94	80	87	94	6	13	20
Chimpanzees **Forest mosaic**	Feeding	19	29	40	80	87	94	80	87	94	6	13	20
	Drinking	18	29	39	80	86	93	80	87	93	6	13	20
	Nesting	20	30	40	80	88	94	81	87	94	6	13	19
	Resting	19	30	40	81	87	94	81	87	94	6	13	19
	Travel	16	27	39	78	85	93	78	85	93	7	15	22
Chimpanzees **Savannah**	Feeding	16	26	38	77	85	93	77	85	93	7	15	23
	Drinking	16	25	38	76	84	93	76	84	92	7	16	24
	Nesting	17	26	38	78	85	93	77	85	93	7	15	23
	Resting	17	26	38	78	85	92	78	85	93	7	15	22
	Travel	11	15	24	30	61	84	30	61	84	16	39	70
Ardipithecus **Dense Forest**	Feeding	20	30	40	81	87	94	81	87	94	6	13	19
	Drinking	19	30	40	81	88	94	81	87	93	6	13	19
	Nesting	20	30	40	80	87	94	81	88	94	5	12	18
	Resting	20	30	40	81	87	94	81	87	94	6	12	19
	Travel	19	30	40	81	87	94	81	87	94	6	13	19
Ardipithecus **Forest mosaic**	Feeding	18	29	39	80	87	94	80	87	94	6	13	20
	Drinking	19	30	40	80	87	93	80	87	94	6	13	20
	Nesting	19	30	40	81	88	94	81	87	94	6	13	19
	Resting	20	30	40	81	87	94	81	87	94	6	13	19
	Travel	17	28	39	79	86	93	79	86	93	7	14	21
Ardipithecus **Savannah**	Feeding	13	19	34	55	79	90	54	79	90	11	21	53
	Drinking	15	24	37	75	84	92	75	84	92	8	17	25
	Nesting	16	27	39	78	86	93	78	86	93	6	14	22
	Resting	17	28	40	79	87	93	79	86	93	7	14	21
	Travel	11	16	25	37	65	84	37	64	84	16	36	64
Australopiths **Dense Forest**	Feeding	19	29	40	80	87	94	80	87	94	6	13	20
	Drinking	19	30	40	81	88	94	81	87	94	6	13	19
	Nesting	20	30	40	81	88	94	81	88	94	6	12	19
	Resting	20	30	40	81	88	94	81	88	94	6	12	19
	Travel	19	29	40	80	87	94	80	87	94	6	13	20
Australopiths **Forest mosaic**	Feeding	17	28	39	79	86	93	79	86	93	7	14	21
	Drinking	19	29	40	80	87	94	80	87	94	7	13	20
	Nesting	20	29	40	81	88	94	81	87	93	6	13	19
	Resting	20	30	40	81	87	94	81	87	94	6	13	19
	Travel	16	27	39	78	85	93	78	85	93	7	15	22
Australopiths **Savannah**	Feeding	13	19	33	50	78	89	49	78	90	11	22	54
	Drinking	16	24	37	75	84	92	75	84	92	8	16	25
	Nesting	17	27	38	78	86	93	78	86	93	7	14	22
	Resting	19	29	40	80	86	93	80	87	94	6	13	20
	Travel	11	15	23	31	60	83	31	60	83	17	40	69

b)		**Tree density (%)**			**Food tree density (%)**			**Number fruit**			**Amount water**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Chimpanzees **Dense Forest**	Feeding	81	87	94	81	87	94	6	9.5	13.5	27	53	77
	Drinking	81	87	94	81	88	94	3.5	8	13	62	75	88
	Nesting	81	88	94	81	87	93	5.5	8.5	12.5	63	75	88
	Resting	81	87	94	81	87	94	6	8.5	12.5	62	75	88
	Travel	80	87	94	80	87	94	0.5	2	3	20	41	67
Chimpanzees **Forest mosaic**	Feeding	80	87	94	80	87	94	6	9.5	13.5	25	50	75
	Drinking	80	87	94	80	87	94	3.5	7.5	12.5	61	73	87
	Nesting	81	87	93	81	87	93	6	9	13	61	73	88
	Resting	81	87	94	81	87	94	6	8.5	12.5	62	75	87
	Travel	78	85	93	78	85	93	1	2	3	19	39	64
Chimpanzees **Savannah**	Feeding	77	85	93	77	85	93	6	9	13	21	44	69
	Drinking	76	82	92	76	82	92	2.5	6.5	11.5	60	71	84
	Nesting	77	85	93	77	85	93	7	10.5	14.5	61	72	86
	Resting	78	85	93	78	85	93	6.5	10	14	62	72	86
	Travel	32	64	84	32	63	84	1	3	6	16	34	52
Ardipithecus **Dense Forest**	Feeding	81	87	94	81	87	94	6	9.5	13.5	28	54	77
	Drinking	81	87	94	81	87	94	4.5	8.5	13.5	62	75	87
	Nesting	81	87	94	81	88	94	6	8.5	13	63	76	89
	Resting	81	87	94	81	87	94	6	8.5	12.5	62	75	88
	Travel	81	87	94	81	87	94	0.5	1.5	2.5	21	43	69
Ardipithecus **Forest mosaic**	Feeding	80	87	93	80	87	94	6	9.5	13.5	27	53	76
	Drinking	80	87	94	80	87	94	4.5	9	13.5	62	75	87
	Nesting	81	88	93	81	87	93	6	9	13	62	74	87
	Resting	81	87	94	81	88	94	6	8.5	12.5	62	75	87
	Travel	79	86	93	79	86	93	0.5	1.5	3	20	42	68
Ardipithecus **Savannah**	Feeding	63	79	89	63	78	90	5	8	12	20	41	64
	Drinking	75	84	92	75	84	92	3.5	8	12.5	60	70	84
	Nesting	78	86	94	78	86	94	7	10	14	60	71	85
	Resting	79	86	94	79	86	93	6	9	13	61	73	86
	Travel	46	68	84	45	67	84	1	2.5	6	16	34	53
Australopiths **Dense Forest**	Feeding	80	87	94	80	87	94	6	9.5	14	28	54	78
	Drinking	81	88	94	81	88	94	5.5	9.5	14	62	75	88
	Nesting	81	87	94	81	88	94	6	9	13	62	75	88
	Resting	81	87	94	81	87	94	6	9	13	62	75	88
	Travel	80	87	94	80	87	94	1	2	3	21	42	69
Australopiths **Forest mosaic**	Feeding	79	86	93	79	87	93	6	9	13.5	27	53	75
	Drinking	80	87	94	80	87	94	5	9.5	14	62	74	88
	Nesting	81	88	95	80	87	94	6	9.5	13.5	63	75	88
	Resting	81	88	94	81	87	94	6	9	13	62	75	88
	Travel	78	85	93	78	85	93	1	2	3.5	20	41	66
Australopiths **Savannah**	Feeding	58	78	89	58	78	89	5	8	12	19	41	64
	Drinking	75	84	92	75	84	92	4	8.5	13	60	71	85
	Nesting	79	86	93	79	85	93	6.5	10	14	60	72	85
	Resting	80	87	94	80	87	94	6	9	13	61	74	87
	Travel	33	63	83	33	63	83	1	3	7	16	33	51

c)		**Temperature day**			**Luminosity day**			**Amount USOs (#)**			**Amount meat (#)**		
		Q_1	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**	**Q_1**	**Median**	**Q_3**
Chimpanzees **Dense Forest**	Feeding	6	12	19	6	13	19	-	-	-	-	-	-
	Drinking	6	13	19	6	13	19	-	-	-	-	-	-
	Nesting	5	12	18	6	13	20	-	-	-	-	-	-
	Resting	6	12	19	6	13	19	-	-	-	-	-	-
	Travel	6	13	20	6	13	19	-	-	-	-	-	-
Chimpanzees **Forest mosaic**	Feeding	6	13	20	6	13	20	-	-	-	-	-	-
	Drinking	6	13	20	7	13	20	-	-	-	-	-	-
	Nesting	6	13	19	6	12	19	-	-	-	-	-	-
	Resting	6	13	19	6	12	19	-	-	-	-	-	-
	Travel	7	15	22	7	15	22	-	-	-	-	-	-
Chimpanzees **Savannah**	Feeding	7	15	23	7	15	23	-	-	-	-	-	-
	Drinking	8	16	24	7	16	24	-	-	-	-	-	-
	Nesting	8	15	23	7	14	22	-	-	-	-	-	-
	Resting	7	14	22	8	15	22	-	-	-	-	-	-
	Travel	16	36	68	16	36	67	-	-	-	-	-	-
Ardipithecus **Dense Forest**	Feeding	6	13	19	6	13	19	2	4	6	-	-	-
	Drinking	6	13	19	6	13	19	2	4	6	-	-	-
	Nesting	6	12	20	6	13	19	2	4	5	-	-	-
	Resting	6	13	19	6	12	19	2	4	6	-	-	-
	Travel	6	13	20	6	13	19	2	4	6	-	-	-
Ardipithecus **Forest mosaic**	Feeding	6	13	20	6	13	20	2	4	6	-	-	-
	Drinking	6	13	20	7	13	20	2	4	6	-	-	-
	Nesting	6	13	19	6	12	19	1	4	6	-	-	-
	Resting	6	13	19	6	12	19	2	4	6	-	-	-
	Travel	7	14	21	7	14	21	1	4	6	-	-	-
Ardipithecus **Savannah**	Feeding	11	21	44	10	21	44	2	5	7	-	-	-
	Drinking	8	17	25	8	17	25	2	4	6	-	-	-
	Nesting	7	15	22	7	15	22	2	4	6	-	-	-
	Resting	7	14	21	7	14	21	2	4	6	-	-	-
	Travel	16	34	62	16	35	61	2	4	7	-	-	-
Australopiths **Dense Forest**	Feeding	6	13	20	6	13	20	2	4	6	0	0	0.5
	Drinking	6	13	19	6	13	19	2	3	6	0	0	0
	Nesting	6	12	19	6	13	19	2	4	6	0	0	0
	Resting	6	13	19	6	13	19	2	3	5	0	0	0
	Travel	6	13	20	6	13	20	2	4	6	0	0	0
Australopiths **Forest mosaic**	Feeding	7	14	21	7	14	21	2	4	6	0	0	0.5
	Drinking	6	13	20	7	13	20	2	4	6	0	0	0
	Nesting	6	13	19	6	12	19	2	3	5	0	0	0
	Resting	6	12	19	6	12	19	2	4	5	0	0	0
	Travel	7	15	22	7	15	22	2	4	6	0	0	0
Australopiths **Savannah**	Feeding	11	21	48	11	21	48	2	5	7	0	0	1.5
	Drinking	8	16	25	8	17	25	2	4	6	0	0	0
	Nesting	7	15	22	7	15	22	2	4	6	0	0	0
	Resting	6	13	20	6	14	21	1	4	6	0	0	0
	Travel	17	38	68	18	39	68	2	5	8	0	0	0

Table 6.17. Inter-individual variability in internal states for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* across model runs in dense forests, forest mosaic and savannah landscapes.

Species	**Landscape**	**Internal state**	**Minimum**	**Maximum**	**% positive individuals**	**% negative individuals**
Ardipithecus	**Dense Forest**	Energy (kCal)	-68.0	10.8	99.3	0.7
		Hydration	-8.1	49.0	99.9	0.1
		Fatigue	-69.0	1.5	0.1	99.9
	Forest Mosaic	Energy (kCal)	-208.6	10.8	93.7	6.3
		Hydration	-30.0	50.0	98.6	1.4
		Fatigue	-70.1	67.4	1.2	98.8
	Savannah	Energy (kCal)	-1,311.3	10.8	29.8	70.2
		Hydration	-294.4	50.0	51.7	48.3
		Fatigue	-69.1	435.6	58.9	41.1
Australopithecus	**Dense Forest**	Energy (kCal)	-35.9	18.2	99.6	0.4
		Hydration	-4.2	49.0	99.9	0.1
		Fatigue	-87.0	-11.0	0.0	100.0
	Forest Mosaic	Energy (kCal)	-262.2	18.3	95.3	4.7
		Hydration	-55.6	49.8	98.9	1.1
		Fatigue	-90.0	66.6	0.72	99.3
	Savannah	Energy (kCal)	-1,165.5	18.1	41.8	58.2
		Hydration	-255.0	50.0	69.9	30.1
		Fatigue	-89.0	402.	42.9	57.1

Table 6.18. Inter-individual variability in daily path length and forest use for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* across model runs in dense forest, forest mosaic and savannah landscapes.

Species	**Landscape**	**Internal state**	**Minimum**	**Maximum**
Ardipithecus	**Dense Forest**	Daily path length	300m	2,250m
		Time spent in forest	44.4%	100.0%
	Forest Mosaic	Daily path length	250m	4,850m
		Time spent in forest	29.2%	100.0%
	Savannah	Daily path length	300m	21,150m
		Time spent in forest	0.0%	100.0%
Australopithecus	**Dense Forest**	Daily path length	200m	1,700m
		Time spent in forest	46.5%	100.0%
	Forest Mosaic	Daily path length	150m	6,200m
		Time spent in forest	11.1%	100.0%
	Savannah	Daily path length	200m	2,1850m
		Time spent in forest	0.0%	100.0%

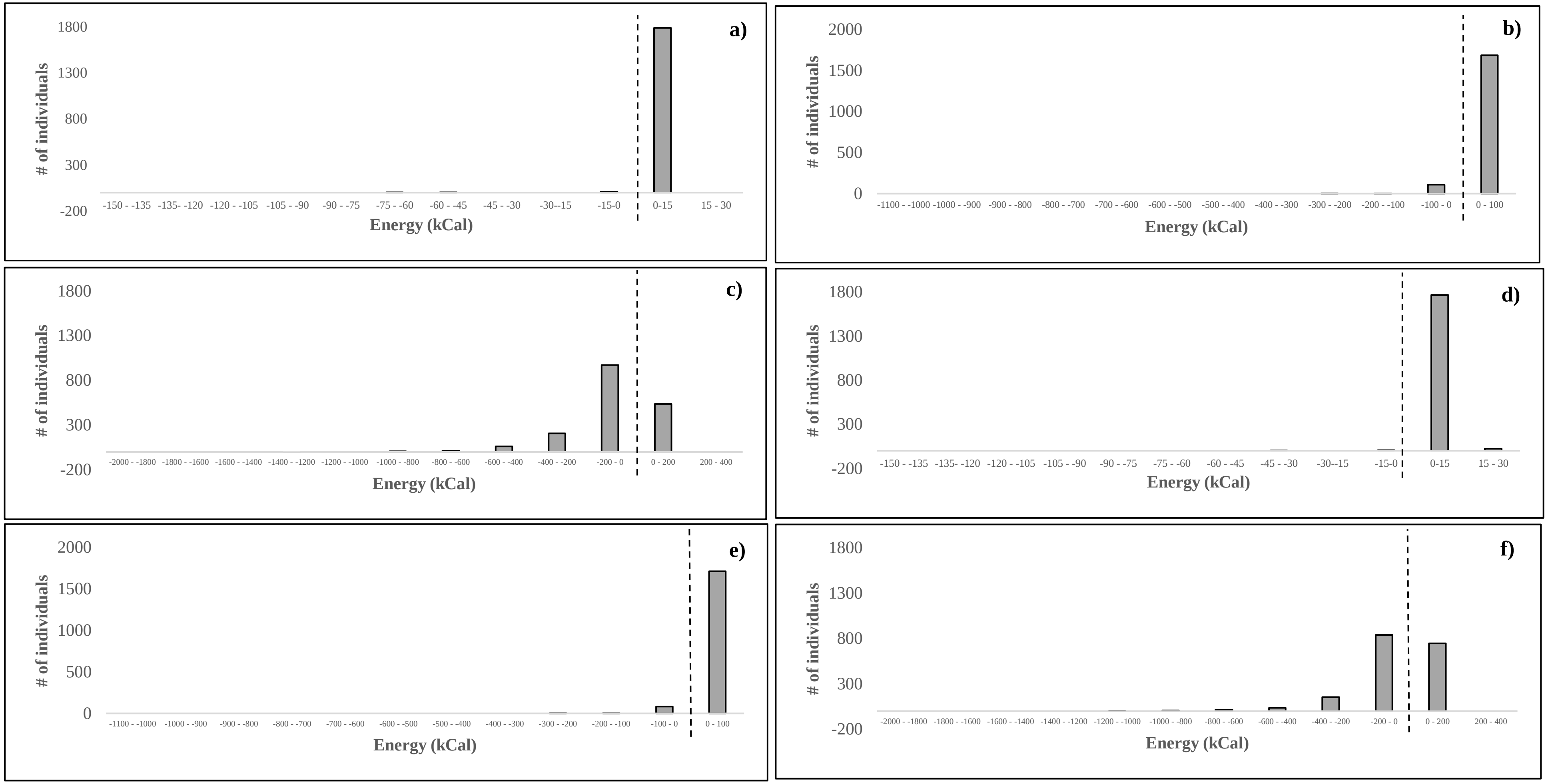

Figure 6.15. Frequency distribution of energy budgets for *Ardipithecus* in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs, and for *Australopithecus* **d)** dense forests, **e)** forest mosaics, and **f)** savannahs. The total number of individuals equals 1,800 individuals per landscape (i.e. 60 individuals per model run, 30 model runs per landscape). Note that scaling is different between graphs. The dotted line indicates the cut-off between positive and negative energy budgets.

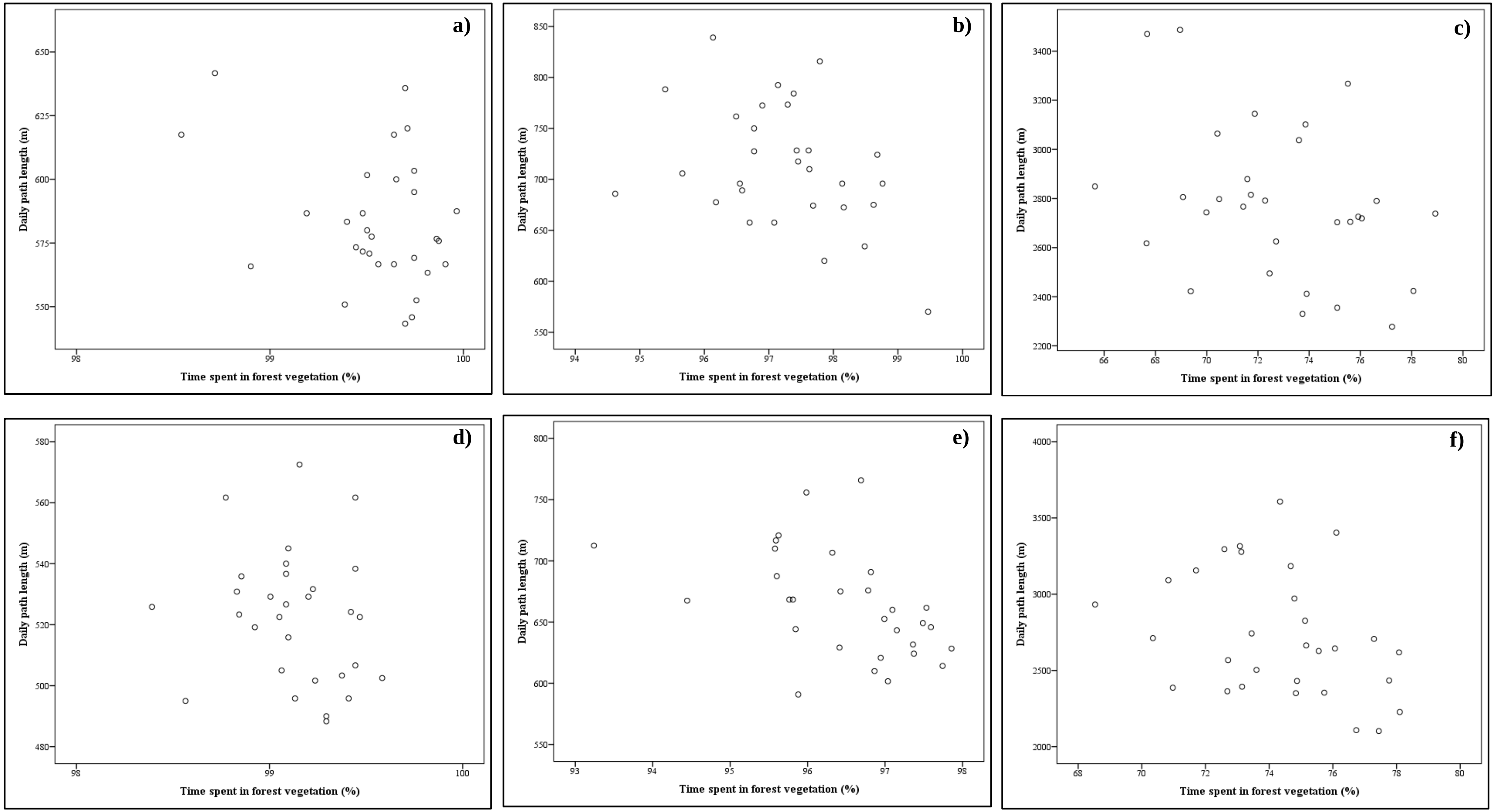

Figure 6.16. Time spent in forest vegetation (%, 24 hours) against daily path lengths for *Ardipithecus ramidus* in **a)** dense forests, **b)** forest mosaics, and **c)** savannahs, and for *Australopithecus anamensis*/ *afarensis* in **d)** dense forests, **e)** forest mosaics, and **f)** savannahs. In all cases, N = 30

Early hominin landscape use in different environments

When comparing *Ardipithecus* and *Australopithecus* landscape use across dense forest, forest mosaic and savannah environments, model output showed that early hominins increased their feeding time, drinking time, travel time and travel distance, decreased their nesting time and resting time, increased their usage of more open vegetation types, and retained a strong preference for forest vegetation when environments were more open. As a result, early hominin individuals in more open landscapes had greater food intake, water intake and fatigue budgets, and lower energy budgets and hydration budgets as compared to individuals in forests. These responses were also highlighted for the generic chimpanzee model of Chapter 4, and field studies on various primate species have observed largely similar behavioural adjustments as a result of (anthropogenic) habitat fragmentation and disturbance (e.g. howlers (*Alouatta palliata*, *Alouatta palliata mexicana* and *Alouatta clamitans*): e.g. Clarke et al. 2002, Asensio et al. 2007, Jung et al. 2015; macaques (*Macaca fascicularis* and *Macaca nemestrina*): e.g. Sha and Hanya 2013, Ruppert et al. 2018).

Even though insufficient data were available to quantitatively classify early hominin environments, environmental descriptions of *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* fossil localities suggested the usage of a wide range of habitats, including dense forests, forest mosaics and savannahs (e.g. Reed 1997, Aronson et al. 2008, White et al. 2009, Cerling et al. 2011). This indicates that early hominins were not as restricted to the open savannah landscapes that supposedly gave rise to early hominin evolution as traditionally assumed in the savannah hypotheses (Dart 1925; reviewed in: e.g. Potts 1998, Bender et al. 2012, Dominguez-Rodrigo 2014). Within the models, early hominins used more open vegetation types such as woodland and grassland more often in more open environments, but forest remained the preferred vegetation type overall and for each behaviour. Micro-habitat characteristics observed in forest vegetation types were used predominantly across environments, though the range of vegetation features and micro-climates used gradually became wider and shifted towards the inclusion of micro-habitat characteristics observed in woodland when landscapes were more open. Nonetheless, with their predominant use of forest micro-habitat characteristics which may have followed in part from model rules, early hominins used the same criteria in selecting a site for a specific activity regardless of the overall landscape and did not alter their site selectivity. This indicates that their minimal landscape requirements and constraints remained constant across habitats. The persistent reliance on forest and the usage of more suboptimal vegetation for their daily activities when the environment became more open is also observed in other primate species (e.g. howlers: e.g. Clarke et al. 2002; chimpanzees: e.g. Russak 2014, Bryson-Morrison et al. 2017; capuchins (*Cebus capucinus*): e.g. McKinney 2011). Although published evidence for *Australopithecus* suggests no preference for any single type of vegetation (Bonnefille et al. 2004, Reed 1998), wooded environments including forest were expected to be more optimal (Su and Harrison 2008).

Early hominin activity budgets differed between environments, with longer travel, feeding and drinking times, and longer travel distances, but shorter nesting and resting times when environments differed from dense forests to savannahs. Whereas longer feeding, drinking and travel times, longer daily path lengths, and shorter resting times confirmed the predictions set out in this study, decreased nesting times were not expected. Similar landscape use patterns were observed for chimpanzees in the generic model, and explanations follow a similar rationale (Chapter 4, p. 122). Longer feeding times, drinking times, travel times and travel distances in forest mosaics and savannahs as compared to dense forests, could presumably be attributed to the more scarce and seasonal availability and distribution of resources in more open landscapes (e.g. McGrew et al. 1981, Hunt and McGrew 2002, Arroyo-Rodríguez and Mandujano 2009). Shorter resting times in forest mosaics and savannahs as compared to dense forests could potentially be ascribed to limited time available after performing the other daily activities. Decreased nesting times could be explained by the increasing difficulty of finding suitable nesting locations in more open environments. In the field, chimpanzees have been observed to engage in other nightly activities such as feeding or travel (Pruetz and Bertolani 2009, Tagg et al. 2018), which could additionally explain shorter nesting times.

Observed activity budgets for *Australopithecus* in this study differed from the australopithecine time budget model presented by Bettridge (2010). This time budget model correctly predicted australopith presence in 47.6% of locations based on fossil evidence, and time budgets were calculated as 16.1% travel, 43.1% feeding, and 32.5% resting (see Dunbar and Gowlett (2014) for review). This would have left 8% of time available for social activities (following Dunbar and Gowlett 2014). Bettridge’s (2010) time budget models included all *Australopithecus* species, and focused on distribution patterns across Eastern and Southern Africa. As both modelling efforts took a different approach and had different goals, direct comparisons of activity budget results are not helpful. Both models, however, showed that australopithecines generally travelled less than chimpanzees (Bettridge 2010).

Differences in activity budgets for *Ardipithecus* and *Australopithecus* in dense forests, forest mosaics and savannahs led to differences in internal states, with higher food intake, water intake and fatigue budgets, and lower energy budgets and hydration budgets in more open landscapes. Interestingly, for both hominins, fruit intake slightly increased when landscapes changed from dense forest to forest mosaics, but significantly dropped in savannahs. At this time, USO intake sharply increased for *Ardipithecus*, and USO and meat intake sharply increased for *Australopithecus*, indicating a shift towards a more mixed diet based on more readily available resources in marginal savannahs. The wider dietary breadth of *Ardipithecus* and *Australopithecus* thus became increasingly more important in more open environments, and had a significant effect when inhabiting seasonally scarce savannahs. Considering their availability and energetic gain, both early hominins showed a persistent preference for fruit, and USOs showed to be important fallback foods, which is in accordance with published literature (Ungar 2004, Laden and Wrangham 2005, Wrangham et al. 2009). Meat was furthermore expected to be an important food item for *Australopithecus* spp. due to its high caloric gain (Stanford 2006, Griffith et al. 2010, Hammond and Ward 2013), but carcass availability was low and opportunistic. A shift towards more readily available, lower quality resources was also observed for various primates as a result of food scarcity and/or habitat loss (e.g. gorillas (*Gorilla* spp.): e.g. Kuroda et al. 1996, Head et al. 2011; howlers: e.g. Asensio et al. 2007; bonobos (*Pan paniscus*): e.g. Serckx et al. 2015; chimpanzees: e.g. Chancellor et al. 2012a).

Both hominin species were able to maintain homeostasis in dense forest and forest mosaic environments, but sustaining positive energy and hydration budgets, and negative fatigue budgets became increasingly more difficult in open savannahs. As resources in savannahs were particularly scarce, seasonal and widely distributed (e.g. McGrew et al. 1981, Moore 1996, Hunt and McGrew 2002), hominins had to increase their travel time and distance to find their required resources, which resulted in less time available for feeding, drinking, nesting and resting, and consequently in lower hydration and energy budgets, and higher levels of fatigue. Although *Australopithecus* was able to maintain slightly negative fatigue budgets and slightly positive hydration budgets in savannah landscapes, *Ardipithecus* was not able to do so. Energy budgets were highly negative for both hominin species in savannahs. Regardless of their morphological adaptations to a wider dietary breadth and less costly terrestrial locomotor patterns, *Ardipithecus* and *Australopithecus* were thus still relatively unsuccessful in savannah habitats as compared to more wooded landscapes, and would likely have had to cope with reduced fitness when inhabiting marginal savannahs. In contrast to the traditional view that hominins would have thrived in savannah environments (e.g. Potts 1998, Bender et al. 2012, Dominguez-Rodrigo 2014), environmental changes towards more open habitats challenged *Ardipithecus* and *Australopithecus* for survival. This supports the findings of White et al. (2009, 2015) of more wooded habitats for *Ardipithecus ramidus*, and adaptations to wooded habitat are also considered for *Australopithecus anamensis* (Cerling et al. 2013).

Similar to the generic chimpanzee model (Chapter 4, p. 124), inter-individual variability in landscape use patterns became more evident when environments were more open, and some early hominin individuals were better able to successfully inhabit more open environments than others. Inter-individual variances could only partly be attributed to model stochasticity, and are likely a result of the environments' carrying capacity. Modelled savannah environments were especially scarce in resources, and food and water items were depletable, leading to competition between individuals and the assumption that savannah environments were not providing enough resources to sustain every simulated individual. Lower population sizes and/or lower population densities may have been a required adaptation for *Ardipithecus* and *Australopithecus* in open environments. Although no data exist on *Ardipithecus* population size and published *Australopithecus* spp. population size estimates are not linked to environmental variability (Dunbar 2014, Dunbar et al. 2014), lower population sizes and densities in more open environments are observed for chimpanzees (e.g. Tutin et al. 1983, Hunt and McGrew 2002).

Early hominins were thus able to adapt their landscape use patterns to suit the resource availability of a wide variety of environments. Even though this suggests remarkable flexibility for early hominins, *Ardipithecus* and *Australopithecus* faced particular survival challenges in open habitats and were better able to successfully inhabit more wooded environments such as dense forests and forest mosaics. Validation of the *Ardipithecus* model followed from model output for feeding time and food intake in savannah landscapes: Literature specified that *Ardipithecus ramidus* diets consisted for 10 – 15%, or 10 – 25%, of food items other than fruit, i.e. C_4 food items such as nuts and tubers, including USOs (Suwa et al. 2009, White et al. 2009, Grine and Daegling 2017). Without this aspect being modelled for, model output outlined that *Ardipithecus* fed for 16.5% of their total feeding time on USOs and 83.5% on fruit in savannahs.

Similarly, also the *Australopithecus* model could be validated based on model output for feeding time and food intake in savannah landscapes: Stable isotope analyses showed that the diets of *Australopithecus* spp. consisted of > 30% of C_4 food items, such as grasses, sedges, nuts, seeds and USOs (Sponheimer et al. 2006, Suwa et al. 2009), and also meat, and potentially insects, presumably played an important role (e.g. McPherron et al. 2010, O'Malley and Power 2014). Without it being modelled for, model output on feeding time in savannah habitats showed that *Australopithecus* spent about 34% of their feeding time on meat and USOs (i.e. 21% and 13%, respectively). The exact distinction between time spent feeding on USOs and meat is not yet optimal, i.e. it could be expected that the dietary contribution of meat for hominins would only have been small, due to their lower masticatory and gut efficiency in processing raw meat, and the risk of ingesting bacteria (e.g. Smith et al. 2015, Carmody 2017, Wrangham 2017). Both models were thus validated to correctly predict the feeding patterns, and thereby potentially also the landscape use patterns, of early hominins. This study thus provided detailed null-models of early hominin landscape use in a variety of environments, and findings can provide new insights into early hominin behavioural ecology and human origins, as well as early hominin susceptibility and adaptability to cope with environmental change.

Ardipithecus and *Australopithecus* landscape use compared

Patterns of landscape use differed in important ways between *Ardipithecus* and *Australopithecus*. *Australopithecus* had shorter feeding times, travel times and travel distances, longer resting times, lower fruit intake and fatigue budgets, higher energy budgets, different USO intake, and used more open vegetation types more frequently as compared to *Ardipithecus*. In open savannah landscapes *Australopithecus* was able to maintain positive hydration budgets and negative fatigue budgets, whereas *Ardipithecus* was not able to sustain this. Both hominins had decreased, negative energy budgets in savannahs, but *Australopithecus*' energy budgets were more positive than those presented for *Ardipithecus*. Within published literature, *Ardipithecus* and *Australopithecus* comparisons remain restricted to those of environment (e.g. Potts 1998, Cerling et al. 2011, Hammond and Ward 2013), diet (e.g. Suwa et al. 2009, White et al. 2009, Grine and Daegling 2017) and mode of travel (e.g. White et al. 2009, Hammond and Ward 2013, Kozma et al. 2018).

Model results confirm the hypothesis that *Australopithecus* was better able to successfully exploit more open vegetation, and *Ardipithecus* was more restricted to wooded environments, due to *Australopithecus*' wider dietary breadth, greater adaptability to less energetically costly terrestrial bipedal locomotion, and the subsequent reduced thermoregulatory stress to open areas and wider access to high-quality and/or isolated food sources (e.g. Laden and Wrangham 2005, Pontzer et al. 2009, Lieberman 2015, Pobiner 2015, Kozma et al. 2018). Although site selection was largely similar for the two early hominin species, *Australopithecus* used a slightly wider range of vegetation features and micro-climates for feeding and travelling, partly following from model rules. This highlights that australopithecines were more tolerant to more extreme micro-habitats, as a consequence of their morphological adaptations. As a result of wider dietary breadth, as is the case for *Australopithecus* as compared to *Ardipithecus* (e.g. Suwa et al. 2009, Grine and Daegling 2017), also other primate species have been shown to use a wider range of more open vegetation for their daily feeding activities as compared to primate species with a more restricted diet (e.g. sympatric frugivorous chimpanzees and more folivorous gorillas (*Gorilla gorilla* spp.): e.g. Yamagiwa et al. 1996, Stanford 2006, Head et al. 2012).

Across landscapes, *Australopithecus* spent less time feeding, more time resting and equal times nesting as compared to *Ardipithecus*, which is in agreement with the predictions. Contrary to expectations, however, travel times and distances were generally shorter for *Australopithecus* than for *Ardipithecus*. These differences could likely be attributed to the wider dietary breadth simulated for australopithecines: with more dietary items to choose from, and thus a higher food availability, australopiths had to feed and travel less, in time and distance, to obtain their required resources (following Masi et al. 2009). *Australopithecus*' adaptations to a wider dietary breadth, more efficient terrestrial bipedalism, and subsequent reduced thermoregulatory stress to open areas as compared to *Ardipithecus*, thus not only led to a wider access to high-quality and/or isolated food sources, but also to a wider range of lower quality, but more readily available food items (e.g. Laden and Wrangham 2005, Pobiner 2015). *Ardipithecus*' shorter resting times across habitats presumably indicated that increased feeding and travel times constrained their resting times (following Masi et al. 2009). Variable resting times may also follow from differences in diet, with longer resting times required for species with more fibrous diets as a result of digestion (i.e. enforced resting time: e.g. Masi et al. 2009, Korstjens et al. 2010). Environments with higher temperatures often provide foods, such as leaves, with lower protein-to-fibre ratios than environments with lower temperatures (e.g. Rothman et al. 2014). Fluctuations in temperature and the effect of fibrous foods (e.g. USOs) on resting time are not currently included in the models, but in view of climate change and increasing temperatures, additional impacts on hominin time budgets could be expected. Even though both hominins included USOs in their diets, *Ardipithecus* were assumed to be more frugivorous than *Australopithecus* due to the latter's wider dietary breadth (e.g. Suwa et al. 2009, Grine and Daegling 2017). Differences in activity budgets for *Ardipithecus* and *Australopithecus* from model output are largely similar to observed differences in activity budgets for sympatric frugivorous chimpanzees and more folivorous gorillas (e.g. Stanford 2006), and for contemporary frugivorous western lowland gorillas (*Gorilla gorilla gorilla*) and more folivorous mountain gorillas (*Gorilla beringei beringei*: e.g. Masi et al. 2009), and link to a positive influence of frugivory on travel distance (e.g. Ganas and Robbins 2005, Coward and Grove 2011).

Differences in activity budgets between *Ardipithecus* and *Australopithecus* led to differences in food and water intake, and in hydration, energy and fatigue budgets. *Ardipithecus* always fed on fruit for more time and had higher fruit intake than *Australopithecus*. Time spent feeding on USOs and USO intake was higher for *Australopithecus* in dense forests, similar for both hominins in forest mosaics, and higher for *Ardipithecus* in savannahs. As australopithecines were simulated to also include meat within their diet, *Australopithecus* diets were more variable than those of *Ardipithecus* following model rules. Nonetheless, the increased consumption of USOs in dense forests for *Australopithecus* as compared to *Ardipithecus* showed that australopiths were better adapted to include lower quality food items when available, even when inhabiting more optimal environments. This observation is in agreement with the findings on *Australopithecus*' more frequent use of open vegetation types as compared to *Ardipithecus*, even in dense forest landscapes. Whereas *Ardipithecus* showed a sharp, sudden shift towards a high consumption of USOs in savannahs, the inclusion of USOs in the australopithecine diet was slightly more gradual. Although this highlighted the importance of USOs as fallback foods (e.g. Laden and Wrangham 2005), australopiths were less reliant on USOs and fruit than *Ardipithecus*, due to their ability to include meat. Literature data on stable isotope analyses also showed that *Australopithecus* spp. included a wider variety of food items within in their diet as compared to *Ardipithecus* (Sponheimer et al. 2006, Suwa et al. 2009, Grine and Daegling 2017).

Australopithecus was more successful in sustaining positive energy and hydration budgets, and negative fatigue budgets across landscapes than *Ardipithecus*. Fatigue levels were always higher for *Ardipithecus* than for *Australopithecus*, and only australopithecines were able to maintain negative fatigue budgets in savannah landscapes as a result of their longer resting times and shorter travel times. Hydration budgets were comparable for *Ardipithecus* and *Australopithecus* in forest mosaic landscapes, higher for *Ardipithecus* in dense forests, and higher for *Australopithecus* in savannah environments, and only australopiths were able to maintain positive hydration budgets in savannahs. The higher hydration budgets for *Ardipithecus* in dense forest environments could potentially be explained as a consequence of australopithecines being more selective in their food intake. Regardless of their overall travel distance, *Australopithecus* in dense forests occasionally travelled further within a single time frame (i.e. a model time step of 10 minutes) to access high-quality, opportunistic scraps of meat (Griffith et al. 2010), and thus lost slightly more hydration than *Ardipithecus*. In more open landscapes such as forest mosaics, there were less opportunities to be selective, as the resources in mosaic habitats were scarcer, hence the similarities in hydration budgets between species in this environment. Higher hydration budgets for *Australopithecus* in savannah landscapes are a result of longer drinking times, higher water intake and shorter travel times as compared to *Ardipithecus*. Energy budgets were comparable for *Ardipithecus* and *Australopithecus* in dense forests environments, but *Australopithecus* had higher energy budgets in forest mosaics and savannahs. Both early hominins had highly negative energy budgets in savannahs. Higher energy budgets for *Australopithecus* in forest mosaics and savannahs are a result of shorter travel times and longer feeding times as compared to *Ardipithecus*. Increased energy gains for *Australopithecus* may also follow from the wider dietary breadth simulated for australopithecines, and thus the inclusion of more high-quality food items. The differences in energy, hydration and fatigue budgets between *Ardipithecus* and *Australopithecus* thus became especially evident in savannah environments, and showed that australopithecines were more successful in exploiting open environments as a consequence of their morphological adaptations to a wider dietary breadth and less costly locomotor patterns.

Australopithecines were thus more tolerant and better able to successfully exploit more open environments than *Ardipithecus*. *Australopithecus*’ enhanced morphological adaptations to a wider dietary breadth and more efficient terrestrial bipedalism led to reduced thermoregulatory stress to open areas and broader access to both high-quality and isolated, as well as low-quality and abundant, food items as compared to *Ardipithecus* (e.g. Laden and Wrangham 2005, Pontzer et al. 2009, Lieberman 2015, Pobiner 2015). These differences are widely acknowledged in hominin literature (e.g. Estebaranz et al. 2012, Kozma et al. 2018), and are also used for comparisons with later hominins (e.g. Ungar 2004, Sponheimer et al. 2013, Ibanez-Gimeno et al. 2017, Kozma et al. 2018). The *Ardipithecus – Australopithecus* comparisons of this study provided detailed insights into previously unidentified differences and similarities in landscape use patterns and the effect of morphological adaptations among hominin species, and can be used to shed new light on human origins. Findings provide a framework for comparing patterns of early hominin landscape use to extant (sympatric and/or contemporary) animal species.

Comparisons of landscape use between early hominins and chimpanzees

Early hominin patterns of landscape-scale habitat use differed from those observed for extant chimpanzees. Model results showed that comparative differences between chimpanzees and early hominins were not always consistent, with comparisons across landscapes, between chimpanzees and *Ardipithecus ramidus,* and between chimpanzees and *Australopithecus anamensis*/ *afarensis* sometimes leading to contradictory results. The following discussion focuses on the general comparative insights between chimpanzees and early hominins across landscapes only, and highlights main differences observed in hominid landscape use patterns. Generally, chimpanzees had shorter resting times, longer travel times, longer travel distances, lower energy budgets, and higher fatigue budgets as compared to early hominins across environments. Early hominins used a considerably wider range of micro-habitats for feeding and travel than chimpanzees. Compared to early hominins, feeding times and fruit intake were higher for chimpanzees in dense forest and forest mosaic environments, but lower in savannah habitats. Drinking times, water intake and hydration budgets were lower for chimpanzees in savannahs. Model output indicated more goal-directed travel for early hominins as compared to chimpanzees. Published literature data on chimpanzee-hominin comparisons remain restricted to comparisons of diet (e.g. Sponheimer et al. 2006, Sponheimer et al. 2013), travel patterns (e.g. Pontzer et al. 2009, Kozma et al. 2018), habitats (e.g. Simpson 2013), population size (Dunbar and Gowlett 2014, Dunbar et al. 2014) social systems (e.g. White et al. 2009, Dunbar and Gowlett 2014), and similarities in sleeping patterns (e.g. Sabater-Pi et al. 1997, Boyd and Silk 2012, Stanford 2012).

Vegetation type usage was highly variable between the three hominid species across landscapes, but forest was preferred overall and for each behaviour separately. Generally, early hominins used a wider range of vegetation features and micro-climates for feeding and travelling (which partly followed from model rules), and also included more open vegetation types such as woodland and grassland, as compared to chimpanzees. Simulated morphological adaptations to a wider dietary breadth, less costly bipedal locomotor patterns, and subsequent reduced thermoregulatory stress to open areas and wider access to resources (e.g. Laden and Wrangham 2005, Pontzer et al. 2009, Lieberman 2015, Kozma et al. 2018), allowed early hominins to more optimally use a wider range of more open vegetation types. This is in agreement with the hypothesis that early hominins would more optimally use more open vegetation as compared to chimpanzees, and a wider access for hominins to more open vegetation types is also outlined in published literature (e.g. Wheeler 1991, Wheeler 1992, Lieberman 2015). Early hominins were considered to have a more flexible diet than frugivorous chimpanzees (e.g. Suwa et al. 2009), and a wider use of more open vegetation is also observed for other primate species with more flexible diets as compared to those with less flexible diets (e.g. Yamagiwa et al. 1996, Stanford 2006, Head et al. 2012).

Chimpanzees generally had longer travel times and distances, and shorter resting times than early hominins across landscapes. Feeding and drinking times were generally longer for chimpanzees in dense forests and forest mosaics, but were considerably shorter in savannahs as compared to early hominins. Decreased travel times and daily path lengths for early hominins were not expected, but could be attributed to early hominins' wider dietary breadth and wider access to resources, which allowed early hominins to travel less (following Masi et al. 2009). This is also observed when comparing other sympatric and/or contemporary primate species with more or less flexible diets (e.g. Stanford 2006, Masi et al. 2009). Contrary to expectations, resting times were generally shorter for chimpanzees as compared to early hominins in dense forests and forest mosaics. Increased travel times for chimpanzees likely led to decreased times available for resting (following Masi et al. 2009). Resting time did not differ significantly between early hominins and extant chimpanzees in savannah environments, which is likely a result of minimal resting time requirements for chimpanzees. Nesting times varied between the three hominid species across landscapes, but were generally comparable. This may have followed partly from model rules based on literature statements of early hominins having similar nesting and sleeping patterns as extant chimpanzees (e.g. Sabater-Pi et al. 1997, Boyd and Silk 2012, Stanford 2012), but it indicates similar selective forces in nesting time and nest site selection across species and landscapes. Increased feeding times for chimpanzees in dense forests as compared to early hominins again highlight the adaptive advantages of early hominins' wider dietary breadth: with the inclusion of a wider range of (high-quality) food items, less feeding time is needed for the required energetic gains, and/or less travel time is needed to access the necessary resources resulting in lower energy loss (e.g. Ganas and Robbins 2005, Stanford 2006, Masi et al. 2009). Longer feeding and drinking times for chimpanzees in forest mosaics than early hominins are likely a result of increased travel times for chimpanzees. Across landscapes, chimpanzees increased their travel time more than early hominins, and thus needed to compensate for the resulting extra loss of energy and hydration by increasing their drinking and feeding times significantly more than early hominins. Following this rationale, in savannahs, chimpanzee travel times became too demanding, indicating insufficient time for drinking and feeding, and/or inabilities in finding the necessary food and water resources. Even though hominins also experience these difficulties, these are less evident than those observed for chimpanzees.

Energy budgets, hydration budgets, fatigue budgets, food intake and water intake differed between the three hominid species as a result of differences in activity budgets. Fruit was the preferred food item for all species, but chimpanzees generally had higher fruit intake than early hominins. Although this followed from model rules with simulated chimpanzees only including fruit as a dietary item and early hominins including fruit, USOs and meat, it indicated that a simulated wider dietary breadth allowed early hominins to be less reliant on one single food type. The dependence on fruit for chimpanzees as compared to the more flexible and wider dietary breadth for early hominins is also outlined in hominin literature (e.g. Ungar 2004, White et al. 2009, Ungar et al. 2010). Hominins' wider dietary breadth and the inclusion of food items that required less digestive processing, such as meat, potentially led to higher energetic gains for hominins (e.g. Coward 2014). Savannah chimpanzees have been observed to include small quantities of USOs into their diet (e.g. McGrew et al. 1988, Hernandez-Aguilar 2009), indicating a necessary shift towards more flexible diets in marginal landscapes. Whereas early hominins were able to maintain homeostasis in forests and mosaics, chimpanzees were only able to do so in dense forests. All three hominids struggled to maintain homeostasis in savannahs, but early hominins were more successful in doing so than chimpanzees. Fatigue budgets were always higher for chimpanzees than for early hominins due to their longer travel and shorter resting times. Hydration budgets were similar between species in dense forests and forest mosaics, but lower in savannahs as a result of observed increased travel time and decreased drinking time for chimpanzees as compared to early hominins. Energy budgets were similar in dense forests, but lower for chimpanzees than early hominins in forest mosaics and savannahs, as a consequence of decreased feeding times and increased travel times. Early hominin spp. were thus more successful in exploiting the available resources of more open habitats such as forest mosaics and savannahs than extant chimpanzees, as a consequence of their more flexible and high-quality diet and their less costly terrestrial locomotor patterns (e.g. Pontzer et al. 2009, Sponheimer et al. 2006).

Model output showed less circular travel paths for early hominins as compared to chimpanzees (see figures in Appendices 4.4, 6.3 and 6.8). Although this finding may follow from model rules on the wider range of resources used by early hominins, it may also indicate an adaptation to more goal-directed travel. In turn, this would highlight diverging cognitive abilities between early hominin spp. and extant chimpanzees, as more goal-directed travel would require more detailed knowledge of the environment, the inclusion of memory functions, and/or the evolution of causal cognition (e.g. Stuart-Fox 2015). On top of morphological adaptations for travel and feeding, if present in early hominins (and not in chimpanzees), these cognitive skills may have enhanced early hominin success in more optimally using their habitats as compared to extant chimpanzees, and would have likely played a role in hominins colonising increasingly open mosaic and savannah habitats. Higher cognitive abilities were likely to have given rise to other observed behavioural innovations of later hominins, such as the use of fire and cooking (e.g. Dunbar and Gowlett 2014, Wrangham 2017).

Overall, early hominins were thus more successful in exploiting the available resources of their landscapes than chimpanzees. This is a consequence of their (simulated) morphological adaptations to efficient terrestrial bipedalism and wider dietary breadth, and the consequent reduced thermal stress and broader access to open area resources (e.g. Laden and Wrangham 2005, Pontzer et al. 2009, Lieberman 2015, Pobiner 2015, Kozma et al. 2018). This allowed early hominins to more optimally use more open vegetation types and landscapes, which is often emphasised in published literature (e.g. Ungar 2004, Lieberman 2015). Comparisons thus highlighted important differences and similarities in landscape use patterns between hominids, which provide new insights into early hominin evolution. These insights can aid in understanding how hominins would have eventually been able to adapt and survive in more open areas than chimpanzees, as well as chimpanzees' strengths, weaknesses and applicability in providing early hominin referential models.

Model limitations, implications and future perspectives

Models are always simplifications of real-life systems (e.g. van der Vaart et al. 2016), and the *Ardipithecus* and *Australopithecus* models are thus subject to certain limitations. Specifically, the early hominin models could be improved whenever new evidence on *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* becomes available. Additionally, the circular movement patterns of early hominins in model outputs should be further explored. Even though circular movement patterns were already observed within the chimpanzee model (Chapter 4), circularity within the early hominin models was less 'extreme', which could indicate more goal-directed travel (i.e. more resources) and more detailed environmental knowledge in early hominins as compared to chimpanzees. However, the circular movement patterns could also follow from model rules per se, and code improvements for movement, foresight and model run time, and/or adding model codes on grouping, seasonality and varying food quality could investigate whether circularity persists. Other model improvements could include temperature, rainfall and micro-climate changes, behavioural *where* and *when* additions, and energy, hydration and fatigue updates for additional insights into hominin landscape use. These, and other, potential model improvements are outlined in detail in Chapter 4 (p. 127), and are currently not implemented in the models due to time constraints, data shortage, comparison reasons with the chimpanzee model, and/or because newly presented results would have been beyond the scope of this study.

Whereas the current early hominin models presented detailed null-models on early hominin landscape use in different environments, for future studies the *Ardipithecus* and *Australopithecus* models could be used to outline even more innovative insights into human origins and evolution. For example, following the rationale outlined in Chapter 4 for chimpanzees (p. 129), scenario testing of the current early hominin models could be used to predict the impacts of various environmental changes on early hominin behaviour, survival and patterns of landscape use. According to published literature, hominins have had to adapt to a wide variety of environmental changes throughout the Plio-Pleistocene, including changes in habitat cover, global warming and/or cooling, and increased environmental aridity (e.g. Vrba 1999, Bobe et al. 2002, Potts 2007, Maslin et al. 2014). Additionally, scenario testing of the *Ardipithecus* and *Australopithecus* models could highlight the outcomes of different behavioural strategies on early hominin landscape use and survival. Within current literature, many behavioural strategies have been put forward to explain the increasing success of hominins over other species, including adaptations in locomotor patterns towards more efficient (and obligate) terrestrial bipedalism, increased dietary breadth, increasingly elaborate tool use and manufacture, tool and food transportation, the usage of fire, and cooking (e.g. Ungar 2004, Potts 2007, Fleagle 2013, Dunbar and Gowlett 2014, Wrangham 2017). Only some of these adaptations are included in the current models, and scenario testing of the effects of other behavioural innovations could aid in explaining why certain behavioural strategies flourished and persisted, whereas others ceased to exist. These findings combined provide a framework for understanding the underlying role of landscapes in early hominin survival, adaptation and evolution. Testing of various environmental change scenarios and various behavioural strategies would highlight detailed insights into early hominin origins and their adaptability to change, and would extrapolate the current findings of this study. It would emphasise hominins’ tipping points for coping versus non-coping with environmental change, when, in time and space, innovative behavioural adaptations would have become advantageous, and which strategies would have been most successful. These insights would provide even more detailed knowledge on how early hominins would have coped with the environmental changes of their time, how this differed among various hominin species and between hominins and chimpanzees, and would broaden the current perspective of hominins eventually colonising, surviving and thriving in open savannahs.

Conclusion

To investigate how early hominin landscape use differed when their paleoenvironments varied along an environmental gradient from forest to more open environments, and how this differed among early hominin species, and between early hominins and extant chimpanzees, this study created two individual-based models (i.e. for *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) based on early hominin evidence combined with findings from chimpanzees (i.e. taking a referential modelling approach). Similar to chimpanzees (Chapter 4), *Ardipithecus* and *Australopithecus* were able to adjust their landscape use patterns to fit the resource abundance of their environments. When environments became more open, early hominins increased their feeding times, travel times, drinking times and daily path lengths, increased their reliance on forest vegetation, used more open vegetation types more often, and decreased their resting and nesting times. Early hominin fatigue budgets increased, and energy and hydration budgets decreased, in forest mosaics and savannahs as compared to dense forests. Early hominins faced increasing survival challenges in more open environments, and both species likely experienced reduced fitness in savannahs. Patterns of landscape use differed in important ways between the two early hominin species, and across landscapes *Australopithecus* was more comfortably maintaining homeostasis, and thus fitness, than *Ardipithecus*. Australopithecines were more tolerant and better able to successfully exploit more open environments as a consequence of their enhanced morphological adaptations to a wider dietary breadth, more efficient terrestrial bipedalism, and the subsequent reduced thermoregulatory stress and broader access to open area resources. Early hominin patterns of landscape use also differed from those observed for chimpanzees. Early hominins were more successful than chimpanzees and were able to more optimally use more open habitats due to their morphological adaptations. Findings on early hominin landscape use and their comparisons between environments, among hominin species, and between early hominins and chimpanzees supplied detailed insights into early hominin behaviour, evolution and origins, as well as into hominin adaptability to change, the differences and similarities in landscape use patterns across species and environments, and chimpanzee applicability as early hominin referential models. Potential future model applications include predicting the impacts of various landscape change scenarios on early hominin behaviour, evaluating the outcomes of different behavioural strategies on early hominin survival, and providing a framework for understanding the underlying role of landscapes in early hominin adaptation and evolution through scenario testing.

CHAPTER 7

General overview and conclusions

Primate habitat worldwide is changing rapidly, leading to declining primate populations (e.g. Estrada et al. 2017). Primates constantly have to adapt to new environmental conditions, and it is therefore of immense importance to study primate landscape use at large spatial scales to determine their responses to habitat alterations and assess their flexibility and adaptability to change (e.g. Arroyo-Rodriguez and Fahrig 2014). Chimpanzees (*Pan troglodytes*) are a primate species facing habitat loss and degradation throughout their range (e.g. Humle et al. 2016b), but it remains unclear how susceptible they are to changing environments. Similarly, changing landscapes in the past are expected to have played a vital role in human evolution (e.g. Bobe et al. 2002, Potts 2007), but limited evidence is available on the behavioural patterns of early hominins (e.g. Plavcan 2013). As chimpanzees are closely related to humans, insights into chimpanzee behavioural ecology in changing landscapes may provide new information into the patterns of early hominin landscape use (e.g. Moore 1996, Mitani 2013). This thesis therefore explored the landscape-scale habitat use of three hominid species (i.e. chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) across a wide range of environments. It investigated the minimal landscape requirements and constraints for chimpanzees and early hominins to determine how flexibly hominids can adapt to changing environments. Specifically, two main research questions were addressed:

I) How will chimpanzee (*Pan troglodytes*) landscape use vary when environments differ from forests to more open habitats, and how is this linked to the presence of specific vegetation features and micro-climate characteristics?

II) How would the landscape use of the early hominins *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis* have differed when environments varied from forests to more open habitats, how would this have differed between the early hominin species, and among early hominins and extant chimpanzees?

Due to difficulties in observing direct hominid responses to present, past and future landscape changes, an individual-based modelling approach based on hominid-habitat relationships from field studies was used. Additionally, due to limited data on early hominins, a referential modelling approach based on findings from chimpanzees was used to explore human origins.

Part I: Chimpanzee landscape use

Chimpanzee behaviour

Chimpanzees select specific types of vegetation (e.g. forest, woodland, grassland) for specific behavioural activities and at different times of day based on vegetation features (e.g. tree height, (food) tree density, canopy cover, canopy connectivity, presence of food and water) and micro-climate characteristics (e.g. local temperature, local luminosity; e.g. Pruetz 2007, Koops et al. 2012a, Duncan and Pillay 2013). Site selection has been linked to various drivers, and factors hypothesised to drive chimpanzee site choice include the thermoregulation hypothesis, the antipredation hypothesis, the antivector hypothesis and the optimal foraging theory (e.g. Koops et al. 2012a. Samson et al. 2013. Stewart and Pruetz 2013, Potts et al. 2016). Even though details on the micro-habitat characteristics preferred and required by chimpanzees for different behavioural activities could help focus conservation strategies towards more efficient chimpanzee habitat protection, such data remain scarce and often descriptive. **Chapter 2** of this thesis explored this knowledge gap and aimed to identify the minimal landscape requirements and constraints for chimpanzees in selecting a site for a specific activity based on a review of published chimpanzee-habitat interactions and preferences from field studies. Specifically, Chapter 2 reviewed current knowledge on the hypothesis that chimpanzees would select specific sites for specific activities to optimise their predator avoidance, thermoregulation, and foraging efficiency, and that specific vegetation features and micro-climates, such as tall trees, closed canopies, low temperatures and high food availability, would be selected accordingly.

Chimpanzee site selection for feeding, drinking, nesting, resting and travelling activities across sites and studies was addressed using a thorough literature review. Results showed that, whereas the environmental context of nest building was relatively well studied, and detailed information on *where* and *when* this activity is performed was available (e.g. Koops 2011, Stewart 2011, Hernandez-Aguilar et al. 2013), information on the required and preferred micro-habitat characteristics for feeding, drinking, resting and travelling remained limited (e.g. Brownlow et al. 2001, Hunt and McGrew 2002, Ban et al. 2016). It was therefore difficult to review the exact hypotheses outlined in this chapter, and findings argued for more detailed studies on the environmental determinants of chimpanzee site selection to quantify *where*, *when* and *why* chimpanzees select specific locations.

Based on reviews of chimpanzee experts (K. Koops, A. Pascual-Garrido, and V. Reynolds) and landscape-scale studies (e.g. Isabirye-Basyta and Lwanga 2008, Arroyo-Rodriguez and Mandujano 2009, Estrada et al. 2017), Chapter 2 made a first attempt to characterise the importance of various vegetation features and micro-climate characteristics in chimpanzee site selection. This led to more detailed and comprehensive insights into the micro-habitat features responsible for chimpanzee site choice, which could be combined with the quantitative data presented in the literature review of chimpanzee behavioural activities for future (modelling) purposes.

This chapter thus brought together the current knowledge on chimpanzee site selection. It was emphasised that chimpanzees are selective in their site choice for specific activities, and some detailed information on chimpanzee-habitat relationships was presented based on findings from field studies. Findings showed that chimpanzees were flexible in their use of different vegetation features, micro-climate characteristics and vegetation types, which argued in favour of chimpanzee adaptability to different environments. These findings provide important implications for chimpanzee conservation. More detailed insights into the environmental determinants of chimpanzee site selection would furthermore allow investigations and comparisons of the underlying reasons and functions of variability in site selection between sites and studies (e.g. Fruth and Hohmann 1996, Koops et al. 2012a), and may reveal new information on the selective pressures shaping chimpanzee landscape use. Findings may be extended to other species, such as closely related early hominins and other primates (e.g. Fruth and Hohmann 1996, Pruetz 2007, Jolly 2013). For this thesis, identified chimpanzee-habitat relationships formed the basis of the chimpanzee landscape use models presented in Chapter 4 and Chapter 5.

Chimpanzee landscapes

Chimpanzees are often referred to as ‘forest chimpanzees’ and ‘savannah chimpanzees’ based on their environment of habitation (e.g. McGrew et al. 1981, Moore 1992, Pruetz and Bertolani 2009, Russak 2013). Nevertheless, exact environmental conditions under which chimpanzee researchers call a chimpanzee landscape a ‘forest’, or a ‘savannah’ had yet to be fully defined. It also remained unclear how these categorisations matched with traditional biome classifications. **Chapter 3** of this thesis addressed this question, and aimed to provide a quantitatively measurable definition of the various landscapes inhabited by chimpanzees, using a qualitative to quantitative process based on existing biome classifications, published field site descriptions, and environmental data.

Forty-three chimpanzee study sites were reviewed for this purpose (e.g. McGrew et al. 1981, Boesch and Boesch-Archerman 2000, Matsuzawa et al. 2011). The 43 study sites were separated into three chimpanzee landscape ‘classes’, i.e. dense forests, forest mosaics and savannahs, based on qualitative landscape descriptions by chimpanzee researchers. Chimpanzee study sites were matched with WWF terrestrial ecoregions (WWF 2018), the Whittaker Biome Diagram (e.g. Whittaker 1975, Ricklefs 2008) and White’s Vegetation Map of Africa (White 1983) to assess whether existing biome classification schemes could consistently separate the chimpanzee researcher classifications. Quantitative data on vegetation cover and climate from chimpanzee study sites were used for k-means clustering analysis, and the creation of boxplots, data range tables and scatterplots to assess whether chimpanzee researchers’ landscape classification of study sites naturally grouped into three objectively-defined landscape classes on the basis of their mean annual temperature (°C), mean annual rainfall (mm), length of the longest consecutive dry season (#), total number of dry months (#), forest cover (%), and tree cover (%).

Results showed that chimpanzee researcher definitions did not match with selected biome, vegetation and climate classification schemes: the three selected bio-climatic schemes lacked sufficient detail to separate chimpanzee forest and savannah field study sites as outlined by chimpanzee researchers. Chimpanzee researcher classifications of sites were, however, separable based on environmental data. Chimpanzee forest and savannah sites could be separated based on forest cover and rainfall. Within forest landscapes, a further distinction was highlighted between dense forest and forest mosaic sites, based on identified relationships between forest cover, annual temperature and length of the longest consecutive dry season. Generally, chimpanzee savannah sites were hot, dry and had only a minimal amount of forest cover, dense forest sites were wet, cool and had a high amount of forest cover, and forest mosaic sites were intermediate.

Even though chimpanzee landscapes ultimately form a natural environmental gradient from forests to savannahs, this chapter is the first to succeed in quantifying definitions of forest and savannah chimpanzees. Furthermore, a new class of mosaic chimpanzees was formalised. The main drivers of chimpanzee landscape classifications were forest cover, rainfall, precipitation seasonality and temperature. These findings highlight the exact range of environments used by chimpanzees, which can be examined to address the underlying reasons of behavioural variability across environments. Findings can also be extended to the landscapes of early hominins and other primates, and it may facilitate classifications of other chimpanzee study sites when environmental data become available. The proposed chimpanzee landscape classification scheme provides consistency and transparency to the chimpanzee literature. In this thesis, chimpanzee landscape findings formed the basis for the individual-based models on chimpanzee landscape use presented in Chapter 4 and Chapter 5.

Chimpanzee landscape use

Landscape use studies investigate how an individual uses the habitats and micro-habitats in its environment to find its required resources (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). Landscape use is guided by an individual's internal states, and is primarily determined by the spatial arrangement of resources across the landscape (e.g. Harvey and Weatherhead 2006, Sutton et al. 2017). Studies on primate habitat use across a wide range of environments are scant, and it remains unclear how flexibly primates can adapt to changing landscapes. As chimpanzees inhabit a wide range of habitats (e.g. Hunt and McGrew 2002, Inskipp 2005) and are threatened with extinction throughout their range (e.g. Humle et al. 2016b, Estrada et al. 2017), they are an ideal species for studying behavioural adaptability to a variety of landscapes. **Chapter 4** of this thesis aimed to determine how activity budgets, energy budgets, and daily path lengths varied for chimpanzees when their habitats differed along an environmental gradient from dense forest to forest mosaics and savannahs.

Due to the challenges faced when studying landscape use under field conditions (i.e. relevant spatial scales, time commitments, complexities in species-habitat interactions, and difficulties in observing direct responses to landscape changes), individual-based models provide an important tool in landscape use studies (e.g. Dunbar 2002, Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014). An individual-based model on chimpanzee landscape use was created in this chapter using NetLogo; environments and individuals followed detailed rules based on findings from Chapter 2 and Chapter 3. The resulting generic chimpanzee landscape use model produced output on daily activity budgets, path lengths, energy, hydration and fatigue budgets, food and water intake, vegetation type usage, and site selection for chimpanzees in dense forests, forest mosaics and savannahs.

Model output showed that chimpanzees adjusted their patterns of landscape use to suit their environment. Forest was the preferred vegetation type overall and for each behaviour across environments, and chimpanzees preferentially used forest vegetation. Generally, individuals increased their feeding time, drinking time, travel time and travel distance, decreased their resting time, and used more suboptimal woodland and grassland vegetation types more often when the environment was more open. In savannahs, however, travel time and distance increased exponentially at the cost of feeding, drinking, nesting and resting time, leading to highly negative energy and hydration budgets, and highly positive levels of fatigue. Model output was compared to literature data on forest, mosaic and savannah chimpanzees where available, and models were generally validated to correctly predict chimpanzee landscape use patterns in different environments, i.e. within 3%, 13% and 25% of their observed range for forest, mosaic and savannah chimpanzees, respectively.

Model findings of Chapter 4 confirmed that chimpanzees in different environments use different behavioural strategies to balance their energy, hydration and fatigue budgets. Chimpanzees were flexible to adjust their behavioural patterns to fit the resource availability of various environments, but maintaining homeostasis became increasingly more difficult in more open landscapes. In particular, savannah chimpanzees faced increasing survival challenges, and additional adaptations seemed necessary to safeguard their survival. Chimpanzee responses to more open environments were similar to observed behavioural alterations of other primate species in degraded habitats (e.g. Clarke et al. 2002, Asensio et al. 2007, Sha and Hanya 2013), and link to the observed correlations between resource abundance, frugivory and travel distance (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005, Coward and Grove 2011). Model output characterised forest vegetation as chimpanzee critical habitat. This chapter thus presented a first null-model of chimpanzee landscape use. The model identified chimpanzee behavioural flexibility across realistic, present-day environments, and highlighted specific behavioural patterns, adaptations and challenges to different landscapes. Findings have implications for future research and conservation, as environmental manipulation of the model in scenario testing can provide insights into chimpanzee responses to future landscape changes and the underlying reasons for adaptation, behavioural innovation and evolution of hominids. It can furthermore present a referential model to study human origins.

Chimpanzee landscape use in marginal savannahs

Savannah chimpanzees live at the edge of their ecological niche in challenging savannah landscapes, and may form the key to understanding how chimpanzees may cope with increasing habitat fragmentation and climate change throughout their range (Pruetz 2018). However, compared to the wealth of information that is known on forest chimpanzees, relatively little is known about the behavioural ecology of savannah chimpanzees (e.g. Hunt and McGrew 2002, Pruetz et al. 2002, Russak 2013). As such, it remains unclear how well the generic chimpanzee landscape use model of Chapter 4 was able to accurately assess savannah chimpanzee circumstances based on general chimpanzee literature only, and it remains to be assessed how the inclusion of site-specific details of particular study sites influences model output on chimpanzee landscape use. **Chapter 5** aimed to explore the landscape-scale habitat use of chimpanzees at Issa Valley, a savannah chimpanzee field site in Tanzania (e.g. Piel et al. 2017, Stewart et al. 2018), using an individual-based modelling approach based on field-collected data. Output of the generic and Issa models were compared, and it was predicted that only the Issa model encompassed sufficient detail (i.e. site-specific data on Issa chimpanzee behaviour, habitat and characteristics), to present a realistic picture of chimpanzee landscape use at this site.

Methods for the development of the Issa model included a literature review on Issa chimpanzee behaviour and habitat, as well as field data collection using vegetation plots and micro-climate data loggers (May – July 2017), and analyses of available, long-term Issa data (2014-2016) gathered through chimpanzee follows, reconnaissance walks and fauna transects by GMERC (i.e. Greater Mahale Ecosystem Research and Conservation). These data were used to set out detailed model rules. The Issa model was developed using NetLogo. Similar to the generic chimpanzee model, the Issa model produced output on the daily activity budgets, path lengths, energy, hydration and fatigue budgets, food and water intake, vegetation type usage, and site selection for Issa chimpanzees.

Model results showed that Issa chimpanzees travelled long distances, spent relatively large amounts of time on travel and small amounts on feeding, drinking, nesting and resting, were reliant on forest vegetation and selective in their site choice for different activities, had negative energy and hydration budgets, low food and water intake, and positive fatigue budgets. Whereas the generic model of Chapter 4 also highlighted these general trends for savannah chimpanzees, differences in output showed that the Issa model presented more detailed, site-specific landscape use patterns for this site. As the Issa landscape is more marginal than the savannah landscape simulated in the generic model, this accurately resulted in greater difficulties for Issa chimpanzees in managing their time and energy budgets.

This chapter was the first to present a site-specific landscape use model for chimpanzees in a savannah environment, and model findings provide detailed insights into savannah chimpanzee behavioural patterns. Model results generally supported published findings from other savannah chimpanzee study sites when available, but some inconsistencies were also encountered, which may be due to observed behavioural adaptations not included in the model (e.g. dietary adaptations, time budget adaptations: Wessling et al. 2018a, Pruetz 2018). Due to the scarce and seasonal distribution of resources in savannahs (e.g. McGrew et al. 1981, Moore 1996), savannah chimpanzee patterns of landscape use differed remarkably from those observed for forest chimpanzees. Model findings therefore emphasised chimpanzee behavioural flexibility to a wide variety of landscapes. However, regardless of this adaptability, the low hydration and energy budgets, and high fatigue budgets indicated that savannah chimpanzees still faced particular challenges and, with impending habitat alterations at the edge of their ecological niche, savannah chimpanzees were challenged for survival. The Issa model included additional detail of chimpanzee landscape use at this site based on site-specific data on the spatial arrangement, cover and structural characteristics of different vegetation types, and chimpanzee preferences for vegetation features and micro-climates in selecting a site for a specific behaviour. Nevertheless, the generic chimpanzee landscape use model could be verified to accurately predict general trends and present-day challenges faced by savannah chimpanzees. These findings support future conservation efforts in measuring chimpanzee behaviour and landscapes in the most effective and time-efficient way. Through scenario testing, the Issa model can provide a site-specific case study to facilitate predictions on priority habitat for savannah chimpanzee conservation, savannah chimpanzee responses to future landscape changes, and the adaptations of early hominins in marginal savannahs.

Part II: Early hominin landscape use

Hominin landscape use

Reconstructing early hominin behaviour remains a daunting challenge in human evolution studies as behaviour does not fossilise (e.g. Mitani 2013, Plavcan 2013). It therefore remains largely unknown how early hominins behaved in their landscapes, and how flexibly they were able to adapt to changing environments. Chimpanzees can provide a referential model to reconstruct early hominin behaviour, due to their phylogenetic relatedness, morphological similarities, and similar variety of habitats (e.g. Moore 1996, Mitani 2013). Based on the findings of chimpanzee landscape use in this thesis (Chapter 2 – Chapter 5), **Chapter 6** explored how early hominin (i.e. *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) landscape use would have differed when paleoenvironments varied from dense forests to forest mosaics and savannahs, and how this differed among early hominin species and between early hominins and chimpanzees. Early hominins were expected to adjust to more open environments in a similar way as is observed for chimpanzees. Furthermore, because of differences in morphological adaptations, patterns of landscape use were expected to vary between early hominin species and between early hominins and extant chimpanzees.

Two individual-based models were created in NetLogo to explore early hominin landscape use in different environments. The *Ardipithecus* and *Australopithecus* models followed rules on early hominin behaviour, habitat and characteristics based on literature review (e.g. Reed 1997, Ungar et al. 2010, Stanford 2012), in combination with findings from chimpanzees whenever early hominin data remained absent. The early hominin models differed from the generic chimpanzee model (Chapter 4) by including a wider dietary breadth (i.e. fruit and underground storage organs (USOs) for *Ardipithecus*, and fruit, USOs and meat for *Australopithecus*), and less costly travel patterns for early hominins (e.g. Grine and Daegling 2017, Kozma et al. 2018). The early hominin models produced output on daily activity budgets, path lengths, food and water intake, energy, hydration and fatigue budgets, vegetation type usage, and site selection in forests, mosaics and savannahs.

Model output showed that, similar to chimpanzees (Chapter 4), early hominins increased their drinking, feeding and travel time and travel distance, and decreased their nesting and resting time, when their environments were more open. Across environments, *Ardipithecus* generally had longer feeding, travel and drinking times and travel distances, shorter resting times, higher fruit intake and fatigue budgets, lower energy and hydration budgets, and a decreased usage of more open vegetation types than *Australopithecus*. Chimpanzees generally had shorter resting times, longer travel times and distances, lower energy and hydration budgets, higher fatigue budgets, and more restricted range use than early hominins. Feeding and drinking times, and fruit and water intake were generally higher for chimpanzees than for early hominins in dense forests and forest mosaics, but were considerably lower for chimpanzees in savannahs.

All three hominid species preferred fruit as a food source, and preferentially used forest vegetation types. The early hominin models were validated to provide predictions of landscape-scale patterns of habitat use that reasonably matched known landscape use and diets for *Ardipithecus* and *Australopithecus*.

This chapter thus provided detailed early hominin landscape use models, and thereby presented important new information for early human origins and adaptability to change. As expected, model output showed that behavioural strategies differed between species and landscapes. All species were flexible to adjust their behavioural patterns in various environments, but maintaining homeostasis in more open environments was increasingly more difficult, which contradicts the traditional view that hominins thrived in open landscapes (e.g. Potts 1998, Bender et al. 2012, Dominguez-Rodrigo 2014). Travel times in savannahs were far greater for all three hominids than in forests and mosaics, which could be linked to the relationship between travel distance, resource abundance and frugivory (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005, Coward and Grove 2011). Whereas increases in travel time for chimpanzees happened at the cost of feeding and drinking time and resulted in highly negative energy and hydration budgets, early hominins were better able to compensate for their increase in travel time as a result of their wider dietary breadth and increased locomotor efficiency (e.g. Grine and Daegling 2017, Kozma et al. 2018). All species preferred forest vegetation, but early hominins were able to use open vegetation types more optimally due to their morphological adaptations (e.g. Wheeler 1984, Lieberman 2015). Species thus differed in their ability to successfully exploit more open landscapes, with *Australopithecus* being more successful than *Ardipithecus*, and early hominins being more successful than chimpanzees. The early hominin models can be used to facilitate predictions on the impacts of landscape changes and behavioural innovations on hominin survival, and to provide a framework for understanding the role of landscapes in hominin evolution.

Combining hominid landscape use findings and addressing research questions

When combining the findings of the results chapters of this thesis, a detailed picture emerges with regards to the overall research questions on hominid landscape use. Findings from Chapter 2 – Chapter 5 showed that chimpanzee patterns of landscape use changed when environments differed along an environmental gradient from dense forests to forest mosaics and savannahs, and that this was tightly linked to the presence of specific vegetation features and micro-climate characteristics. Chimpanzees select specific sites for specific activities and at different times of day based on micro-habitat characteristics (Chapter 2), and inhabit various environments where the abundance and distribution of these resources differed (Chapter 3). The overall resource availability across environments shaped the landscape-scale patterns of habitat use for chimpanzees (Chapter 4 and Chapter 5), which is also observed for other primates (e.g. Asensio et al. 2007, Sha and Hanya 2013), and other animals (e.g. Deppe and Rotenberry 2008, Sutton et al. 2017). In more open environments such as savannahs, resources are scarcer, more seasonal and widely distributed, which affects species' activity budgets (e.g. McGrew et al. 1981, Moore 1996, Clarke et al. 2002). Travel distance, and thus travel time, is influenced by resource availability and frugivory, with more widely distributed resources and a higher amount of frugivory in a species' diet leading to longer travel times and distances, which, in turn, influences the time required and available for other time budget components, such as feeding, drinking, nesting, and resting (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005, Korstjens et al. 2010). Chimpanzees were able to adjust their landscape use to fit the resource distribution of various environments (Chapter 4 and Chapter 5), but maintaining homeostasis was increasingly more difficult in savannahs, especially marginal savannahs like Issa (Chapter 5). Field studies showed that chimpanzees flexibly changed their behavioural patterns in savannahs (e.g. behavioural innovations such as lower population densities, a wider dietary breadth, using caves for thermoregulation, and digging wells for drinking water; e.g. Hunt and McGrew 2002, Pruetz 2007, Wessling et al. 2018a) in order to maintain their fitness. Chimpanzees are thus able to cope with the extreme conditions of savannahs at various sites (e.g. Hunt and McGrew 2002, Pruetz and Bertolani 2009, Piel et al. 2017), but it remains unknown how chimpanzees may cope with further environmental changes throughout their range. With detailed insights into chimpanzee behavioural ecology in various landscapes, the chimpanzee landscape use models presented in Chapter 4 and Chapter 5 provided an original contribution to knowledge by quantitatively identifying the selective pressures that shape chimpanzee patterns of landscape use. Findings on chimpanzee habitat dependence, behaviour-habitat relationships, as well as minimal landscape requirements and constraints present important information for chimpanzee conservation efforts, and the models are able to provide a useful tool for conservationists in exploring chimpanzee responses to future landscape changes in general (Chapter 4) or at specific study sites (Chapter 5).

Similarly, findings from Chapter 6 showed that early hominin landscape use differed in dense forest, forest mosaic and savannah environments due to the presence of specific vegetation features and micro-climate characteristics. Hominins adapted to various environmental changes during the Plio-Pleistocene, with landscapes generally becoming gradually more open (e.g. Bobe et al. 2002, Potts 2007). Model output from Chapter 6 showed that early hominins adapted their activity budgets to suit the resource abundance and distribution of their landscapes in order to cope with the environmental changes of their time. Similar to chimpanzees, time budget alterations were linked to the influence of resource availability and frugivory on travel distance (e.g. Palacios and Rodriguez 2001, Ganas and Robbins 2005). Early hominin morphological adaptations to bipedality decreased their energy expenditure and their bipedal posture reduced exogenous solar heat gain (e.g. Wheeler 1984, Lieberman 2015). As such, early hominins had reduced thermoregulatory stress and a higher tolerance to open areas, and subsequently had a wider access to high-quality and/ or isolated resources (e.g. USOs, meat from carcasses; e.g. Laden and Wrangham 2005, Lieberman 2015, Pobiner 2015). Within the early hominin species, *Australopithecus* was better adapted to increased locomotor efficiency and a wider dietary breadth than *Ardipithecus* (e.g. Kozma et al. 2018). The wider range and resource use of early hominins due to these morphological adaptations led to differences in landscape use patterns between the three hominid species (i.e. chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis*/ *afarensis*) investigated in this thesis. *Australopithecus* was generally more successful in more optimally exploiting the available resources of more open vegetation types and maintaining homeostasis (and thus fitness) than *Ardipithecus* and chimpanzees, and chimpanzees were less successful than *Ardipithecus*. These differences were especially evident in more open habitats such as marginal savannahs. With these findings, the early hominin models presented in Chapter 6 provide a unique contribution to human evolution studies, with detailed new insights into early hominin behaviour, as well as into hominin adaptability and susceptibility to change, the differences and similarities in landscape use patterns across species and environments, and chimpanzee applicability as early hominin referential models. The early hominin models provide an important tool for exploring early hominin origins, and can be adapted for future purposes.

Current research limitations

The main research limitations of this thesis were literature-based data shortages, the individual-based modelling approach, and referential modelling. Chimpanzees have been studied across a wide range of study sites and in a wide variety of environments (e.g. Goodall 1986, Reynolds 2005). As such, an extensive literature database exists on the behavioural ecology of chimpanzees in their natural habitat across equatorial Africa. Nonetheless, data on various topics remain limited, including detailed outlines of the specific environments inhabited by chimpanzees at various sites (Chapter 3), the importance of specific vegetation features, micro-climate characteristics and general environmental variables in deciding *where* and *when* to perform a particular activity (especially feeding, drinking, resting and travelling; Chapter 2), the internal changes in energy, hydration and fatigue following from different behaviours (Chapter 2), and the underlying motives to *why* certain sites are selected, preferred and/or required for specific activities (Chapter 2). Similarly, based on fossil evidence, some detailed knowledge currently exists on the behavioural ecology of early hominins such as *Ardipithecus ramidus*, *Australopithecus anamensis*, and *Australopithecus afarensis* (e.g. Reed 1997, Ungar et al. 2010), but extensive insights into especially early hominin behaviour, specific habitats, and behaviour-habitat relationships remain incomplete (Chapter 6). As detailed data on chimpanzee and early hominin behaviour, landscapes, and characteristics were necessary to develop realistic model rules for the individual-based models (Chapter 4 – Chapter 6), this thesis dealt with these data shortages in various ways, such as expert-based reviews on chimpanzee site selection (Chapter 2), literature-based reviews of important landscape-scale variables in species' habitat use (Chapter 2), general knowledge-based considerations (Chapter 4 – Chapter 6), field data collection (Chapter 5), and referential modelling (Chapter 6). Nevertheless, the publication of more detailed and quantitative data for chimpanzees and early hominins will provide more insights, and may lead to more appropriate model rules.

The second limitation of this thesis was the individual-based modelling approach, as models are always simplifications of 'real-life' systems (e.g. van der Vaart et al. 2016). Due to constraints in processing power and complexities in interpreting cause-effect relationships, models are approximate representations of the 'real world' (e.g. Dunbar 2002). Nonetheless, models provide a valuable solution to study complex systems, where challenges such as relevant spatial scales, time commitments, complexities in species-habitat interactions, and difficulties in observing responses to landscape changes render direct observations and field studies difficult (Dunbar 2002, Arroyo-Rodriguez and Fahrig 2014). Guidelines on how to develop, test and analyse individual-based models exist (e.g. Grimm et al. 2006, Railsback and Grimm 2012), but these guidelines are not set in stone, as can be seen from the variety of approaches to individual-based modelling in published research (e.g. Jepsen et al. 2005, Sellers et al. 2007, Bialozyt et al. 2014). In this thesis, the individual-based modelling guidelines were followed to such an extent as to make the models developed as clear, accessible and easy to interpret as possible. Chapter 4 – Chapter 6 highlighted specific points on how the individual-based models on hominid landscape use could be improved. These improvements were not implemented due to time constraints, data shortages, comparison reasons between models (i.e. keep model output similar for detailed comparisons), and/or because new model output was beyond the current scope of this thesis, but could provide important applications for future models.

As early hominin behaviour, landscapes and characteristics cannot be observed directly, behavioural patterns have to be reconstructed by extrapolating insights from fossil remains, and/or by using a referential modelling approach based on living species (e.g. Jolly 2013). Chapter 6 reviewed the criticism on referential modelling in the study of human evolution, and focused on referential modelling per se (e.g. Tooby and DeVore 1987), as well as on the chimpocentrism of early hominin models (e.g. Sayers and Lovejoy 2008). Whereas Tooby and DeVore (1987) argued that referential models based on homology between species are inferior to conceptual models based on evolutionary theory (i.e. no rules exist on how to select a living species as a referential model, and referential models tend to focus on observed similarities rather than differences between model and referent), referential models provide essential data points for the construction of conceptual models (e.g. Moore 1996, Stanford 2012). Similarly, whereas the chimpocentrism argument focuses on the overemphasis of behavioural similarities between chimpanzees and early hominins, as well as on the underemphasised applicability of other species (Sayers and Lovejoy 2008, Sayers et al. 2012), chimpanzees' close phylogenetic relatedness to humans, their similar habitats and their similar morphological adaptations provide a useful model for exploring important *similarities* and *differences* between chimpanzees and hominins (e.g. Moore 1996, Mitani 2013). Chimpanzees are therefore useful referential models in the study of human origins. It should be taken into account, however, that chimpanzees are not the only option to reconstruct early hominin behaviour, and behavioural reconstructions based on other species (e.g. bonobos) should also be considered (e.g. Zihlman 1996). Also, similar to individual-based models, referential models are *models* which always provide an approximate representation of reality.

Future perspectives

Chapter 2 – Chapter 6 highlighted various areas for future academic research. First and foremost, future studies should focus on collecting more data (where possible) on the landscapes, behaviours, characteristics and behaviour-habitat relationships of chimpanzees and early hominins. More detailed insights into hominid behavioural ecology and the environmental context of hominid behavioural patterns will highlight innovative information into hominid adaptability, flexibility and vulnerability to change, and may be extended to other species. These detailed and quantified insights into hominid-habitat interactions may provide useful information for chimpanzee conservation and the development of appropriate mitigation strategies (e.g. reforestation, green corridors, afforestation, deforestation avoidance, forest management, buffer zones) for the protection of chimpanzees, their habitat and their required resources, as well as shed new light onto human evolution. Findings would additionally provide more detailed information for the outline of specific model rules in the development of individual-based landscape use models. Specific gaps and future research avenues that could be addressed in future studies to generate new insights and knowledge into hominid behaviour and ecology, and to test and validate current model assumptions (indicated with '*' below) and output include:

- Further quantifying chimpanzee and early hominin environments within their home-ranges across (fossil) sites, i.e. for each site addressing the exact:
    - vegetation types (e.g. forest, woodland, grassland, cultivated fields).
    - vegetation cover.
    - spatial vegetation arrangement*.
    - vegetation features per vegetation type (e.g. tree height, DBH, canopy cover, tree density, food and water availability)*.
    - fragmentation*.
    - climate (e.g. temperature, temperature variability, rainfall, rainfall variability, seasonality)*.
    - micro-climates per vegetation type (e.g. local temperature, local luminosity, local humidity)*.
- Further exploring chimpanzee and early hominin behaviours (e.g. feeding, drinking, nesting, resting, travelling) across sites, seasons, landscapes and species, i.e. investigating hominid:
    - activity budgets.
    - daily path lengths.

    - dietary breadths*.
    - material culture.
    - behavioural repertoires*.
    - behavioural innovations.
    - behavioural flexibility.
- Further specifying chimpanzee and early hominin behaviour-habitat relationships across (fossil) sites, i.e. studying:
    - *where* and *when* hominids perform their daily activities (e.g. feeding, drinking, nesting, resting, travelling) in relation to various vegetation features (e.g. tree height, DBH, canopy cover, tree density, food and water availability), micro-climates (e.g. local temperature, local luminosity, local humidity) and general environmental variables (e.g. time of day, precipitation, temperature)*.
    - the relative and landscape-scale importance of these environmental variables in selecting a site for a specific activity*.
    - *why* hominids select specific sites for their daily activities (e.g. thermoregulation hypothesis, antivector hypothesis, antipredation hypothesis, optimal foraging theory).
- Further examining how chimpanzee and early hominin behaviour is guided by internal states (e.g. energy, hydration, fatigue) across sites, seasons, landscapes and species, i.e. assessing:
    - *how much* (e.g. energy, hydration, fatigue, macronutrients, micronutrients) can be gained and lost when hominids perform their daily activities (e.g. feeding, drinking, nesting, resting, travelling)*.
    - what typical strategies exist for energy, hydration, fatigue and nutrient balancing*.
    - what are realistic total daily budgets of gain and loss (e.g. for energy, hydration, fatigue, and nutrients)*.
    - how do hominid internal states vary throughout the day.
    - what are plausible internal states for hominids to start off and finish their day*.
    - *how much* (e.g. energy, nutrients) can be gained and lost through various food items and food processing activities*.

Second, through scenario testing, the individual-based models on hominid landscape use created in this thesis have important future applications. As explained in detail in Chapter 4 – Chapter 6, small manipulations of the current model codes may ***i)*** facilitate predictions on the impact of various behaviour and landscape changes on hominid patterns of landscape use, ***ii)*** present a framework for understanding the underlying reasons of behavioural innovation and adaptation to specific landscapes in hominid evolution, and ***iii)*** provide a referential model for the behaviour and ecology of closely related species. The models can also easily be adapted to suit the characteristics of other species. Whenever detailed information is available for a particular species, model codes can be adapted accordingly. Thereby, the models created in this study present a unique contribution to human evolution studies and have various implications for future research on other species, including chimpanzees. The models furthermore provide a powerful tool for conservationists in exploring the landscape-scale habitat use of various species. Model output can inform conservation studies on the applicability, appropriateness and effectiveness of various mitigation strategies (e.g. green corridors, reforestation) for species protection and survival. Potential, high priority research questions (per discipline) that can be addressed with the models using scenario testing include:

- **Climate and landscape change #1**: Considering the combined effect of climate and (human-induced) landscape changes to chimpanzee habitat, what will be the effect of future environmental change scenarios on chimpanzee landscape use and survival abilities, under which environmental conditions will entire chimpanzee populations be able to survive, when will chimpanzee population reductions and/or behavioural adaptations become necessary, when will chimpanzee populations become (locally) extinct, and what will chimpanzees' tipping points be of coping vs. non-coping with environmental change? This can be tested with the current models by, for example:
    - Adding various landscape changes to the current model environments, such as the conversion of forest vegetation into cultivated fields, habitat loss, habitat fragmentation and the insertion of human infrastructure.
    - Adding various climatic changes to the current model environments, such as global warming and drying, and changes in local micro-climates.
    - Adding detailed model rules on climate and landscape change interactions, such as tree cover and habitat loss interactions with (micro-) climate changes.
- **Conservation #1**: Considering that climate and landscape changes have various effects on chimpanzee habitat and different mitigation strategies currently exist,

which environmental changes have the largest influence on chimpanzee activity budgets, daily path lengths, internal states and survival abilities, mitigation against which environmental changes should be prioritised, what is the effectiveness and relative importance of various mitigation strategies with regards to patterns of chimpanzee landscape use, and which strategy (or combination of strategies) is most effective in safeguarding chimpanzee survival? This can be tested with the current models by, for example:

  - Adding different environmental changes to the model one-by-one, such as habitat fragmentation, habitat loss and habitat isolation per se.
  - Adding the outcomes of various mitigation activities to the models one-by-one and combined, such as reforestation areas, green corridors and buffer zones.

- **Chimpanzee behaviour and ecology #1**: Considering the wide variability in dietary breadths and the use of material culture across sites, as well as within and between landscapes, what is the impact of diet and tool use on chimpanzee activity budgets, daily path lengths and internal states? This can be studied with the current models by, for example:
  - Adding new dietary items, such as crops and insects, with detailed rules on caloric and nutrient gains, intake rates, and distributions across the landscape.
  - Adding detailed rules on tool use processes, such as ant-dipping and termite-fishing, with respect to energetic gains and losses, and time commitments.
- **Chimpanzee behaviour and ecology #2**: Considering the costs and benefits of group living and the increasing marginality of environments under past and current climate and landscape change scenarios, which ecological conditions promote the adoption of fission-fusion social systems, and how does this influence patterns of chimpanzee landscape use? This can be researched with the current model by, for example:
  - Adding detailed model rules on chimpanzee grouping patterns, cooperation and competition.
  - Adding detailed model rules on chimpanzee subgroup formation with regards to various social and ecological conditions.
- **Chimpanzee behaviour and ecology #3**: Considering the increasing human encroachment on chimpanzee habitat, how are chimpanzee patterns of landscape

use affected by the presence of, and interactions with, humans? This can be investigated with the current models by, for example:

  - Adding human individuals as new species to the model, with detailed rules on their behaviour, environment, and behaviour-habitat relationships.
  - Adding detailed model rules on chimpanzee – human interactions.

- **Hominin evolution #1**: Considering the wide variety of landscapes in hominin paleoenvironmental reconstructions and the randomization of hominin landscapes in the current models, how would early hominins have adapted their landscape use to real-world environments? This can be tested with the current models by, for example:
  - Adding hominin individuals with detailed model rules on behaviour, behaviour-habitat relationships and characteristics to the currently quantified, present-day environment of the Issa model, or to other models of real-life environments.
- **Hominin evolution #2**: As many hominin species are currently identified and species often differ in their morphological adaptations, how would other hominin species have used their landscapes, and how would this have differed along an environmental gradient? This can be investigated with the current models by, for example:
  - Adding new hominin species to the model, such as species from the genera *Australopithecus*, *Paranthropus* and *Homo*, with detailed model rules on behaviour, environments, and behaviour-habitat relationships within realistic landscapes for these hominin species.
- **Hominin evolution #3**: Considering the faunal assemblages found in association with hominin fossils, how would the presence of other species have positively and negatively impacted hominin fitness and survival abilities, as measured in activity budgets, daily path lengths and internal states, for example with regards to competition, cooperation, hunting opportunities and predator avoidance? This can be studied with the current models by, for example:
  - Adding individuals of other species to the models, with detailed rules on their behaviour, habitat, and behaviour-habitat relationships in realistic landscapes.
  - Adding detailed model rules on hominin – sympatric species interactions, such as competition, cooperation, hunting opportunities and predation.

- **Hominin evolution #4**: As considerable debate exists on the origins and functions of hominin behavioural innovations and adaptations, when, how and why would bipedalism and material culture have evolved, why was it advantageous, and what would have been the effects on patterns of hominin landscape use? This can be tested (and the debate potentially solved) with the current models by, for example:
    - Adding detailed model rules on the various assumed functions of bipedality, such as reductions in energetic costs, thermoregulatory advantages and freeing the hands for other activities, with respect to their gains and losses (e.g. energy, hydration, fatigue).
    - Adding various tool use processes, such as stone tool use, tool manufacture and hunting, with regards to their energetic and nutrient gains and losses, as well as time commitments.

Although outlined per discipline above, addressing these questions and testing the various presented scenarios can be beneficial for multiple disciplines at once.

Insights from this thesis also lead to the outline of some practical recommendations. For example, the landscape-based classifications of chimpanzees and their environments (Chapter 3) showed a lack of consistency in environmental terminologies, and no universally accepted climate and vegetation classification scheme currently exists (e.g. Torello-Raventos et al. 2013, Dominguez-Rodrigo 2014). This argued for the establishment of clearly outlined and realistically scaled definitions for environments, landscapes and vegetation types across disciplines, preferably with respect to geographical and climatological literature, and this should be addressed in future studies. Additionally, this study encountered that no strict rules are outlined for individual-based and referential modelling approaches, and methods differ between studies. For individual-based modelling, detailed guidelines are set out (e.g. Grimm et al. 2006, Railsback and Grimm 2012), and future modelling research should adhere to these guidelines to make the modelling process more accessible. Detailed procedures should likewise be highlighted for referential modelling, i.e. how to select model and referent, how to deal with differences and similarities between model and referent, how to create, analyse and test referential models, etc., to make this approach transparent and comparable between species. One of the main criticisms of individual-based models, and perhaps of models in general, is that models are often complex and irreproducible due to poor documentation (e.g. Grimm et al. 2010); clear, accessible and enforced guidelines for model development and documentation will deal with this criticism.

Furthermore, within published literature, habitat suitability studies for chimpanzees often focus on the presence of forest (e.g. Junker et al. 2012). Whereas this thesis emphasised the importance of forest for chimpanzee survival and highlighted forest vegetation as chimpanzee critical habitat, it also showed that other vegetation types were important for chimpanzee persistence, especially where forest was scarce. When only limited amounts of forest vegetation were present, chimpanzees relied increasingly on other vegetation types such as woodland to meet their daily requirements and find their necessary resources. This indicates that a limited availability of forest does not necessarily prohibit chimpanzee inhabitancy, as can be seen for many mosaic and savannah chimpanzee field study sites (e.g. Pruetz and Bertolani 2009, Humle 2011). Future studies of habitat suitability modelling should, therefore, include a wide range of predictor variables with regards to suitable vegetation for more realistic predictions of chimpanzee habitat suitability across equatorial Africa (e.g. Jantz et al. 2016, Heinicke et al. 2019). Similarly, whereas this thesis highlighted the importance of landscape-scale studies in investigating the effects of habitat alterations on primate behaviour and survival across a wide range of environments (e.g. Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez and Fahrig 2014), patch-scale studies are also significant, especially with regards to the implementation of local-scale mitigation strategies (e.g. reforestation, forest management) for primate protection and survival. Ideally, chimpanzee conservation would take a global approach, protecting chimpanzees and their habitat simultaneously across their range (e.g. Humle 2015, Korstjens and Hillyer 2016). Realistically, however, this is often not feasible, as chimpanzee habitat stretches over several countries, which are each subject to their own governmental laws and regulations (e.g. Humle 2015). A local-scale approach of implementing mitigation strategies for chimpanzee protection is therefore more likely (e.g. Humle 2015, Korstjens and Hillyer 2016), and patch-scale implementations together should work towards the greater goal of globally safeguarding chimpanzee survival.

Conclusion

This thesis explored chimpanzee, *Ardipithecus* and *Australopithecus* landscape use across a wide range of environments to determine their flexibility and adaptability to changing landscapes using individual-based and referential modelling. Based on literature review, this thesis successfully classified chimpanzee landscapes as dense forests, forest mosaics and savannahs, and accordingly was the first to present detailed chimpanzee landscape definitions based on published vegetation cover and climate data

(Chapter 3). Detailed chimpanzee-habitat relationships were highlighted based on literature and expert-based reviews, and showed specific preferences and requirements for vegetation features, micro-climate characteristics and general environmental variables for chimpanzees in selecting a site for a specific activity (Chapter 2). These data were used to set out detailed rules for the individual-based landscape use models created with NetLogo. The generic chimpanzee landscape use model indicated that patterns of chimpanzee landscape use differed between landscapes, with the maintenance of homeostasis and fitness becoming increasingly more difficult in more open landscapes due to the scarce and wide distribution of resources (Chapter 4). A specific case study for Issa Valley, a savannah chimpanzee field site in Tanzania, verified these findings and showed that especially savannah chimpanzees faced particular survival challenges (Chapter 5). The marginal, 'real life' Issa landscape was demonstrated to be even more challenging than the savannah environment used in the generic chimpanzee model; additional adaptations and behavioural innovations seemed necessary to safeguard savannah chimpanzee survival (Chapter 5). Using a referential modelling approach based on findings from chimpanzees combined with early hominin evidence, the *Ardipithecus* and *Australopithecus* landscape use models showed that early hominins adjusted their behavioural patterns to forests, mosaics and savannahs in a similar way as was observed for chimpanzees, but early hominins were more successful in more optimally using open vegetation types and landscapes due to their morphological adaptations to increased locomotor efficiency and a wider dietary breadth (Chapter 6). Similarly, *Australopithecus* showed to be more successful than *Ardipithecus* (Chapter 6). This thesis therefore showed that landscape-scale patterns of hominid habitat use were dependent upon the overall environment, and were tightly linked to the presence and distribution of valuable resources. All three hominid species thrived in forest environments, and were challenged for survival in more open landscapes such as savannahs. By quantitatively characterising the selective pressures that shape hominid landscape use, this thesis provides a unique contribution to the field of primatology and the study of human origins, which can be extended to other species. The created individual-based models on hominid landscape use have important future applications, including presenting a framework for understanding the underlying reasons of behavioural innovation and adaptation to specific landscapes in hominid evolution, and providing a tool for conservation studies in exploring the impacts of future landscape changes.

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APPENDICES

APPENDIX 2.1

Expert-based review questionnaire for chimpanzee experts

To support the data collection on chimpanzee site selection for different activities (Chapter 2), a questionnaire was developed on the environmental determinants of chimpanzee site selection for chimpanzee experts. This questionnaire is outlined on the next two pages and reviewed the relative importance of various vegetation features, micro-climate characteristics and general environmental variables for the chimpanzees at the study sites of the chimpanzee experts. Questionnaires were sent out to the JISCMAIL mailing list for members of the Primate Society of Great Britain (PSGB), and were additionally shared through the social media pages of the PSGB and the International Primatological Society (IPS). Three questionnaires were returned, and were completed by Dr. Kathelijne Koops, Dr. Alejandra Pascual-Garrido, and Prof. Vernon Reynolds.

EXPERT-BASED REVIEWS

Environmental determinants of chimpanzee site selection for specific activities

By completing this questionnaire, you are consenting to the information provided in the participant information sheet. The participant information sheet can be found here.

Name of the expert:
Date:
Study site:
Country:

Vegetation (habitat) types present at the study site (e.g. forest, woodland, swamp, grassland):

Proportion of different vegetation types (e.g. percentage, area) present at the study site:

WHERE TO PERFORM A SPECIFIC ACTIVITY

Importance of specific vegetation features and micro-climate characteristics

Please outline the order of importance (i.e. **1** (*very* important), **2** (important), **3** (*not very* important), **4** (*not* important), or **9** (unknown)) of the outlined vegetation features and micro-climate characteristics in selecting a site for a specific activity for chimpanzees at your study site. Please insert a number in every blank cell. If exact quantitative information is available, please indicate where this information is published or accessible.

Environmental Variable	**Chimpanzee Behaviour**				
	Drinking	**Feeding**	**Nesting**	**Resting***	**Travel**
Vegetation feature					
Tree species					
Tree height					
Tree DBH**					
Tree LBH***					
Tree crown width					
Tree crown height					
Tree crown connectivity					
Tree leaf cover					
Tree branch architecture					
Canopy cover					
Canopy connectivity					
Understory density					
Tree density					
Food tree density					
Food availability					
Water availability					
Micro-climate					
Local temperature					
Sun exposure					
General variable					
Slope					
Altitude					
Vegetation type					

* Resting includes social time
** Diameter at breast height (DBH)
*** Lowest branch height (LBH)

Notes:

PARTICIPANT INFORMATION SHEET

Dear chimpanzee expert,

You are being invited to fill out a short questionnaire to provide some expert knowledge for my research project. Please read the following information carefully in order to decide whether you would like to take part. Let me first introduce myself, my name is Kelly van Leeuwen, and I am a PhD student (2015 – 2018) at Bournemouth University in the UK. My PhD project aims to investigate how flexibly chimpanzees can adapt their behaviour to changing environments. To investigate this, I am using an individual-based modelling approach based on published chimpanzee-habitat relationships from field studies and field data from Issa Valley, Ugalla, Tanzania (the 'Ugalla Primate Project'). It is hoped that the outcomes of this project will contribute to our current understanding of chimpanzees' habitat requirements. This information can be used to predict how chimpanzees will, or will not, cope with future landscape change scenarios, and for exploring the role of landscapes in driving hominid evolution.

As a part of the modelling cycle, I need to come up with specific model rules on chimpanzee behaviour and habitat based on literature from different chimpanzee field study sites. During my literature review, I encountered that knowledge on the environmental context of locations used for specific chimpanzee activities (e.g. feeding, resting, and travel) remains only scarcely presented at this point. This makes it difficult for me to set out specific model rules on where and when the chimpanzees should perform these daily activities. My question to you is whether you would be willing to help me with this, by filling out the attached questionnaire on the importance of various vegetation features and micro-climate characteristics for chimpanzees in selecting a specific location for a specific activity (i.e. feeding, drinking, nesting, resting, and travel) at your study site. Of course, filling out the questionnaire is by no means mandatory, you are free to decide whether you would like to take part in this study, or not.

By completing the questionnaire, you are consenting to take part in this study. Participants are free to withdraw at any time, simply by not returning the questionnaire to my email address. Please note that once you have submitted the questionnaire, I will not be able to remove your responses from the study. Data will not be anonymized for further analyses; in this case, your name can be linked to your study site and appropriate reference can be provided.

All information collected will be kept strictly in accordance to the Data Protection Act 1998. Information will be saved in password-protected files on my personal computer and hard drive. As such, I will be the only person with direct access to the data. The information provided may be discussed with the supervisors of this project. All data relating to this project will be held until 1 year after the award of the degree.

Within my PhD thesis, data from the questionnaire will be used to create an overview (for each chimpanzee study site individually and for all sites combined) on the (relative) importance of different vegetation and micro-climate characteristics for chimpanzees in selecting a location for a specific activity. Where possible, quantitative data and information on the presence and proportions of different vegetation types at each study site will be added. This information will be used to set out model rules for the individual-based models created in the study. As the data will not be anonymized, your name and the date of completion of the questionnaire will be provided as a reference whenever your data will be used. You will also be named in the acknowledgements section of the thesis. In agreement with Bournemouth University's open-access policy, the PhD thesis will be made publicly available after submission. In case the information will be used for publication in peer-reviewed journals, appropriate reference to you will again be provided, as well as credits in the acknowledgements.

For further information, please do not hesitate to contact me. You are also free to contact my supervisors (Dr. Amanda Korstjens, akorstjens@bournemouth.ac.uk; and Prof. Ross Hill, rhill@bournemouth.ac.uk). If you have any concerns regarding this study, please contact the Deputy Dean for Research & Professional Practice of the Faculty of Science and Technology, Prof. Tiantian Zhang (researchgovernance@bournemouth.ac.uk).

Many thanks for considering taking part in my PhD research project. In case you decide to take part, I am looking forward to receiving your questionnaire by email (kvanleeuwen@bournemouth.ac.uk) by November 3rd, 2017.

Yours sincerely,
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APPENDIX 4.1

The 'Overview, Design concepts and Detail' (ODD) protocol for communicating individual-based models

Model descriptions in this study follow the Overview, Design concepts and Details (ODD) protocol for communicating individual-based models (Grimm et al. 2006, Grimm et al. 2010). The basic idea of the ODD protocol is to always structure information about individual-based models in the same sequence, making models more accessible, repeatable and understandable (Grimm et al. 2006, Grimm et al. 2010). The ODD protocol consists of seven elements: 1) purpose; 2) entities, state variables and scales; 3) process overview and scheduling; 4) design concepts; 5) initialization; 6) input; and 7) submodels (Grimm et al. 2006, Grimm et al. 2010). The first three elements can be grouped under the term 'Overview', the fourth element comes under the term 'Design concepts', and the last three elements can be grouped under the term 'Details' (Grimm et al. 2006, Grimm et al. 2010). Table A4.1.1 provides an overview of the different elements of the ODD protocol with their relevant definitions and descriptions. In contrast to the other elements, the element 'design concepts' in itself encapsulates eleven modelling concepts (i.e. basic principles, emergence, adaptation, objectives, learning, prediction, sensing, interaction stochasticity, collectives, and observation) to describe how models implement a set of basic conceptions (e.g. Railsback and Grimm 2012). Design concepts are defined in Table A4.1.2.

Table A4.1.1. Systematic overview of the ODD protocol with relevant definitions and descriptions for each element. Information based on Grimm et al. (2006, 2010) and Railsback and Grimm (2012).

Block	**Element**	**Explanation**
Overview	*Purpose*	The element *purpose* encapsulates the purpose of the model, or the question addressed.
	Entities, State Variables and Scales	The element *entities, state variables and scales* describes what entities (i.e. agents, patches) are in the model, by which state variables these entities are characterized, and what the temporal and spatial resolutions of the model are.
	Process Overview and Scheduling	The *process overview and scheduling* element explain the processes that change the state variables of the model entities, and on what spatial and temporal scale this is done.
Design Concepts	*Design Concepts*	The element *design concepts* addresses how the model implements a set of important basic modelling concepts: basic principles, emergence, adaptation, objectives, learning, prediction, sensing, interaction, stochasticity,

Block	Element	Explanation
		collectives, and observation.
Details	*Initialization*	The *initialization* element outlines the initial state of the model world at the start of a run.
	Input	The element *input* focuses on whether the model needs input from external sources in order to run properly, and if so, which.
	Submodels	The element *submodels* describes the design of the submodels (or subprocesses) that combined represent the processes listed in the *process overview and scheduling* element in more detail.

Table A4.1.2. Definitions of the modelling concepts specified under the design concepts element of the ODD protocol. Information based on Grimm et al. (2006, 2010) and Railsback and Grimm (2012).

Design Concept	Explanation
Basic principles	The concept *basic principles* addresses what general concepts, theories or hypotheses underlie the design of the model.
Emergence	The concept *emergence* specifies which results, behaviours or model outputs emerge from the model, and are not simply imposed by model rules alone.
Adaptation	The *adaptation* concept addresses the question of what adaptive traits (or behaviours) the agents have, how they respond to changes in their environment and within themselves, which decisions they make, and how these behaviours are modelled.
Objectives	The concept *objectives* explains which (internal) objectives guide agents in their behavioural decisions.
Learning	The concept *learning* addresses the question of whether agents change their (adaptive) behaviours over time as a consequence of their experience.
Prediction	The *prediction* concept outlines if and how agents predict the future conditions they are likely to experience.
Sensing	The concept *sensing* outlines which internal and environmental state variables an agent is assumed to know and consider in making its decisions.
Interaction	The concept *interaction* addresses how the agents in the model interact with one another.
Stochasticity	The *stochasticity* concept explains what random processes are put into the model and why this is done.
Collectives	The concept *collectives* addresses if aggregations of agents are formed within the model and how these aggregations affect, and are affected by, the agents that are in it.
Observation	The concept *observation* explains what data are collected from the model, how and when they are collected, and how they can be used for testing, understanding and analysing it.

APPENDIX 4.2

Model parameters of the generic chimpanzee landscape use model of Chapter 4

Table A4.2.1 below outlines the model parameters that were used to set up the generic chimpanzee landscape use model presented in Chapter 4. The table includes information on the parameter values, the source of these parameter values, and whether these parameters were used for calibration and/or sensitivity analysis. Parameter values are either based on empirical data, or on general knowledge considerations. The rationale behind the outlined values for each of the model input parameters is outlined in Appendix 4.5.

Table A4.2.1. Model parameters for the generic chimpanzee landscape use model presented in Chapter 4. The column 'Data source' indicates whether the parameter value is based upon empirical data or knowledge-based considerations; Output indicates that this parameter value was selected in order to produce model output for analyses. The 'Calibration process?' and 'Sensitivity analysis?' columns outline whether a parameter was used for these processes. When a parameter value is specified as, for example, 0 – 21, this indicates that a random value was chosen between 0 and 21 at the onset of each model run for each individual or patch as appropriate. When 'scaled' appears behind a variable, this indicates that this variable was specified on a scale of 0 – 100 as exact data remained absent. Within the table, F stands for dense forests, M for forest mosaics, and S for savannah environments.

Model parameter	Value	Data source	Calibration process?	Sensitivity analysis?
home range size	36km2	Empirical data	No	No
patch size	50mx50m	General knowledge	No	No
% forest cover	80% (F), 45% (M), 10% (S)	Empirical data	No	No
% woodland cover	10% (F), 40% (M), 55%(S)	Empirical data	No	No
% savannah cover	10% (F), 15% (M), 35%(S)	Empirical data	No	No
fragmentation	0.05	General knowledge	No	No
temperature	25°C	General knowledge	No	No
rainfall	0mm	General knowledge	No	No
tree height forest	10 - 50m	Empirical data	No	No
tree height woodland	8 - 20m	Empirical data	No	No
tree height savannah	3 - 15m	Empirical data	No	No
canopy cover forest	75 – 100%	Empirical data	No	No
canopy cover woodland	25 – 75%	Empirical data	No	No
canopy cover savannah	0 – 25%	Empirical data	No	No
canopy connectivity forest	75 – 100%	Empirical data	No	No
canopy connectivity woodland	25 – 75%	Empirical data	No	No
canopy connectivity savannah	0 – 25%	Empirical data	No	No
understory density forest	0 – 25%	Empirical data	No	No
understory density woodland	25 – 75%	Empirical data	No	No

Model parameter	**Value**	**Data source**	**Calibration process?**	**Sensitivity analysis?**
understory density savannah	75 – 100%	Empirical data	No	No
tree density forest	75 – 100%	Empirical data	No	No
tree density woodland	25 – 75%	Empirical data	No	No
tree density savannah	0 – 25%	Empirical data	No	No
food tree density forest	75 – 100%	Empirical data	No	No
food tree density woodland	25 – 75%	Empirical data	No	No
food tree density savannah	0 – 25%	Empirical data	No	No
number of fruit forest	0 - 21	General knowledge	Yes	Yes
number of fruit woodland	0 - 14	General knowledge	Yes	Yes
number of fruit savannah	0 - 7	General knowledge	Yes	Yes
amount of water forest	0 - 100	General knowledge	No	Yes
amount of water woodland	0 - 75	General knowledge	No	Yes
amount of water savannah	0 - 50	General knowledge	No	Yes
temperature-day forest	0 – 25 (scaled)	Empirical data	No	No
temperature-day woodland	25 – 75 (scaled)	Empirical data	No	No
temperature-day savannah	75 – 100 (scaled)	Empirical data	No	No
temperature-night forest	75 – 100 (scaled)	Empirical data	No	No
temperature-night woodland	25 – 75 (scaled)	Empirical data	No	No
temperature-night savannah	0 – 25 (scaled)	Empirical data	No	No
luminosity-day forest	0 – 25 (scaled)	Empirical data	No	No
luminosity-day woodland	25 – 75 (scaled)	Empirical data	No	No
luminosity-day savannah	75 – 100 (scaled)	Empirical data	No	No
luminosity-night forest	0 – 25 (scaled)	Empirical data	No	No
luminosity-night woodland	0 – 25 (scaled)	Empirical data	No	No
luminosity-night savannah	0 – 25 (scaled)	Empirical data	No	No
number of chimps	60	Empirical data	No	No
where - canopy cover criterion	>0	Empirical data	No	No
where–canopy connectivity criterion	>0	Empirical data	No	No
where - understory density criterion	≤50	General knowledge	Yes	Yes
where - tree density criterion	≥50	General knowledge	Yes	Yes
where - food tree density criterion	≥50	General knowledge	Yes	Yes
where - tree height criterion	≥1	Empirical data	No	No
where - local temperature criterion	≤50	General knowledge	Yes	Yes
where - local luminosity criterion	≤50	General knowledge	Yes	Yes
when - feeding criterion	≤144	General knowledge	Yes	Yes
when - drinking criterion	≤72	General knowledge	Yes	Yes
when - resting criterion	>73	General knowledge	No	Yes
when - nesting criterion	≥72	Empirical data	No	No
when - temperature criterion	>29	Empirical data	No	No
when - rainfall criterion	>25	Empirical data	No	No
Initial - energy	0 – 10 kCal	General knowledge	No	Yes
Initial - hydration	0 – 10	General knowledge	No	Yes
Initial - fatigue	0 - 10	General knowledge	No	Yes
Step - energy	-2 kCal	General knowledge	Yes	Yes

Model parameter	**Value**	**Data source**	**Calibration process?**	**Sensitivity analysis?**
Step - hydration	-1	General knowledge	No	Yes
Step - fatigue	+1	General knowledge	No	Yes
Feeding - energy	+3.1kCal per fruit	Empirical data	No	No
Feeding - number fruits eaten	3.5	General knowledge	Yes	Yes
Drinking - hydration	+50	General knowledge	No	No
Drinking - amount water drunk	50	General knowledge	No	Yes
Resting - fatigue	-2	General knowledge	No	Yes
Nesting - fatigue	-2	General knowledge	No	Yes
Travel - energy	-3.5kCal per 50m	Empirical data	No	No
Travel - hydration	-1 per 50m	General knowledge	No	Yes
Travel - fatigue	-1 per 50m	General knowledge	No	Yes
Feed-forest	+1 for each time step	Output	No	No
Feed-woodland	+1 for each time step	Output	No	No
Feed-savannah	+1 for each time step	Output	No	No
Drink-forest	+1 for each time step	Output	No	No
Drink-woodland	+1 for each time step	Output	No	No
Drink-savannah	+1 for each time step	Output	No	No
Rest-forest	+1 for each time step	Output	No	No
Rest-woodland	+1 for each time step	Output	No	No
Rest-savannah	+1 for each time step	Output	No	No
Nest-forest	+1 for each time step	Output	No	No
Nest-woodland	+1 for each time step	Output	No	No
Nest-savannah	+1 for each time step	Output	No	No
Travel-forest	+1 for each time step	Output	No	No
Travel-woodland	+1 for each time step	Output	No	No
Travel-savannah	+1 for each time step	Output	No	No
Daily-path-length	+50m for each patch	Output	No	No
Energy	Update with behaviour/run	Output	No	No
Hydration	Update with behaviour/run	Output	No	No
Fatigue	Update with behaviour/run	Output	No	No
Food intake	+3.5 for each feed	Output	No	No
Water intake	+50 for each drink	Output	No	No

APPENDIX 4.3

Model code of the generic chimpanzee landscape use model of Chapter 4

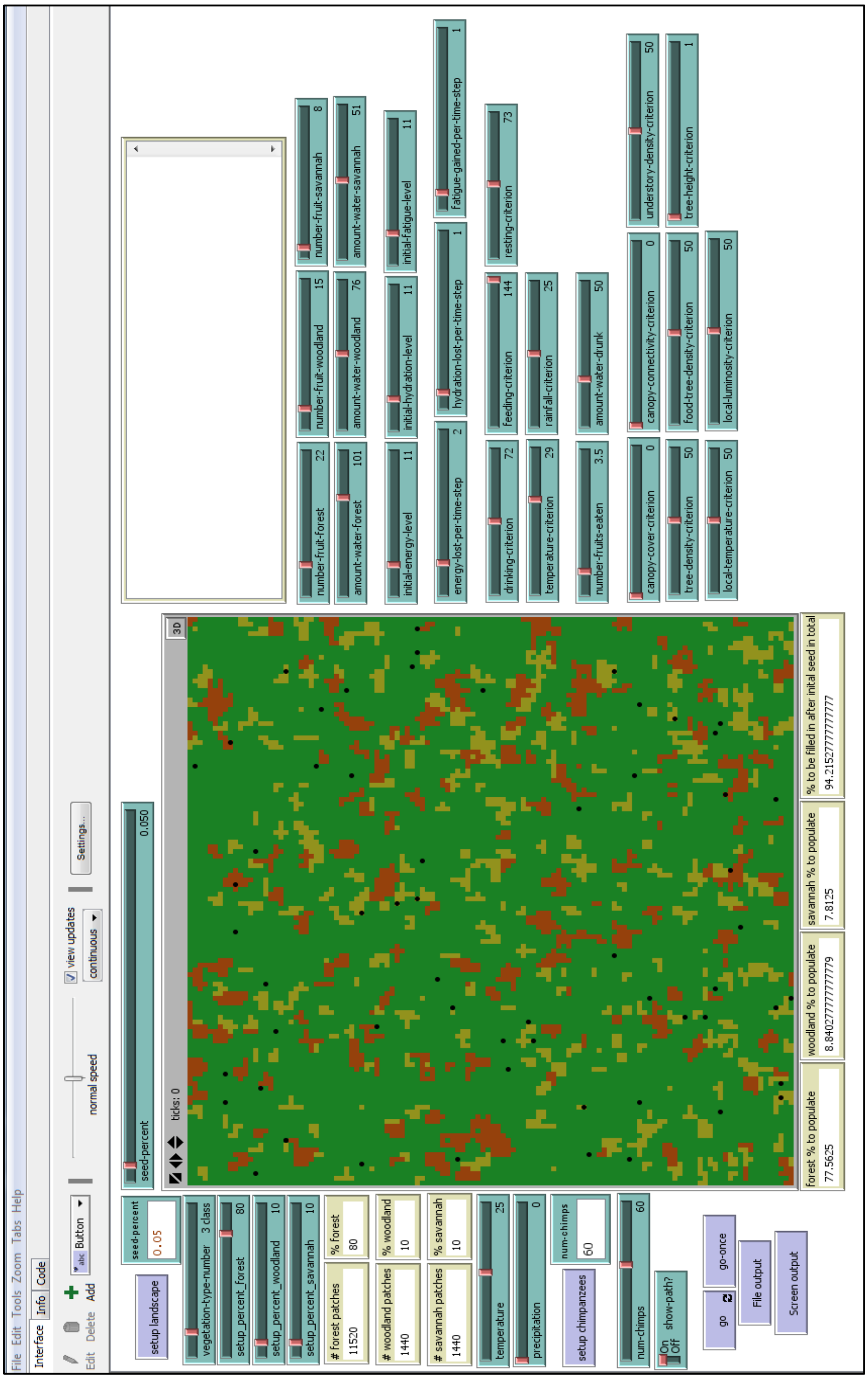
The generic chimpanzee landscape use model presented in Chapter 4 was developed using NetLogo software (version 5.2.1; Willensky 1999). See http://ccl.northwestern.edu/netlogo/ for NetLogo information and downloads. The model code can be accessed online, using the specifications below. Italics within model code indicate code explanations. The rationale behind the model code is outlined in Appendix 4.5.

Webpage: http://kellyvanleeuwen.com/thesis/
Username: klvanleeuwen
Password: please contact the author

APPENDIX 4.4

Model interface of the generic chimpanzee landscape use model of Chapter 4

The model interface, or ‘front screen’, of the generic chimpanzee landscape use model presented in Chapter 4 is outlined below. Figure A4.4.1 shows the model before it is run, whereas Figure A4.4.2 shows the model after it has been run. The rationale behind the parameter values outlined on the interface tab is specified in Appendix 4.5.



seed-percent 0.05

vegetation-type-number 3 class

setup_percent_forest 80

setup_percent_woodland 10

setup_percent_savannah 10

% forest 80

% woodland 10

% savannah 10

forest patches 11520

woodland patches 1440

savannah patches 1440

temperature 25

precipitation 0

num-chimps 60

num-chimps 60

show-path? On Off

seed-percent 0.050

forest % to populate 77.5625

woodland % to populate 8.8402777777779

savannah % to populate 7.8125

% to be filled in after inital seed in total 94.2152777777777

number-fruit-forest 22

number-fruit-woodland 15

number-fruit-savannah 8

amount-water-forest 101

amount-water-woodland 76

amount-water-savannah 51

initial-energy-level 11

initial-hydration-level 11

initial-fatigue-level 11

energy-lost-per-time-step 2

hydration-lost-per-time-step 1

fatigue-gained-per-time-step 1

drinking-criterion 72

feeding-criterion 144

resting-criterion 73

temperature-criterion 29

rainfall-criterion 25

number-fruits-eaten 3.5

amount-water-drunk 50

canopy-cover-criterion 0

canopy-connectivity-criterion 0

understory-density-criterion 50

tree-density-criterion 50

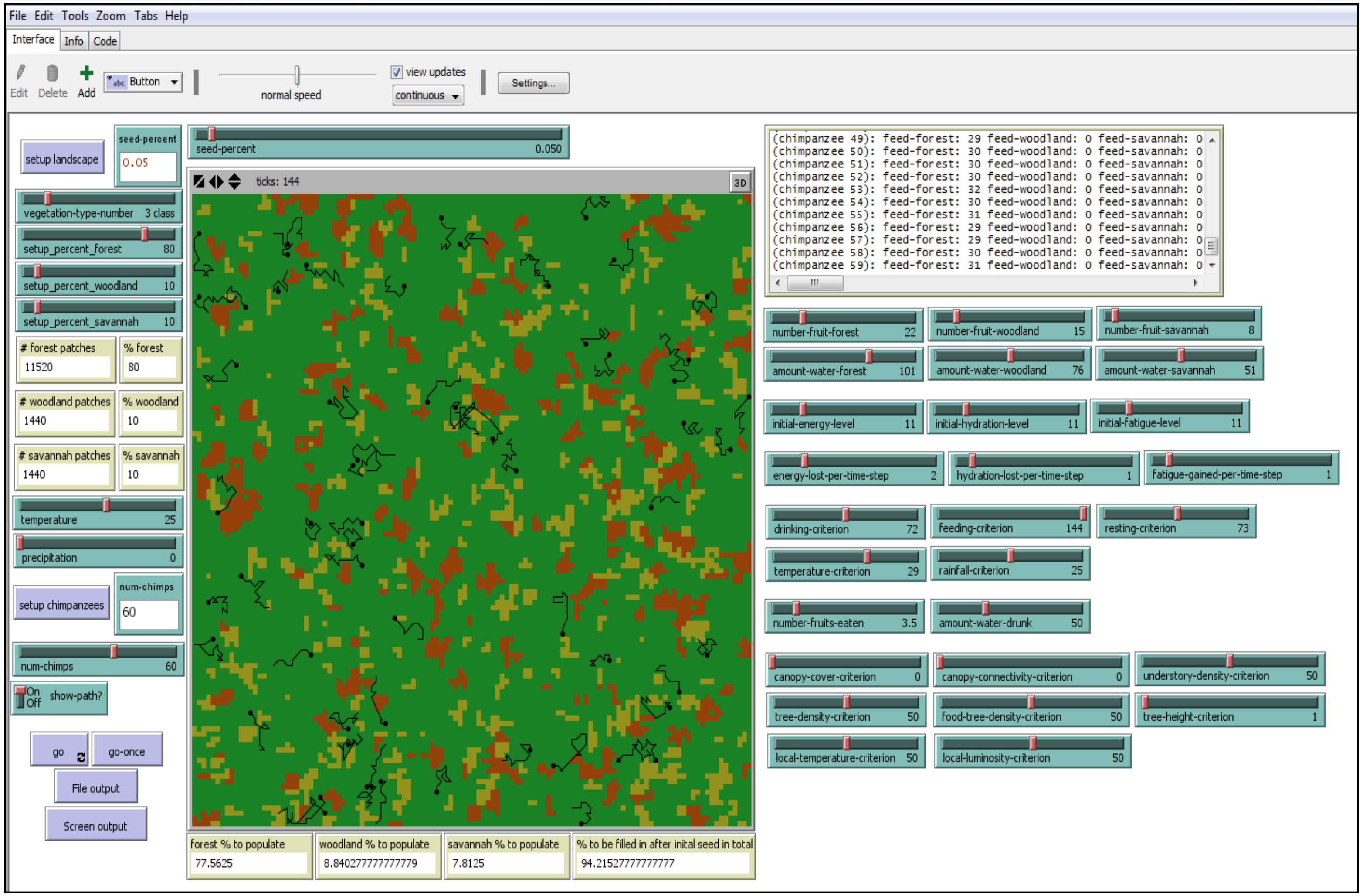
food-tree-density-criterion 50

tree-height-criterion 1

local-temperature-criterion 50

local-luminosity-criterion 50

Figure A4.4.1. Interface tab of the generic chimpanzee model at the onset of a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).



seed-percent 0.05

seed-percent 0.050

vegetation-type-number 3 class

setup_percent_forest 80

setup_percent_woodland 10

setup_percent_savannah 10

forest patches 11520

% forest 80

woodland patches 1440

% woodland 10

savannah patches 1440

% savannah 10

temperature 25

precipitation 0

num-chimps 60

num-chimps 60

show-path? On

forest % to populate 77.5625

woodland % to populate 8.840277777777779

savannah % to populate 7.8125

% to be filled in after inital seed in total 94.21527777777777

```
(chimpanzee 49): feed-forest: 29 feed-woodland: 0 feed-savannah: 0
(chimpanzee 50): feed-forest: 30 feed-woodland: 0 feed-savannah: 0
(chimpanzee 51): feed-forest: 30 feed-woodland: 0 feed-savannah: 0
(chimpanzee 52): feed-forest: 30 feed-woodland: 0 feed-savannah: 0
(chimpanzee 53): feed-forest: 32 feed-woodland: 0 feed-savannah: 0
(chimpanzee 54): feed-forest: 30 feed-woodland: 0 feed-savannah: 0
(chimpanzee 55): feed-forest: 31 feed-woodland: 0 feed-savannah: 0
(chimpanzee 56): feed-forest: 29 feed-woodland: 0 feed-savannah: 0
(chimpanzee 57): feed-forest: 29 feed-woodland: 0 feed-savannah: 0
(chimpanzee 58): feed-forest: 30 feed-woodland: 0 feed-savannah: 0
(chimpanzee 59): feed-forest: 31 feed-woodland: 0 feed-savannah: 0
```

number-fruit-forest 22

number-fruit-woodland 15

number-fruit-savannah 8

amount-water-forest 101

amount-water-woodland 76

amount-water-savannah 51

initial-energy-level 11

initial-hydration-level 11

initial-fatigue-level 11

energy-lost-per-time-step 2

hydration-lost-per-time-step 1

fatigue-gained-per-time-step 1

drinking-criterion 72

feeding-criterion 144

resting-criterion 73

temperature-criterion 29

rainfall-criterion 25

number-fruits-eaten 3.5

amount-water-drunk 50

canopy-cover-criterion 0

canopy-connectivity-criterion 0

understory-density-criterion 50

tree-density-criterion 50

food-tree-density-criterion 50

tree-height-criterion 1

local-temperature-criterion 50

local-luminosity-criterion 50

Figure A4.4.2. Interface tab of the generic chimpanzee landscape use model of Ch4 after a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).

APPENDIX 4.5

Model code rationale for the generic chimpanzee landscape use model of Chapter 4

Table A4.5.1 presents the rationale behind the model rules and input parameters of the generic chimpanzee landscape use model presented in Chapter 4. Model rules are based upon findings from Chapter 2 and Chapter 3, on published literature and/or on general knowledge-based considerations.

Table A4.5.1. Rationale behind the model code and rules of the generic chimpanzee landscape use model of Chapter 4.

Model Rule/ Parameter	**Value**	**Justification**
Global		
Model size	36km^2	Average home-range size of chimpanzee communities across sites based on published literature.
Patch size	50m x 50m	A patch of 50m x 50 m is small enough to contain the necessary detail for each vegetation type, but not too small to affect processing power and difficulty.
Model run (time)	24 hours	As the model simulated daily activity budgets, path lengths, and vegetation type usage, a run of 24 hours was chosen.
Time step (time)	10 minutes	A time step of 10min is small enough to capture the necessary behavioural details, but not too small to affect processing power.
Landscape		
Overall landscape	3	Results of Chapter 3 indicated that chimpanzee landscapes can be grouped into three different environments: dense forests, forest mosaics, and savannahs. This study looks at the behavioural differences for chimpanzees within these three environments.
Vegetation types	3	Results of Chapter 3 indicated that every chimpanzee study site contained the vegetation type forest (F). Furthermore, results showed that woodland (W) and savannah grassland (S) is available at each site classified as a savannah landscape. The presence of all other vegetation types is variable. It was therefore chosen to only use the three vegetation types above in order to be consistent.
Vegetation cover	<u>Dense forest:</u> Forest (F) = 80%, woodland (W) = 10%, savannah grassland (S) = 10%; <u>Forest mosaic:</u> F = 45%, W = 40%, S = 15%; <u>Savannah:</u> F = 10%, W = 55%, S = 35%.	Forest cover is the main driver of landscape-based classifications of chimpanzees and their environments and therefore, the amount of forest cover was specified first, so that it nicely fits within the definitions outlined in Chapter 3 and is evenly spaced between landscapes. The remaining percentage of cover was then filled with woodland and savannah grassland in a way that is roughly similar to the woodland and grassland cover averages within the different environments based on literature descriptions.
Fragmentation	0.05	The fragmentation is set to 0.05, as no data are available on the average percent of fragmentation across study sites. This value was allocated randomly.
Temperature	25°C	The overall temperature is set to 25°C, which nicely falls within the thermos-neutral zone for chimpanzees (20 - 29°C). This value was allocated randomly.
Precipitation	0mm	The amount of rainfall is set to 0mm, indicating that this day is 'dry' and there is no interference of precipitation. This value was allocated randomly.
Vegetation features		Only landscape-scale environmental variables are included in the model: tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, amount

Model Rule/ Parameter	Value	Justification
		food, and amount water (Chapter 2). Other variables are not included because they are too small-scale and/or correlated with the other variables. Slope and altitude are not included in the model as there is no consistency between sites, which would impair the model rules.
• Tree height	F: 10-50m; W: 8-20m; S: 3-15m.	Chapter 3 showed that literature specified tree height as either high, medium or low, with the exact heights specified as high = 10-50m, medium = 8-20m, and low = 3-15m.
• Canopy cover	F: 75-100%; W: 25-75%, S: 0-25%.	Chapter 3 showed that literature specified canopy cover as either high, medium or low, without exact percentages specified. It was therefore scaled for the model to 0 – 100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Canopy connectivity	F: 75-100%; W: 25-75%, S: 0-25%.	Chapter 3 showed that literature specified canopy connectivity as either high, medium or low, without exact percentages specified. It was therefore scaled to 0-100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Understory density	F: 0-25%; W: 25-75%, S: 75-100%.	Chapter 3 showed that literature specified understory density as either high, medium or low, without exact percentages specified. It was therefore scaled to 0-100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Tree density	F: 75-100%; W: 25-75%, S: 0-25%.	Chapter 3 showed that literature specified tree density as either high, medium or low, without exact percentages specified. It was therefore scaled for the model to 0-100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Food tree density	F: 75-100%; W: 25-75%, S: 0-25%.	Chapter 3 showed that literature specified food tree density as either high, medium or low, without exact percentages specified. It was therefore scaled for the model to 0-100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Number fruit	F: 0-21; W: 0-14; S: 0-7.	Based on a knowledge-based assumption, forest has more fruit than woodland, and woodland has more fruit than savannah. With respect to the amount of fruit eaten per time step (see below), it was specified that chimpanzees can eat occasionally in savannah grasslands, sometimes in woodland, and regularly (and for a maximum of 60min) in forest.
• Amount water	F: 0-100; W: 0-75; S: 0-50.	Based on a knowledge-based assumption, forest has more water available than woodland, and woodland has more water than savannah. With respect to the amount of water drunk per time step (see below), it was specified that chimpanzees can rarely drink in savannah, occasionally in woodland, and sometimes in forest
Micro-climate characteristics		Only landscape-scale environmental variables are included in the model: local temperature and local luminosity.
• Temperature (day)	F: 0-25, W: 25-75; S: 75-100.	Chapter 3 showed that literature specified daytime temperature as either hot, medium, or cold, but no exact values have been specified. It was therefore randomly scaled for the model to 0-100, with hot (i.e. high temperatures) being 75-100, medium 25-75, and cool (i.e. low temperatures) 0-25.
• Temperature (night)	F: 75-100; W: 25-75; S: 0-25.	Chapter 3 showed that literature specified nighttime temperature as either hot, medium or cold, but no exact values are specified. It was therefore scaled for the model to 0-100, with hot being 75-100, medium 25-75, and cool 0-25. Values were allocated randomly.
• Luminosity (day)	F: 0-25, W: 25-75; S: 75-100.	Chapter 3 showed that literature specified daytime luminosity as either high, medium, or low, but no exact values are specified. It was therefore scaled for the model to 0-100, with light being 75-100 (i.e. high luminosity), medium 25-75, and dark 0-25 (i.e. low luminosity). Values were allocated randomly.
• Luminosity (night)	F: 0 -25; W: 0-25, S: 0-25.	Chapter 3 showed that nights are generally dark, but no exact values are specified. It was therefore scaled for the model to 0-100, with light 75-100, medium 25-75, and dark 0-25. Values were allocated randomly.

Model Rule/ Parameter	**Value**	**Justification**
Chimpanzees		
Community size	60	Average population size of chimpanzee communities across sites based on literature, placed randomly in the model environment.
Internal states	3	Based on simplifications of general knowledge, it was decided that model behaviours are driven by internal states for energy, hydration, and fatigue.
Behaviour		
Feeding		Based on published literature (Chapter 2), feeding can be regarded as an important daily behaviour for chimpanzees, where energy can be gained.
Drinking		When investigating complete daily activity budgets for chimpanzees, drinking should be included as an important behaviour to obtain water, even though this is not often specified in the literature (Chapter 2).
Nesting		When investigating chimpanzee behaviour over a 24-hour period, nesting should be included, as this is the only nighttime behaviour for chimpanzees (Chapter 2).
Resting		Based on literature, resting can be regarded as an important daily behaviour for chimpanzees, where fatigue can be lost. It can either be enforced due to, e.g., food processing, or 'extra' which can be used for other activities such as social behaviours (Chapter 2).
Travel		Based on literature, travel can be regarded as an important daily behaviour for chimpanzees, getting an individual from A to B. Travel is therefore often considered goal-directed (Chapter 2). Energy will be lost while travelling.
Where		Results of Chapter 2 showed the important landscape-scale vegetation features and micro-climate characteristics for each modelled behaviour based on expert-based opinions.
• Feeding	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Results of Chapter 2 specified amount fruit, food tree density, tree height, tree density, temperature day and luminosity day as important factors in selecting a feeding location. Exact criteria of any of these environmental variables, however, remain absent. Criteria are therefore chosen randomly for the model, based on general knowledge assumptions: Chimpanzees should feed where there is enough fruit, at least enough to last them one time step, i.e. 3.5 fruits (see below). Chimpanzees should furthermore prefer locations with higher tree and food tree densities (high densities 50-100, low densities 0-50), taller trees (higher trees have larger DBHs and should contain more food, but also short trees can have food), and lower temperatures and luminosities (high temperature /light 50-100, low temperature /dark 0-50).
• Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Results of Chapter 2 specified amount water, temperature day and luminosity day as important variables in selecting a drinking location. Exact criteria of any of these environmental variables, however, are not specified. Criteria are therefore chosen randomly for the model, based on knowledge-based assumptions: Chimpanzees should drink where there is enough water, at least enough to last them one time step, i.e. 50 hydrations. Chimpanzees should furthermore prefer locations where it is not too hot or too light (high temperature /light 50-100, low temperature /dark 0-50).
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and	Results of Chapter 2 specified that tree height, canopy cover, canopy connectivity, tree density, amount fruit, understory density, food tree density, amount water, temperature day and luminosity day were important factors in selecting a nesting location. Exact criteria for tree height, canopy cover, and canopy connectivity for nesting were specified in literature, but exact criteria of any of the other environmental variables remain absent. The criteria set out for these variables for the model are therefore based on general knowledge assumptions: Chimpanzees would prefer to nest at locations with high tree and food tree densities and low understory densities (high densities 50-100, low densities 0-50), at locations where there is enough food (i.e. more than 3.5 fruits) and water (i.e. more

Model Rule/ Parameter	Value	Justification
	luminosity (day) ≤ 50.	than 50 hydrations), and at locations where it is not too hot or too light (high temperature /light 50-100, low temperature /dark 0-50).
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Results of Chapter 2 specified temperature day, luminosity day, tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, amount fruit and amount water as important variables in selecting a resting location. Exact criteria of any of these environmental variables, however, remained absent. Criteria are therefore chosen randomly for the model, based on knowledge-based assumptions: Chimpanzees would prefer to rest at cooler and shadier locations (high temperature /light 50-100, low temperature /dark 0-50), and at locations with taller trees (use the same criterion as for nesting and feeding, as similar locations can be expected), higher canopy cover and connectivities (use the same criterion as for nesting as similar locations can be expected), lower understory densities and higher tree and food tree densities (high densities 50-100, low densities 0-50), and with enough fruit (i.e. more than 3.5 fruits) and water (i.e. more than 50 hydrations) available.
• Travel		Within the model, travel is assumed to be a goal-directed behaviour, based on findings from literature (Chapter 2). No criteria are set as to where a chimpanzee can or cannot travel, as this would restrict individual decisions and enforce the model rules. Preferred vegetation features and micro-climate characteristics will follow from the model results. In this way, only the ‘goal activities’ will have strict ‘*where*-criteria’. Within the travel procedure, individuals will first check the vegetation features and micro-climate characteristics of their current patch and select this patch for their goal activity if the patch abides to all criteria. If not, individuals will subsequently look at its neighbouring patches within 50m for a suitable patch, will then look at its surrounding patches within 100m for a suitable patch, or will ‘jump’ a random 3 – 6 patches (150 – 300m) to start a search there. Chimpanzees are expected to ‘see’ a maximum of 100m in all directions and are expected to travel a maximum of 300m within 10min (based on literature on maximum average travel speed of 2.02km/hr: Bates and Byrne 2009).
• Relative importance		No relative importance is included within the model. Vegetation features or micro-climate characteristics are either important for a specific behaviour, or they are not. An individual investigates the most important variables first, but all important variables are still included.
When		Base on general knowledge assumptions (Chapter 2), overall for the model, it is specified that chimpanzees must first assess whether it is dark/night. In this case, the only option for chimpanzees is to nest. During daytime, an individual must first decide whether the current weather conditions impair its daily activities, or whether it is too tired. If so, an individual must rest. If not, it is expected that drinking is most important due to the importance of water, followed by feeding for gaining energy. This is, however, relative, as an individual can be more hungry than thirsty, in which case it will feed. If no need for feeding or drinking, an individual can spend ‘extra’ time resting.
• Feeding	Energy ≤ 144, and energy < hydration.	An individual should feed when it is hungry (and more hungry than thirsty). The feeding criterion is based on random variables and the assumption that individuals would like to maintain a neutral energy balance: in total 288 energy will be lost during a model run (see below), 144 of which will be lost during nighttime nesting. As long as an individual keeps its energy above 144 during daytime, it will be prepared for nesting.
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	An individual should drink when it is thirsty (and more thirsty than hungry). The drinking criterion is based on random variables and on the assumption that individuals would like to maintain a neutral hydration (i.e. water) balance: in total 144

Model Rule/ Parameter	Value	Justification
		hydration will be lost during a model run (see below), 72 of which will be lost during nighttime nesting. As long as an individual keeps its hydration above 72 during daytime, it will be prepared for nesting.
- Nesting	Time steps > 72.	An individual should nest when it is dark (i.e. after 12 hours, and thus after 72 time steps of 10 minutes). Nesting is the only option at nighttime.
- Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Chimpanzees should rest when it is too wet (put at > 25mm, as this is generally considered as a wet day), when it is too hot (put at > 29°C, as temperatures above this value are outside the thermoneutral range for chimpanzees), when they are too tired (it could be assumed that individuals would like to maintain a neutral fatigue balance: in total 144 fatigues will be gained during a model run (see below), of which only 72 will be lost during nighttime nesting. As long as an individual keeps its fatigue below 72 during daytime, it will be prepared for nesting), or when there is nothing else to do (i.e. extra resting time).
- Travel		Travel is incorporated within the behavioural procedures of feeding, drinking, nesting and resting, and is goal directed. Chimpanzees will choose to travel if their current patch is not suitable for their selected activity.
How much		
- Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	As there is no literature data (Chapter 2) on how much energy, hydration, and fatigue chimpanzees start off with in the morning, these values are randomly set between 0 and 10, in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step.
- Existing	Energy: -2; hydration: -1; fatigue: +1.	Based on general knowledge (Chapter 2), individuals lose energy and hydration, and gain fatigue simply by existing. The values are randomly set at 1 or 2 in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step and no data exist to inform this study otherwise.
- Feeding	Energy: +10.85 kCal (3.1kCal per fruit)	Based on literature data (Chapter 2), 1 gram of dry weight of fruits contains 3.1kCal of energy (including fig fruit and non-fig fruit). Hourly energy intake rates are not specified for chimpanzees. In reality, individuals would lose a lot of energy every 10 minutes due to mechanisms such as food processing. However, in order to keep the model simple and losses and gains in the same order of magnitude, it is assumed, after model calibration, that chimpanzees would be able to gain at least 10.85 kCal of energy net at each time step, i.e. eating 3.5 fruits. On average, it is assumed that a fruit contains between 70 – 95% water, the remainder is called dry weight.
- Drinking	Hydration + 50	As the amount of hydration while drinking is not specified in current literature (Chapter 2), it is assumed that an individual can gain a lot of hydration during each drinking bout. This is based on the observation that chimpanzees do not spent a lot of time drinking each day.
- Nesting	Fatigue: -2	No data are presented on the amount of fatigue lost while nesting (Chapter 2). It is therefore assumed that individuals lose 1 fatigue each time step spent nesting.
- Resting	Fatigue: -2	No data are presented on the amount of fatigue lost while resting (Chapter 2). It is therefore assumed that individuals lose 1 fatigue each time step spent resting.
- Travel	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	Based on an average daily path length of 3.0km and an average energy expenditure for travel of 207.3kCal/day for chimpanzees, energy lost per 50m travelled equals about 3.5kCal (Chapter 2). As chimpanzees can travel between 50 – 300m, energy loss due to travel is somewhere between -3.5kCal and -21kCal. For every extra 50m travelled (so when travelling between 100 – 300m) an additional hydration will be lost, and an extra fatigue will be gained, as an individual is travelling faster.
Output		
Feeding	+1 for each time	Based on 144 time steps in the model, each time step spent on

Model Rule/ Parameter	Value	Justification
	step spent feeding.	feeding will add +1 to the feeding column in the output table. This way, the amount of time spent feeding over a 24-hour period can easily be assessed.
Drinking	+1 for each time step spent drinking.	Based on 144 time steps in the model, each time step spent on drinking will add +1 to the drinking column in the output table. This way, the amount of time spent drinking over a 24-hour period can easily be assessed.
Nesting	+1 for each time step spent resting.	Based on 144 time steps in the model, each time step spent on nesting will add +1 to the nesting column in the output table. This way, the amount of time spent nesting over a 24-hour period can easily be assessed.
Resting	+1 for each time step spent nesting.	Based on 144 time steps in the model, each time step spent on resting will add +1 to the resting column in the output table. This way, the amount of time spent resting over a 24-hour period can easily be assessed.
Travel	+1 for each time step spent travelling.	Based on 144 time steps in the model, each time step spent on travel will add +1 to the travel column in the output table. This way, the amount of time spent travelling over a 24-hour period can easily be assessed.
Forest	+1 for each time step spent in forest.	Based on 144 time steps in the model, each time step spent in forest will add +1 to the forest column in the output table. This way, the amount of time spent within forest vegetation over a 24-hour period can easily be assessed.
Woodland	+1 for each time step spent in woodland.	Based on 144 time steps in the model, each time step spent in woodland will add +1 to the woodland column in the output table. This way, the amount of time spent within woodland vegetation over a 24-hour period can easily be assessed.
Savannah	+1 for each time step spent in savannah.	Based on 144 time steps in the model, each time step spent in savannah will add +1 to the savannah column in the output table. This way, the amount of time spent within savannah grassland vegetation over a 24-hour period can easily be assessed.
Feed-forest	+1 for each time step spent on feeding in forest.	Based on 144 time steps in the model, each time step spent on feeding in forest will add +1 to the feed-forest column in the output table. This way, the amount of time spent on feeding within forest vegetation over a 24-hour period can easily be assessed.
Feed-woodland	+1 for each time step spent on feeding in woodland.	Based on 144 time steps in the model, each time step spent on feeding in woodland will add +1 to the feed-woodland column in the output table. This way, the amount of time spent on feeding within woodland vegetation over a 24-hour period can easily be assessed.
Feed-savannah	+1 for each time step spent on feeding in savannah.	Based on 144 time steps in the model, each time step spent on feeding in savannah will add +1 to the feed-savannah column in the output table. This way, the amount of time spent on feeding within savannah grassland vegetation over a 24-hour period can easily be assessed.
Drink-forest	+1 for each time step spent on drinking in forest.	Based on 144 time steps in the model, each time step spent on drinking in forest will add +1 to the drink-forest column in the output table. This way, the amount of time spent on drinking within forest vegetation over a 24-hour period can easily be assessed.
Drink-woodland	+1 for each time step spent on drinking in woodland.	Based on 144 time steps in the model, each time step spent on drinking in woodland will add +1 to the drink-woodland column in the output table. This way, the amount of time spent on drinking within woodland vegetation over a 24-hour period can easily be assessed.
Drink-savannah	+1 for each time step spent on drinking in savannah.	Based on 144 time steps in the model, each time step spent on drinking in savannah will add +1 to the drink-savannah column in the output table. This way, the amount of time spent on drinking within savannah grassland vegetation over a 24-hour period can easily be assessed.
Nest-forest	+1 for each time step spent on nesting in forest.	Based on 144 time steps in the model, each time step spent on nesting in forest will add +1 to the nest-forest column in the output table. This way, the amount of time spent on nesting within forest vegetation over a 24-hour period can easily be assessed.
Nest-woodland	+1 for each time	Based on 144 time steps in the model, each time step spent on

Model Rule/ Parameter	Value	Justification
	step spent on nesting in woodland.	nesting in woodland will add +1 to the nest -woodland column in the output table. This way, the amount of time spent on nesting within woodland vegetation over a 24-hour period can easily be assessed.
Nest-savannah	+1 for each time step spent on nesting in savannah.	Based on 144 time steps in the model, each time step spent on nesting in savannah will add +1 to the nest-savannah column in the output table. This way, the amount of time spent on nesting within savannah grassland vegetation over a 24-hour period can easily be assessed.
Rest-forest	+1 for each time step spent on resting in forest.	Based on 144 time steps in the model, each time step spent on resting in forest will add +1 to the rest-forest column in the output table. This way, the amount of time spent on resting within forest vegetation over a 24-hour period can easily be assessed.
Rest-woodland	+1 for each time step spent on resting in woodland.	Based on 144 time steps in the model, each time step spent on resting in woodland will add +1 to the rest -woodland column in the output table. This way, the amount of time spent on resting within woodland vegetation over a 24-hour period can easily be assessed.
Rest-savannah	+1 for each time step spent on resting in savannah.	Based on 144 time steps in the model, each time step spent on resting in savannah will add +1 to the rest-savannah column in the output table. This way, the amount of time spent on resting within savannah grassland vegetation over a 24-hour period can easily be assessed.
Travel-forest	+1 for each time step spent on travelling in forest.	Based on 144 time steps in the model, each time step spent on travelling in forest will add +1 to the travel-forest column in the output table. This way, the amount of time spent on travelling within forest vegetation over a 24-hour period can easily be assessed.
Travel-woodland	+1 for each time step spent on travelling in woodland.	Based on 144 time steps in the model, each time step spent on travelling in woodland will add +1 to the travel -woodland column in the output table. This way, the amount of time spent on travelling within woodland vegetation over a 24-hour period can easily be assessed.
Travel-savannah	+1 for each time step spent on travelling in savannah.	Based on 144 time steps in the model, each time step spent on travelling in savannah will add +1 to the travel -savannah column in the output table. This way, the amount of time spent on travelling within savannah grassland vegetation over a 24-hour period can easily be assessed.
Daily path length	+50m for each patch travelled.	For each 50m travelled, 50m is added to the daily path length column in the output table.
Energy	Various	Each time energy is gained and/or lost, this is updated in the energy column of the output table.
Hydration	Various	Each time hydration is gained and/or lost, this is updated in the hydration column of the output table.
Fatigue	Various	Each time fatigue is gained and/or lost, this is updated in the fatigue column of the output table.
Food intake	+ 3.5 for each feeding bout.	After each feeding bout, the amount of fruits eaten is updated in the food intake column in the output table.
Water intake	+ 50 for each drinking bout.	After each drinking bout, the amount of water drunk is updated in the water intake column in the output table.
Chimp land use	-	Output table (.csv) for further analyses.
Chimp activity	-	Output table (.csv) for further analyses.
Chimp site selection	-	Output table (.csv) for further analyses.

APPENDIX 5.1

Vegetation plot measurements at Issa Valley, Tanzania

Twenty-four vegetation plots (25m x 25m) were set up throughout the Issa study area to measure the structural vegetation characteristics of forest, woodland, swamp and savannah grassland vegetation types. Plot locations were selected according to a stratified random sampling design. Six plots were measured for each vegetation type. Overall plot measurements were taken to assess the characteristics of each plot, e.g. number of trees, altitude, slope, canopy cover, and understory density. Details on overall plot measurements are outlined in Table A5.1.1. Plot tree measurements were taken to assess the characteristics of each tree and vine with a diameter at breast height (DBH) of ≥ 10cm within a plot, e.g. tree species, tree height, lowest branch height (LBH) and crown width. Details on plot tree measurements are outlined in Table A5.1.2.

Table A5.1.1. Overall plot tree measurements for the vegetation plots set out across the Issa study area.

Variable	**Definition**	**Method**
Date	Date of plot measurement.	Watch
Plot #	The number of the plot that is being measured.	Self (count)
Vegetation type	The vegetation type of the plot, classified as forest (F), woodland (W), grassland (G), or swamp (S)	Self (prior classification based on the stratified random sampling design).
Plot name	Name of the plot, with respect to its vegetation type and number	Self (prior identification based on the stratified random sampling design).
Time start	Starting time of measuring the plot.	Watch
Time end	End time of measuring the plot.	Watch
Latitude	Geographical latitude of the plot centre.	GPS (prior identification based on the stratified random sampling design)
Longitude	Geographical longitude of the plot centre.	GPS (prior identification based on the stratified random sampling design)
GPS SW	GPS location of the bottom left corner of the plot. (specific name as plot name + SW)	GPS (specify as name of the plot plus SW)
GPS SE	GPS location of the bottom right corner of the plot (SE).	GPS (specify as name of the plot plus SE)
GPS NW	GPS location of the upper left corner of the plot (NW).	GPS (specify as name of the plot plus NW)
GPS NE	GPS location of the upper right corner of the plot (NE).	GPS (specify as name of the plot plus NE)
Observers	Names of the people measuring the plot.	Self (note)
Altitude	Elevation of the plot.	Altimeter
Topography	Steepness of the slope in the plot, categorized as: 1 = flat; 2 = mild; 3 = medium, 4 = steep.	Self (estimate)
Weather conditions	Climatic conditions (e.g. cloud cover, rain, sun) when the plot was measured.	Self (estimate)
# of trees	Total number of trees (DBH ≥ 10cm) within a plot.	Self (post calculations after plot was measured)
# of feeding trees	Total number of feeding trees (DBH ≥ 10cm) within a plot.	Self (post calculations after plot was measured)

Variable	**Definition**	**Method**
% of feeding trees	Proportion of trees in the plot that are identified as chimpanzee food trees, i.e. dividing the number of feeding trees by the total number of trees within the plot, and multiplying this by 100.	Self (post calculations after plot was measured)
% feeding trees in fruit	Percentage of chimpanzee food trees actually bearing fruit within the plot, i.e. dividing the number of chimpanzee food trees with fruit by the total number of feeding trees, and multiplying this by 100.	Self (post calculations after plot was measured)
# of vines	Total number of vines (DBH ≥ 10cm) within a plot.	Self (post calculations after plot was measured)
# of small trees	Total number of small trees (diameter < 10cm) within a plot.	Self (count after all trees ≥ 10 cm were measured)
Canopy cover (%)	Proportion of the plot covered by the tree canopies, categorized as: 0 = 0% of the plot covered; 1 = 1-25% of the plot covered; 2 = 26-50% of the plot covered; 3 = 51-75% of the plot covered; 4 = 76-100% of the plot covered.	Self (estimate)
Canopy cover (%)	Proportion of the plot covered by tree canopies, as measured by photographs at each corner and in the middle of the plot, and analysing these pictures with CanopyDigi.	Photographs at the centre of the plot and at each corner. *Post* analyses using CanopyDigi.
Canopy connectivity (%)	Percentage of overlap between trees within the plot, categorized as: 0 = 0% of canopy connected; 1 = 1-25% of canopy connected; 2 = 26-50% of canopy connected; 3 = 51-75% of canopy connected; 4 = 76-100% of canopy connected.	Self (estimate)
Understory (%)	Proportion of understory and bushes covering the ground within a plot, categorized as: 0 = 0% of understory cover; 1 = 1-25% of understory cover; 2 = 26-50% of understory cover; 3 = 51-75% of understory; 4 = 76-100% of understory cover.	Self (estimate)
Grass (%)	Proportion of ground covered with grass within a plot, categorized as: 0 = 0% of grass cover; 1 = 1-25% of grass cover; 2 = 26-50% of grass cover; 3 = 51-75% of grass cover; 4 = 76-100% of grass cover.	Self (estimate)
Bare (%)	Proportion of bare land present within a plot, categorized as: 0 = 0% of bare land cover; 1 = 1-25% of bare land cover; 2 = 26-50% of bare land cover; 3 = 51-75% of bare land cover; 4 = 76-100% of bare land cover.	Self (estimate)
THV (%)	Proportion of edible herbs (terrestrial herbaceous vegetation, THV) within a plot, categorized as: 0 = 0% of THV present; 1 = 1-25% of THV present; 2 = 26-50% of THV present; 3 = 51-75% of THV present; 4 = 76-100% of THV present.	Self (estimate)
Food present	Overall presence of food within a plot. If food present, specify item (i.e. fruit, flower, leaf) and amount, categorized as: 0 = food absent; 1 = 1 - 25% of overall canopy covered with food; 2 = 26 - 50% of overall canopy covered with food; 3 = 51 - 75% of overall canopy covered with food; 4 = 76 - 100% of overall canopy covered with food.	Self (estimate)
Water present	Presence of water within a plot. If water present, specify type (i.e. river, pool, puddle), and amount (i.e. number and % of ground covered).	Self (estimate)
Tree density	Number of trees (DBH ≥ 10cm) per plot and per hectare. Hectare tree density calculated by multiplying the total number of trees within a plot by 16 (i.e. 16 * 25x25m = 1 hectare).	Self (post calculations after the plot was measured)
Food tree density	Number of chimpanzee feeding trees (DBH ≥ 10cm) per plot and per hectare. Hectare food tree density calculated by multiplying the total number of feeding trees within a plot by 16 (i.e. 16 * 25x25m = 1 hectare).	Self (post calculations after the plot was measured)
Chimpanzee evidence	Record of evidence of chimpanzee activity observed within a plot. If yes, specify type of evidence (i.e. feeding remains, footprint, nest, faecal sample) and associated behaviour (i.e. feeding, drinking, nesting,	Self (estimate)

Variable	Definition	Method
	resting, travel).	
Termite mound	Indicating whether there are termite mounds present within the plot, and if so, amount and % of ground covered.	Self (estimate)
Ant nest	Indicating whether there are ant nests present within the plot, and if so, amount and % of ground covered.	Self (estimate)
Comments	Notes regarding the overall plot.	Self

Table A5.1.2. Plot tree measurements for trees and vines (≥ 10cm DBH) within the vegetation plots set out across the Issa study area.

Variable	Definition	Method
Plot #	The number of the plot that is being measured.	Self (count)
Vegetation type	The vegetation type of the plot, classified as forest (F), woodland (W), grassland (G), or swamp (S).	Self (prior classification based on the stratified random sampling design).
Plot name	Name of the plot, with respect to its vegetation type and number.	Self (prior identification based on the stratified random sampling design).
Tree #	Number of the tree that is being measured.	Self (count)
Vine #	Number of the vine that is being measured.	Self (count)
Tree/ Vine species	Species of the tree/ vine measured.	Field assistant
Feeding tree or vine	Identify whether it is a chimp feeding tree/ vine.	Field assistant
Feeding tree category	If a chimpanzee feeding tree/ vine identify which part of the tree/vine would be eaten by the chimpanzees (i.e. fruit, bark, flower, leaf, etc.)	Field assistant
Food present	Identify whether chimpanzee food is present within the tree. If so, specify type of food and amount, categorized as: 0 = food absent; 1 = 1 - 25% of food present; 2 = 26 - 50% of food present; 3 = 51 - 75% of food present; 4 = 76 - 100% of food present.	Self (count) and field assistant
DBH (cm)	Diameter (cm) of the tree trunk at breast height.	DBH tape
LBH (m)	Height of the lowest branch (m) measured from the base of the trunk to the underside of the first major branch.	Range finder
Tree height (m)	Height of the tree (m) measured from base of the trunk to tallest point of the crown	Range finder
Crown width (m)	Distance (m) between the north and south ordinal points of the crown, and the west and east ordinal points of the crown.	Tape measure and compass
Crown height (m)	Height of the crown (m) measured from the lowest branch to the tallest point of the crown.	Self (post calculations after the tree was measured)
Crown shape	Shape of the crown, categorized as: spheroid, elongated spheroid, cone, upside down cone, umbrella, or bent over (Figure 5.2, Chapter 5).	Self (estimate)
Crown cover (%)	Proportion of the tree canopy in leaf, categorized as: 0 = 0% of the canopy in leaf; 1 = 1-25% of the canopy in leaf; 2 = 26-50% of the canopy in leaf; 3 = 51-75% of the canopy in leaf; 4 = 76-100% of the canopy in leaf.	Self (estimate)
Crown connectivity (%)	Percentage of overlap between the measured tree and its neighbouring trees, categorized as: 0 = 0% of canopy connected; 1 = 1-25% of canopy connected; 2 = 26-50% of canopy connected; 3 = 51-75% of canopy connected; 4 = 76-100% of canopy connected.	Self (estimate)
Data-logger tree	Identify whether the tree measured is the tree with the data loggers for micro-climate measurements	Self
Comments	Notes regarding the tree or vine.	Self

APPENDIX 5.2

Model parameters of the Issa chimpanzee landscape use model of Chapter 5

The input parameters for the Issa chimpanzee landscape use model presented in Chapter 5 are outlined in Table A5.2.1 below. Within the table, information is included on the source of specific parameters values (i.e. empirical Issa data or knowledge-based considerations), and whether parameters were included within the local sensitivity analysis. Rationales behind the specific values of input parameters are presented in Appendix 5.6.

Table A5.2.1. Input parameters for the Issa chimpanzee landscape use model presented in Chapter 5. Within the table, the column 'Data source' indicates whether the parameter value is based upon empirical data or general knowledge considerations; 'Output' indicates that this parameter value was created to produce model output; The 'Sensitivity analysis' column outlines whether a parameter was used for these processes. When a parameter value is specified as, for example, 1 – 75, this indicates that a random value was chosen between 1 and 75 at the onset of each model run for each individual or patch as appropriate.

Parameter	**Value**	**Data source**	**Sensitivity analysis**
home range size	110km^2	Empirical data	No
patch size	50x50m	General knowledge	No
% forest cover	2.8%	Empirical data	No
% woodland cover	87.6%	Empirical data	No
% savannah cover	0.1%	Empirical data	No
% swamp cover	5.4%	Empirical data	No
% rocky outcrop cover	4.1%	Empirical data	No
fragmentation	Map	Empirical data	No
temperature day	23.3°C	Empirical data	No
temperature night	18.4°C	Empirical data	No
rainfall day	0mm	Empirical data	No
rainfall night	0mm	Empirical data	No
tree height forest	1.5 - 29.5m	Empirical data	No
tree height woodland	2.6 - 18.5m	Empirical data	No
tree height savannah	1.7 - 24.6m	Empirical data	No
tree height swamp	2.3 - 11.6m	Empirical data	No
tree height rocky outcrop	0m	Empirical data	No
canopy cover forest	51 – 100%	Empirical data	No
canopy cover woodland	1 – 75%	Empirical data	No
canopy cover savannah	1 – 50%	Empirical data	No
canopy cover swamp	0 – 50%	Empirical data	No
canopy cover rocky outcrop	0%	Empirical data	No
canopy connectivity forest	26 – 100%	Empirical data	No
canopy connectivity woodland	1 – 75%	Empirical data	No

Parameter	Value	Data source	Sensitivity analysis
canopy connectivity savannah	0 – 25%	Empirical data	No
canopy connectivity swamp	0 – 50%	Empirical data	No
canopy connectivity rocky outcrop	0%	Empirical data	No
understory density forest	0 – 100%	Empirical data	No
understory density woodland	1 – 75%	Empirical data	No
understory density savannah	1 – 100%	Empirical data	No
understory density swamp	0 – 100%	Empirical data	No
understory density rocky outcrop	0%	Empirical data	No
tree density forest	72 – 172 trees	Empirical data	No
tree density woodland	48 – 76 trees	Empirical data	No
tree density savannah	1 – 84 trees	Empirical data	No
tree density swamp	0 – 100 trees	Empirical data	No
tree density rocky outcrop	0 trees	Empirical data	No
food tree density forest	36% of trees	Empirical data	No
food tree density woodland	47% of trees	Empirical data	No
food tree density savannah	6% of trees	Empirical data	No
food tree density swamp	62% of trees	Empirical data	No
food tree density rocky outcrop	0% of trees	Empirical data	No
number of fruit forest	4.0% of feeding trees, 7 fruits per feeding tree	Empirical data, and general knowledge	No
number of fruit woodland	27.9% of feeding trees, 7 fruits per feeding tree	Empirical data, and general knowledge	No
number of fruit savannah	8.3% of feeding trees, 7 fruits per feeding tree	Empirical data, and general knowledge	No
number of fruit swamp	4.2% of feeding trees, 7 fruits per feeding tree	Empirical data, and general knowledge	No
number of fruit rocky outcrop	0% of feeding trees, 7 fruits per feeding tree	Empirical data, and general knowledge	No
amount of water forest	0 – 100 hydrations	General knowledge	Yes
amount of water woodland	0 – 75 hydrations	General knowledge	Yes
amount of water savannah	0 – 50 hydrations	General knowledge	Yes
amount of water swamp	0 – 75 hydrations	General knowledge	Yes
amount of water rocky outcrop	0 hydrations	General knowledge	Yes
temperature-day forest	22.3 - 24.4°C	Empirical data	No
temperature-day woodland	23.9 - 29.0°C	Empirical data	No
temperature-day savannah	28.5 - 31.7°C	Empirical data	No
temperature-day swamp	23.8 - 28.9°C	Empirical data	No
temperature-day rocky outcrop	28.5 - 31.7°C	Empirical data	No
temperature-night forest	16.8 - 20.1°C	Empirical data	No
temperature-night woodland	16.7 - 20.4°C	Empirical data	No
temperature-night savannah	20.7 - 21.8°C	Empirical data	No
temperature-night swamp	14.8 - 16.2°C	Empirical data	No
temperature-night rocky outcrop	20.7 - 21.8°C	Empirical data	No
luminosity-day forest	1012 – 8113 Lux	Empirical data	No
luminosity-day woodland	6854 – 39578 Lux	Empirical data	No
luminosity-day savannah	10093 – 44272 Lux	Empirical data	No
luminosity-day swamp	13059 – 29194 Lux	Empirical data	No
luminosity-day rocky outcrop	10093 – 44272 Lux	Empirical data	No

Parameter	**Value**	**Data source**	**Sensitivity analysis**
luminosity-night forest	0 – 9 Lux	Empirical data	No
luminosity-night woodland	3 – 18 Lux	Empirical data	No
luminosity-night savannah	10 – 50 Lux	Empirical data	No
luminosity-night swamp	11 – 76 Lux	Empirical data	No
luminosity-night rocky outcrop	10 – 50 Lux	Empirical data	No
number of chimps	67	Empirical data	No
where - canopy cover criterion	≥ 5%	Empirical data	No
where - canopy connectivity criterion	≥ 0%	Empirical data	No
where - understory density criterion	≥ 0%	Empirical data	No
where - tree density min criterion	72 trees	Empirical data	No
where - tree density max criterion	172 trees	Empirical data	No
where - food tree min density criterion	4 trees	Empirical data	No
where - food tree max density criterion	84 trees	Empirical data	No
where - tree height min criterion	1.5m	Empirical data	No
where - tree height max criterion	29.5m	Empirical data	No
where - tree height nest/rest criterion	2m	Empirical data	No
where - local temperature day min criterion	22.3°C	Empirical data	No
where - local temperature day max criterion	24.4°C	Empirical data	No
where - local temperature night min criterion	16.8°C	Empirical data	No
where - local temperature night max criterion	20.1°C	Empirical data	No
where - local luminosity day min criterion	1,012 Lux	Empirical data	No
where - local luminosity day max criterion	8,113 Lux	Empirical data	No
where - local luminosity night min criterion	0 Lux	Empirical data	No
where - local luminosity night max criterion	9 Lux	Empirical data	No
where - number of fruits	3.5 fruits	General knowledge	Yes
where - amount water	50 hydrations	General knowledge	Yes
where – feeding (important variables)	number fruits, food tree density, tree height, tree density, temperature day, luminosity day	Empirical data	No
where – drinking (important variables)	amount water, temperature day, luminosity day	Empirical data	No
where – nesting (important variables)	tree height, canopy cover, canopy connectivity, understory density, tree density, number fruit, food tree density, amount water, temperature night, luminosity night	Empirical data	No
where – resting (important variables)	tree height, canopy cover, canopy connectivity, understory density, tree density, number fruit, food tree density, amount water, temperature night, luminosity night	Empirical data	No
where – travel (important variables)	none	Empirical data	No
when - feeding criterion	energy ≤ 144, energy < hydration	General knowledge	Yes
when - drinking criterion	hydration ≤ 72, hydration < energy	General knowledge	Yes
when - resting criterion	fatigue ≥ 73 fatigues	General knowledge	Yes
when - nesting criterion	time > 72 steps	Empirical data	No

Parameter	**Value**	**Data source**	**Sensitivity analysis**
when - temperature criterion	temperature > 29°C	Empirical data	No
when - rainfall criterion	rainfall > 25mm	Empirical data	No
Initial - energy	0 – 10kCal	General knowledge	Yes
Initial - hydration	0 – 10 hydrations	General knowledge	Yes
Initial - fatigue	0 – 10 fatigues	General knowledge	Yes
Step - energy	-2kCal	General knowledge	Yes
Step - hydration	-1 hydration	General knowledge	Yes
Step - fatigue	+1 fatigue	General knowledge	Yes
Feeding - energy	+10.85kCal per 3.5 fruits, 3.1kCal per fruit	Empirical data	No
Feeding - energy per fruit	3.1kCal	Empirical data	No
Feeding - number fruits eaten	3.5 fruits	General knowledge	Yes
Drinking - hydration	50 hydrations	General knowledge	No
Drinking - amount water drunk	50 hydrations	General knowledge	Yes
Resting - fatigue	-2 fatigues	General knowledge	Yes
Nesting - fatigue	-2 fatigues	General knowledge	Yes
Travel - energy	3.5kCal per 50m	Empirical data	No
Travel - hydration	-1 for every extra 50m	General knowledge	Yes
Travel - fatigue	+1 for every extra 50m	General knowledge	Yes
Travel - daily path length	50m per patch travelled	Empirical data	No
Travel - number of patches	in order: 0, 1, 2, 3 - 6 (jump)	General knowledge	No
Feed-forest/ feed-woodland/ feed-savannah/ feed-swamp/ feed-rockyoutcrop	+1 for every step in this activity/veg type	Output	No
Drink-forest/ drink-woodland/ drink-savannah/ drink-swamp/ drink-rockyoutcrop	+1 for every step in this activity/veg type	Output	No
Rest-forest/ rest-woodland/ rest-savannah/ rest-swamp/ rest-rockyoutcrop	+1 for every step in this activity/veg type	Output	No
Nest-forest/ nest-woodland/ nest-savannah/ nest-swamp/ nest-rockyoutcrop	+1 for every step in this activity/veg type	Output	No
Travel-forest/ travel-woodland/ travel-savannah/ travel-swamp/ travel-rockyoutcrop	+1 for every step in this activity/veg type	Output	No
Daily-path-length	+50m for every patch travelled	Output	No
Energy	variable depending on behaviour	Output	No
Hydration	variable depending on behaviour	Output	No
Fatigue	variable depending on behaviour	Output	No
Food intake	+3.5 for each time step eating	Output	No
Water intake	+50 for each time step drinking	Output	No
Current activity	variable depending on behaviour	Output	No
Tick	1 per time step	Output	No

APPENDIX 5.3

Model code of the Issa chimpanzee landscape use model presented in Chapter 5

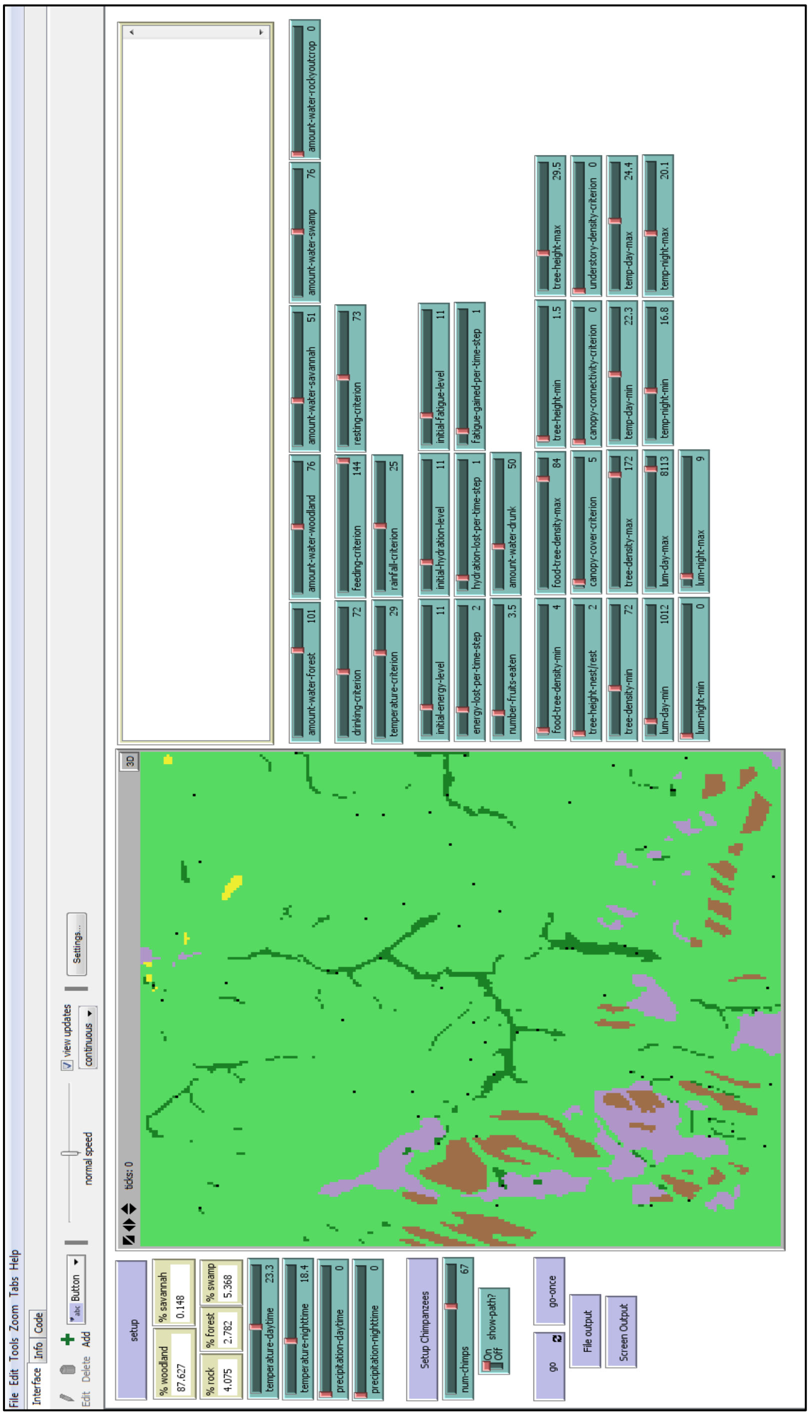
The Issa chimpanzee landscape use model presented in Chapter 5 was developed using NetLogo software (version 5.2.1; Willensky 1999). The model code for the Issa chimpanzee landscape use model can be accessed online, using the specifics outlined below. The Issa model was adapted from the generic chimpanzee landscape use model presented in Chapter 4, and Appendix 5.5 highlights the differences between the models. Rationale behind the Issa model code is outlined in Appendix 5.6.

Webpage: http://kellyvanleeuwen.com/thesis/
Username: klvanleeuwen
Password: please contact the author

APPENDIX 5.4

Model interface of the Issa chimpanzee landscape use model of Chapter 5

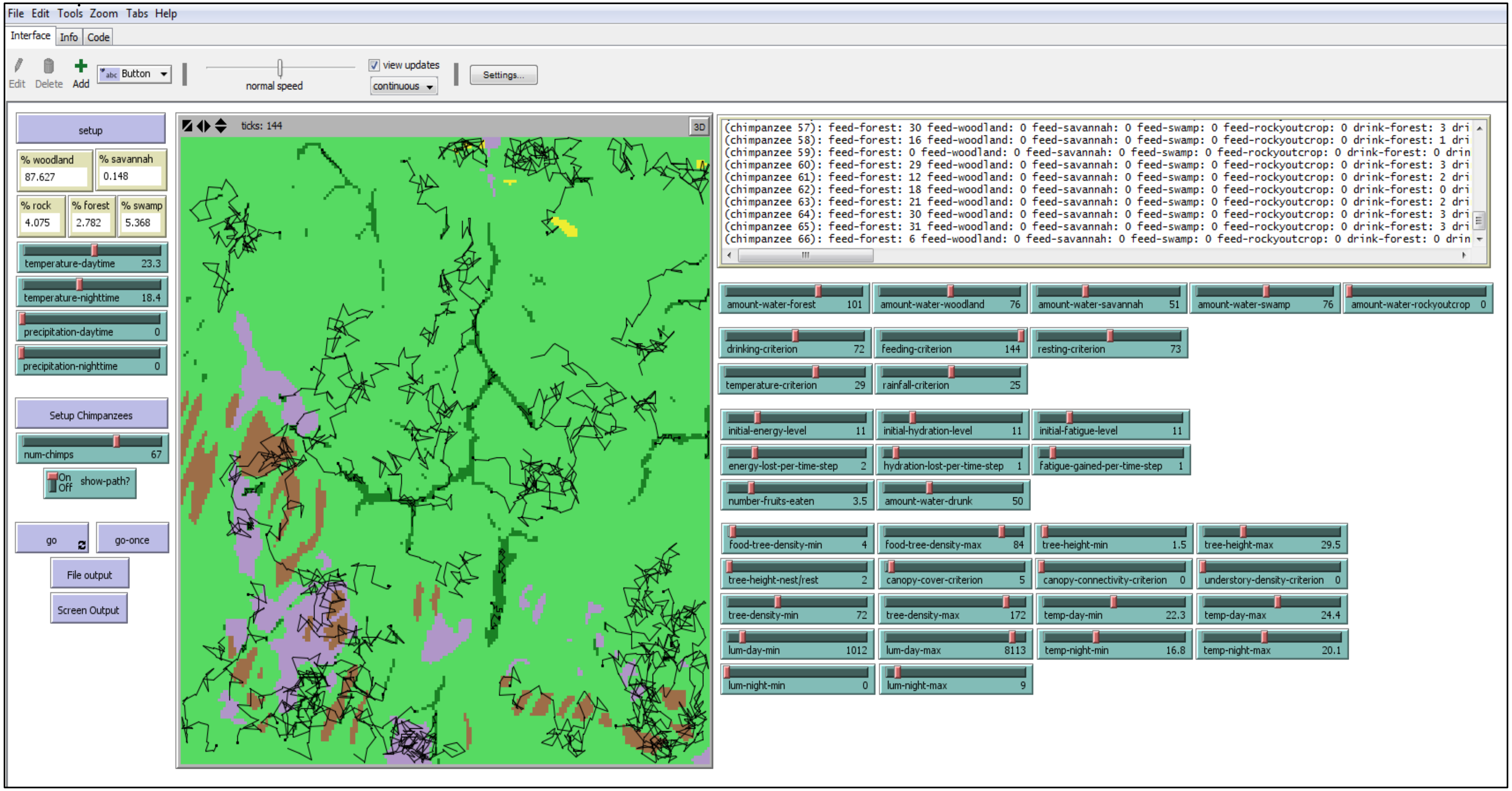
The figures below outline the model interface, or front screen, of the Issa chimpanzee landscape use model presented in Chapter 5. Whereas Figure A5.4.1 shows the model outline at the onset of a model run, Figure A5.4.2 highlights the model interface after a model run. Appendix 5.6 presents the rationale behind the specific parameters settings.



% woodland 87.627
% savannah 0.148
% rock 4.075
% forest 2.782
% swamp 5.368
temperature-daytime 23.3
temperature-nighttime 18.4
precipitation-daytime 0
precipitation-nighttime 0
num-chimps 67
On Off show-path?
ticks: 0

amount-water-forest 101
amount-water-woodland 76
amount-water-savannah 51
amount-water-swamp 76
amount-water-rockyoutcrop 0
drinking-criterion 72
feeding-criterion 144
resting-criterion 73
temperature-criterion 29
rainfall-criterion 25
initial-energy-level 11
initial-hydration-level 11
initial-fatigue-level 11
energy-lost-per-time-step 2
hydration-lost-per-time-step 1
fatigue-gained-per-time-step 1
number-fruits-eaten 3.5
amount-water-drunk 50
food-tree-density-min 4
food-tree-density-max 84
tree-height-min 1.5
tree-height-max 29.5
tree-height-nest/rest 2
canopy-cover-criterion 5
canopy-connectivity-criterion 0
understory-density-criterion 0
tree-density-min 72
tree-density-max 172
temp-day-min 22.3
temp-day-max 24.4
lum-day-min 1012
lum-day-max 8113
temp-night-min 16.8
temp-night-max 20.1
lum-night-min 0
lum-night-max 9

Figure A5.4.1. Model interface of the Issa chimpanzee landscape use model of Chapter 5 before the model run. Environment simulated as 2.8% forest (dark green), 87.6% woodland (light green), 5.4% swamp (purple), 4.1% rocky outcrop (brown), and 0.1% grassland (yellow).



% woodland 87.627
% savannah 0.148
% rock 4.075
% forest 2.782
% swamp 5.368
temperature-daytime 23.3
temperature-nighttime 18.4
precipitation-daytime 0
precipitation-nighttime 0
num-chimps 67
On Off show-path?

```
(chimpanzee 57): feed-forest: 30 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 3 dri
(chimpanzee 58): feed-forest: 16 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 1 dri
(chimpanzee 59): feed-forest: 0 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 0 drin
(chimpanzee 60): feed-forest: 29 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 3 dri
(chimpanzee 61): feed-forest: 12 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 2 dri
(chimpanzee 62): feed-forest: 18 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 0 dri
(chimpanzee 63): feed-forest: 21 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 2 dri
(chimpanzee 64): feed-forest: 30 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 3 dri
(chimpanzee 65): feed-forest: 31 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 3 dri
(chimpanzee 66): feed-forest: 6 feed-woodland: 0 feed-savannah: 0 feed-swamp: 0 feed-rockyoutcrop: 0 drink-forest: 0 drin
```

amount-water-forest 101
amount-water-woodland 76
amount-water-savannah 51
amount-water-swamp 76
amount-water-rockyoutcrop 0
drinking-criterion 72
feeding-criterion 144
resting-criterion 73
temperature-criterion 29
rainfall-criterion 25
initial-energy-level 11
initial-hydration-level 11
initial-fatigue-level 11
energy-lost-per-time-step 2
hydration-lost-per-time-step 1
fatigue-gained-per-time-step 1
number-fruits-eaten 3.5
amount-water-drunk 50
food-tree-density-min 4
food-tree-density-max 84
tree-height-min 1.5
tree-height-max 29.5
tree-height-nest/rest 2
canopy-cover-criterion 5
canopy-connectivity-criterion 0
understory-density-criterion 0
tree-density-min 72
tree-density-max 172
temp-day-min 22.3
temp-day-max 24.4
lum-day-min 1012
lum-day-max 8113
temp-night-min 16.8
temp-night-max 20.1
lum-night-min 0
lum-night-max 9

Figure A5.4.2. Model interface of the Issa chimpanzee landscape use model of Chapter 5 after a model run. Environment simulated as 2.8% forest (dark green), 87.6% woodland (light green), 5.4% swamp (purple), 4.1% rocky outcrop (brown), and 0.1% grassland (yellow).

APPENDIX 5.5

Model code adaptations to create the Issa model of Chapter 5 from the chimpanzee model of Chapter 4

The generic chimpanzee landscape use model presented in Chapter 4 was updated and adapted to suit the behaviour, characteristics and habitat of the chimpanzees at Issa Valley, Tanzania. The resulting individual-based model on Issa chimpanzee landscape use is presented in Chapter 5. Table A5.5.1 outlines the differences and similarities in model codes between the generic model and the Issa model. The rationale behind the model code of the Issa model is presented in Appendix 5.6.

Table A5.5.1. Differences and similarities in the model codes of the generic chimpanzee landscape use model of Chapter 4 and the Issa chimpanzee landscape use model of Chapter 5. The Issa model was adapted from the generic model to suit the behaviour, characteristics, and habitat of the chimpanzees at Issa Valley, Tanzania. The column 'data source' emphasises the source of the Issa model code or adaptation. The rationale behind model rules is outlined in Appendix 5.6.

Parameter	**Generic model (Ch4)**	**Issa model (Ch5)**	**Data source**
Global			
Model size/ Home range	36km^2 (6km x 6km)	110km^2 (10km x 11km)	GMERC data, literature, GIS analyses
Patch size	50m x 50m (120 x 120 patches)	50m x 50m (200 x 220 patches)	Chapter 4
Model run (time)	24 hours	24 hours	Chapter 4
Time step (time)	10 minutes	10 minutes	Chapter 4
Landscape			
Vegetation types	3	5	GMERC data, literature, GIS analyses
Vegetation cover	<u>Savannah:</u> Forest (F) = 10%, woodland (W) = 55%, savannah grassland (G) = 35%.	<u>Issa</u>: Forest (F) = 2.8%, woodland (W) = 87.6%, savannah grassland (G) = 0.1%, swamp (S) = 5.4%, rocky outcrop ® = 4.1%	GMERC data, GIS analyses
Fragmentation	0.05	GIS map	GIS analyses
Temperature	25^{0}C	Day: 23.3^{0}C Night: 18.4^{0}C	HOBO weather station
Precipitation	0mm	Day: 0mm Night: 0mm	HOBO weather station
GIS map or random	Random	Map	GIS analyses
Vegetation features			
• Tree height	F: 10-50m; W: 8-20m; G: 3-15m.	F: 1.5 – 29.5; W: 2.6 – 18.5; S: 2.3 – 11.6; G: 1.7 – 24.6; R: 0m	Field collected data
• Canopy cover	F: 75-100%; W: 25-75%, G: 0-25%.	F: 51 – 100%; W: 1 – 75%; S: 0 – 50%; G: 1 – 50;% R: 0%	Field collected data
• Canopy connectivity	F: 75-100%; W: 25-75%, G: 0-25%.	F: 26 – 100%; W: 1 – 75%; S: 0 – 50%; G: 0 – 25%; R: 0%	Field collected data
• Understory density	F: 0-25%; W: 25-75%, G: 75-100%.	F: 0 – 100%; W: 1 – 75%; S: 0 – 100%; G: 1 – 100%; R: 0%	Field collected data

Parameter	Generic model (Ch4)	Issa model (Ch5)	Data source
• Tree density	F: 75-100%; W: 25-75%, G: 0-25%.	F: 72 – 172 trees; W: 48 – 76 trees; S: 0 – 100; G: 1 – 84 trees; R: 0 trees per 50m x 50m plot	Field collected data
• Food tree density	F: 75-100%; W: 25-75%, G: 0-25%.	F: 36% of trees; W: 47% of trees; S: 62% of trees; G: 6% of trees; R: 0% of trees present in a 50m x 50m patch	Field collected data
• Number fruit	F: 0-21; W: 0-14; G: 0-7.	F: 4.0% of feeding trees; W: 27.9% of feeding trees; S: 4.2% of feeding trees; G: 8.3% of feeding trees; R: 0% of feeding trees providing fruit. One feeding tree is assumed to contain 7 fruits, i.e. twice the number-fruits-eaten)	Chapter 4, GMERC data, field collected data
• Amount water	F: 0-100; W: 0-75; G: 0-50.	F: 0-100; W: 0-75; S: 0 – 75; G: 0-50, R: 0.	Chapter 4
Micro-climate characteristics			
• Temperature (day)	F: 0-25, W: 25-75; G: 75-100.	F: 22.3 – 24.4°C; W: 23.9 – 29.0°C; S: 23.8 -28.9°C; G: 28.5 – 31.7°C; R: 28.5 – 31.7°C	Field collected data
• Temperature (night)	F: 75-100; W: 25-75; G: 0-25.	F: 16.8 – 20.1°C; W: 16.7 – 20.4°C; S: 14.8 – 16.2°C; G: 20.7 – 21.8°C; R: 20.7 – 21.8 °C	Field collected data
• Luminosity (day)	F: 0-25, W: 25-75; G: 75-100.	F: 1,012 – 8,113 Lux; W: 6,854 – 39,578 Lux; S: 1,3059 – 29,194 Lux; G: 10,093 – 44,272 Lux; R: 10,093 – 44,272 Lux	Field collected data
• Luminosity (night)	F: 0 -25; W: 0-25, G: 0-25.	F: 0 – 9 Lux; W: 3 – 18 Lux; S: 11 – 76 Lux; G: 10 – 50 Lux; R: 10 – 50 Lux	Field collected data
Chimpanzees			
Community size	60	67	Literature
Internal states	3	3	Chapter 4
Behaviour			
Feeding	Included	Included	Chapter 4
Drinking	Included	Included	Chapter 4
Nesting	Included	Included	Chapter 4
Resting	Included	Included	Chapter 4
Travel	Included	Included	Chapter 4
Where			
• Feeding	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density between 4 – 84 food trees/patch, tree height between 1.5 – 29.5m, tree density between 72 – 172 trees/patch, temperature (day) between 22.3 – 24.4°C, and luminosity (day) between 1,012 – 8,113 Lux.	Field collected data, literature, GMERC data, Chapter 4
• Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) between 22.3 – 24.4°C, and	Field collected data, literature, GMERC data, Chapter 4

Parameter	**Generic model (Ch4)**	**Issa model (Ch5)**	**Data source**
		luminosity (day) between 1,012 – 8,113 Lux.	
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, tree density between 72 – 172 trees/patch, number fruit ≥ 3.5, understory density > 0%, food tree density between 4 – 84 trees/patch, amount water ≥ 50, temperature (night) between 16.8 – 20.1°C, and luminosity (night) between 0 – 9.	Field collected data, literature, GMERC data, Chapter 4
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Temperature (day) between 22.3 – 24.4°C, luminosity (day) between 1,012 – 8,113 Lux, tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, understory density between > 0%, tree density between 72 – 172 trees/patch, food tree density between 4 – 84 trees/patch, number fruit ≥ 3.5, and amount water ≥ 50.	Field collected data, literature, GMERC data, Chapter 4
• Travel	No specific rules	No specific rules	Chapter 4
• Relative importance	Not included	Not included	Chapter 4
When			
• Feeding	Energy ≤ 144 and energy < hydration.	Energy ≤ 144 and energy < hydration.	Chapter 4
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Hydration ≤ 72 and hydration ≤ energy.	Chapter 4
• Nesting	Time steps > 72.	Time steps > 72.	Chapter 4
• Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Chapter 4
• Travel	No specific rules	No specific rules	Chapter 4
How much			
• Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Chapter 4
• Existing	Energy: -2; hydration: -1; fatigue: +1.	Energy: -2; hydration: -1; fatigue: +1.	Chapter 4
• Feeding	Energy: +10.85 kCal (3.1kCal per fruit)	Energy: +10.85 kCal (3.1kCal per fruit)	Chapter 4
• Drinking	Hydration + 50	Hydration + 50	Chapter 4
• Nesting	Fatigue: -2	Fatigue: -2	Chapter 4
• Resting	Fatigue: -2	Fatigue: -2	Chapter 4
• Travel	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	Chapter 4
Output			
Feeding	+1 for each time step spent feeding.	+1 for each time step spent feeding.	Chapter 4
Drinking	+1 for each time step spent drinking.	+1 for each time step spent drinking.	Chapter 4
Nesting	+1 for each time step spent resting.	+1 for each time step spent resting.	Chapter 4
Resting	+1 for each time step spent	+1 for each time step spent	Chapter 4

Parameter	Generic model (Ch4)	Issa model (Ch5)	Data source
	nesting.	nesting.	
Travel	+1 for each time step spent travelling.	+1 for each time step spent travelling.	Chapter 4
Forest	+1 for each time step spent in forest.	+1 for each time step spent in forest.	Chapter 4
Woodland	+1 for each time step spent in woodland.	+1 for each time step spent in woodland.	Chapter 4
Savannah	+1 for each time step spent in savannah.	+1 for each time step spent in savannah.	Chapter 4
Swamp	Not included	+1 for each time step spent in swamp.	Following Chapter 4
Rocky outcrop	Not included	+1 for each time step spent in rocky outcrop.	Following Chapter 4
Feed-forest	+1 for each time step spent on feeding in forest.	+1 for each time step spent on feeding in forest.	Chapter 4
Feed-woodland	+1 for each time step spent on feeding in woodland.	+1 for each time step spent on feeding in woodland.	Chapter 4
Feed-savannah	+1 for each time step spent on feeding in savannah.	+1 for each time step spent on feeding in savannah.	Chapter 4
Feed-swamp	Not included	+1 for each time step spent on feeding in swamp.	Following Chapter 4
Feed-rockyoutcrop	Not included	+1 for each time step spent on feeding in rocky outcrop.	Following Chapter 4
Drink-forest	+1 for each time step spent on drinking in forest.	+1 for each time step spent on drinking in forest.	Chapter 4
Drink-woodland	+1 for each time step spent on drinking in woodland.	+1 for each time step spent on drinking in woodland.	Chapter 4
Drink-savannah	+1 for each time step spent on drinking in savannah.	+1 for each time step spent on drinking in savannah.	Chapter 4
Drink-swamp	Not included	+1 for each time step spent on drinking in swamp.	Following Chapter 4
Drink-rockyoutcrop	Not included	+1 for each time step spent on drinking in rocky outcrops.	Following Chapter 4
Nest-forest	+1 for each time step spent on nesting in forest.	+1 for each time step spent on nesting in forest.	Chapter 4
Nest-woodland	+1 for each time step spent on nesting in woodland.	+1 for each time step spent on nesting in woodland.	Chapter 4
Nest-savannah	+1 for each time step spent on nesting in savannah.	+1 for each time step spent on nesting in savannah.	Chapter 4
Nest-swamp	Not included	+1 for each time step spent on nesting in swamp.	Following Chapter 4
Nest-rockyoutcrop	Not included	+1 for each time step spent on nesting in rocky outcrops.	Following Chapter 4
Rest-forest	+1 for each time step spent on resting in forest.	+1 for each time step spent on resting in forest.	Chapter 4
Rest-woodland	+1 for each time step spent on resting in woodland.	+1 for each time step spent on resting in woodland.	Chapter 4
Rest-savannah	+1 for each time step spent on resting in savannah.	+1 for each time step spent on resting in savannah.	Chapter 4
Rest-swamp	Not included	+1 for each time step spent on resting in swamp.	Following Chapter 4
Rest-rockyoutcrop	Not included	+1 for each time step spent on resting in rocky outcrops.	Following Chapter 4
Travel-forest	+1 for each time step spent on travelling in forest.	+1 for each time step spent on travelling in forest.	Chapter 4
Travel-woodland	+1 for each time step spent on travelling in woodland.	+1 for each time step spent on travelling in woodland.	Chapter 4
Travel-savannah	+1 for each time step spent on travelling in savannah.	+1 for each time step spent on travelling in savannah.	Chapter 4
Travel-swamp	Not included	+1 for each time step spent on travelling in swamp.	Following Chapter 4
Travel-rockyoutcrop	Not included	+1 for each time step spent on travelling in rocky	Following Chapter 4

Parameter	Generic model (Ch4)	Issa model (Ch5)	Data source
		outcrops.	
Daily path length	+50m for each patch travelled.	+50m for each patch travelled.	Chapter 4
Energy	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chapter 4
Hydration	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chapter 4
Fatigue	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chapter 4
Food intake	+ 3.5 for each feeding bout.	+ 3.5 for each feeding bout.	Chapter 4
Water intake	+ 50 for each drinking bout.	+ 50 for each drinking bout.	Chapter 4
Chimp land use	Output file, calculations	Output file, calculations	Chapter 4
Chimp activity	Output file, calculations	Output file, calculations	Chapter 4
Chimp site selection	Output file, calculations	Output file, calculations	Chapter 4

APPENDIX 5.6

Model code rationale for the Issa chimpanzee landscape use model of Chapter 5

The rationale behind the model rules, decisions and design of the Issa chimpanzee landscape use model presented in Chapter 5 are outlined in Table A5.6.1 below. Model rules are based upon Issa literature, Greater Mahale Ecosystem Research and Conservation (GMERC) data and Issa field collected data, or follow the rationale of the generic chimpanzee landscape use model of Chapter 4 (Appendix 4.5).

Table 5.6.1. Rationale behind the model rules of the Issa chimpanzee landscape use model of Chapter 5.

Parameter	**Value**	**Justification**
Global		
Model size/ Home range	$110km^2$ (10km x 11km)	Minimum Issa chimpanzee home-range size and study area based on chimpanzee evidence (finding derived from published literature and GMERC (GIS) data).
Patch size	50m x 50m (200 x 220 patches)	Similar to Chapter 4, a patch of 50m x 50 m is small enough to contain the necessary detail for each vegetation type, but not too small to affect processing power and difficulty. To create a model environment of $110km^2$, the model contains 200 x 220 patches, equalling 44000 patches in total.
Model run (time)	24 hours	As the model simulated daily activity budgets, path lengths, and vegetation type usage, a run of 24 hours was chosen. This is the same as in Chapter 4 to allow model comparisons.
Time step (time)	10 minutes	A time step of 10min is small enough to capture the necessary behavioural details, but not too small to affect processing power. This is the same as in Chapter 4 to allow model comparisons.
Landscape		
Overall landscapes	1	Only one landscape is simulated for this model: the savannah landscape of Issa Valley, Tanzania.
Landscape implementation	GIS map	Instead of randomly setting up the landscape as was done in Chapter 4, it was chosen to simulate the realistic, present-day environment observed in Issa Valley, Tanzania. Data on the vegetation cover and composition at Issa were outlined in a (GMERC) GIS layer created by Caspian Johnson and were adapted to suit the $110km^2$ area of this study. In GIS, cell size was set to 50m x 50m and each cell contained only one vegetation type based on the majority vegetation of the underlying layer. This map was imported into Netlogo, and was then combined with a layer of 50m x 50m patches. This made it possible to assign each patch a vegetation type and assign necessary vegetation features and micro-climates.
Vegetation types	5	The GIS map of Issa shows that the Issa landscape is composed of 5 different types of vegetation; Forest (F), Woodland (W), Savannah Grassland (G), Swamp (S), and Rocky Outcrops (R).
Vegetation cover	<u>Issa</u>: F = 2.8%, W = 87.6%, G = 0.1%, S = 5.4%, R = 4.1%	Based on the combination of the GIS map and the 50m x 50m patches, the percentage of each vegetation type could be outlined as: forest 2.8%, woodland 87.6%, savannah grassland 0.1%, swamp 5.4%, rocky outcrops 4.1%
Fragmentation	-	As the landscape is based on a real-life map of the study area, no value was set for fragmentation.
Temperature	Day: 23.3^0C Night: 18.4^0C	Based on data from the Issa weather station (HOBO equipment), daily average temperature is 23.3^0C at Issa and nightly average temperature is 18.4^0C. Data were collected between May 5, 2017 and July 2, 2017. It is possible to present more detailed temperature patterns (for example,

Parameter	Value	Justification
		average temperature per hour) based on the HOBO data. However, for comparison reasons with Chapter 4, it was chosen to keep day and night temperatures constant throughout the model run.
Precipitation	Day: 0mm Night: 0mm	Based on data from the Issa weather station (HOBO equipment), daily average rainfall is 0mm at Issa and nightly average rainfall is 0mm. Data were collected between May 5, 2017 and July 2, 2017. It is possible to present more detailed rainfall patterns (e.g. average temperature per hour) based on the HOBO data. However, for comparison reasons with Chapter 4, it was chosen to keep day and night rainfall constant throughout the model run.
Vegetation features		Similar to Chapter 4, only landscape-scale environmental variables were included in the model: tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, amount food, and amount water (Chapter 2). Other variables were not included because they were too small-scale and/or correlated with other variables. Slope and altitude were not included as there is no consistency between sites.
• Tree height	F: 1.5 – 29.5; W: 2.6 – 18.5; S: 2.3 – 11.6; G: 1.7 – 24.6; R: 0m	Based on data from Issa vegetation plots (N = 24, 6 per vegetation type), tree heights for Issa were set for forest between 1.5 – 29.5m, for woodland between 2.6 – 18.5m, for swamp between 2.3 – 11.6m, for grassland between 1.7 – 24.6m and for rocky outcrops to 0m. Tree height for rocky outcrops was not measured. However, based on personal observations, rocky outcrops did not contain vegetation, so tree height was set at 0m.
• Canopy cover	F: 51 – 100; W: 1 – 75; S: 0 – 50; G: 1 – 50; R: 0%	Based on data from Issa vegetation plots and personal observations, canopy cover was set as F: 51 – 100%, W: 1 – 75%, S 0 – 50%, G: 1 – 50% and R: 0%.
• Canopy connectivity	F: 26 – 100; W: 1 – 75; S: 0 – 50; G: 0 – 25; R: 0%	Based on data from Issa vegetation plots and personal observations, canopy connectivity was set as F: 26 – 100%, W: 1 – 75%, S: 0 – 50%, G: 1 – 25% and R: 0%.
• Understory density	F: 0 – 100; W: 1 – 75; S: 0 – 100; G: 1 – 100; R: 0%	Based on Issa vegetation plots and personal observations, understory density and grass cover were set as F: 0 – 100%, W: 1 – 75%, S: 0 – 100%, G: 1 – 100% and R: 0%.
• Tree density	F: 72 – 172; W: 48 – 76; S: 0 – 100; G: 1 – 84; R: 0 trees per 50m x 50m patch	Based on data from Issa vegetation plots and personal observations, the number of trees per patch was set as F: 72 – 172 trees, W: 48 – 76 trees, S: 0 – 100 trees, G: 1 – 84 trees and R: 0 trees.
• Food tree density	F: 36%; W: 47%; S: 62%; G: 6%; R: 0% of all trees present in a 50m x 50m patch	Based on data from Issa vegetation plots and personal observations, amount of feeding trees was set as F: 36% of trees within a patch, W: 47% of trees within a patch, S: 62% of trees within a patch, G: 6% of trees within a patch, and R: 0% of trees within a patch. Normally, forest vegetation types would contain between 4 – 84 feeding trees, woodland between 20 – 44 feeding trees, swamp between 0 – 80 feeding trees, grassland between 0 – 8 feeding trees, and rocky outcrops 0 feeding trees per 50m x 50m plot. However, adding this to the model could result in errors: It was possible that a patch contained more feeding trees than actual trees. To circumvent this problem, it was decided to use the average percentage of feeding trees per patch present in each vegetation type.
• Number fruit	F: 4.0%; W: 27.9%; S: 4.2%; G: 8.3%; R: 0% of all feeding trees in a 50m x 50m patch.	Data from Issa vegetation plots showed that, on average, 4.0% of the food trees within forest bore fruit, as compared to 27.9% of the food trees in woodland, 8.3% of the food trees in grassland, 4.2% of the food trees in swamp. There was no food present in rocky outcrops. This indicates that, based on the amount of feeding trees present, at any time food is most likely to be found in woodland, followed by forest, swamp, and grassland. The finding that woodland had more fruit than forest at Issa is also supported by the Fruit Availability Indices (FAI) data (Chapter 5), although the average percentage of food trees bearing fruit for FAI

Parameter	Value	Justification
		calculations was different. Vegetation plot findings were used here, as all other vegetation features were also based on these data, and no FAI data existed for grassland and only limited FAI data for swamp, i.e. two trees. No data exist on the number of fruits contained by each feeding tree bearing fruit. Therefore, based on the assumption that chimpanzees eat 3.5 fruits each time step (number-fruits-eaten, see below) and the personal observation that chimpanzees usually spend more than 10min within a feeding tree, it is assumed that each tree bearing fruit has 7 fruits, i.e. twice the number of fruits eaten. Usually, chimpanzees spend even longer than 20min within a single feeding tree, but this depends on its size; small trees are generally depleted in short time periods, whereas large trees take more time. 2 x number-of-fruits eaten is therefore an intermediate assumption, taking into account the size of a tree. With this assumption and based on the percentage of trees bearing fruit per vegetation type per patch (based on number of fruit trees), the amount of fruit present in each patch was calculated for the model.
• Amount water	F: 0-100; W: 0-75; S: 0 – 75; G: 0-50, R: 0 hydrations per 50m x 50m patch	As the Issa vegetation plots did not result in sufficient data, amount water per vegetation type was kept similar to Chapter 4: Based on a knowledge-based assumption, forest has more water available than woodland, and woodland has more water than savannah. With respect to the amount of water drunk per time step (see below), it was specified that chimpanzees can rarely drink in savannah, occasionally in woodland, and sometimes in forest. For the Issa model, it was assumed, based on personal observations, that swamp would have similar amounts of water available as woodlands, and that no available water would be present in rocky outcrops.
Micro-climate characteristics		Similar to Chapter 4, only landscape-scale environmental variables are included in the model: local temperature and local luminosity.
• Temperature (day)	F: 22.3 – 24.4; W: 23.9 – 29.0; S: 23.8 -28.9; G: 28.5 – 31.7; R: 28.5 – 31.7 degrees Celsius	Based on data from Issa micro-climate data loggers (N = 36, 12 per vegetation type), average temperature day for forest is set between 22.3 – 24.4 ^{0}C, for woodland between 23.9 – 29.0^{0}C, for swamp between 23.8 -28.9^{0}C, for grassland between 28.5 – 31.7^{0}C, and for rocky outcrops between 28.5 – 31.7^{0}C. Even though no data were collected for rocky outcrops, temperatures were assumed to be similar to grasslands, as these are equally open. Data were collected between May 5, 2017 and July 2, 2017. It is possible to present more detailed daytime temperature patterns (for example, average micro-climate temperature per hour) based on the micro-climate data. However, for comparison reasons with Chapter 4, it was chosen to keep daytime temperature constant throughout the model run.
• Temperature (night)	F: 16.8 – 20.1; W: 16.7 – 20.4; S: 14.8 – 16.2; G: 20.7 – 21.8; R: 20.7 – 21.8 degrees Celsius	Based on data from Issa micro-climate data loggers, average temperature at night was set as F: 16.8 – 20.1 ^{0}C, W: 16.7 – 20.4^{0}C, S: 14.8 -16.2^{0}C, G: 20.7 – 21.8^{0}C, and R: 20.7 – 21.8^{0}C. It is possible to present more detailed nighttime temperature patterns (for example, average micro-climate temperature per hour) based on the micro-climate data. However, for comparison reasons with Chapter 4, it was chosen to keep daytime temperature constant throughout the model run.
• Luminosity (day)	F: 1,012 – 8,113; W: 6,854 – 39,578; S: 13,059 – 29,194; G: 10,093 – 44,272; R: 10,093 – 44,272 Lux	Based on data from Issa micro-climate data loggers, average luminosity day was set as F: 1,012 – 8,113 Lux, W: 6,854 – 39,578 Lux, S: 13,059 – 29,194 Lux, G: 10,093 – 44,272 Lux, and R: 10,093 – 44,272 Lux. It is possible to present more detailed daytime luminosity patterns (for example, average micro-climate temperature per hour) based on the micro-climate data. However, for comparison reasons with Chapter 4, it was chosen to keep daytime temperature constant throughout the model run.
• Luminosity (night)	F: 0 – 9; W: 3 – 18;	Based on data from Issa micro-climate data loggers average

Parameter	**Value**	**Justification**
	S: 11 – 76; G: 10 – 50; R: 10 – 50 Lux	luminosity night was set as F: 0 – 9 Lux, W: 3 – 18 Lux, S: 11 – 76 Lux, G: 10 – 50 Lux, and R: 10 – 50 Lux. It is possible to present more detailed nighttime luminosity patterns (for example, average micro-climate temperature per hour) based on the micro-climate data. However, for comparison reasons with Chapter 4, it was chosen to keep daytime temperature constant throughout the model run.
Chimpanzees		
Community size	67	Minimum population size for Issa chimpanzees (finding derived from published literature). At the start of a model run, chimpanzees are placed on a location that is suitable for nesting, based on the assumption that chimpanzees leave their nest first thing in the morning, and start their day.
Internal states	3	Based on simplifications of general knowledge, it was decided that model behaviours are driven by internal states for energy, hydration, and fatigue. This is the same as in Chapter 4 to allow model comparisons.
Behaviour		
Feeding		Following the rationale of Chapter 4: Based on literature (see Chapter 2), feeding can be regarded as an important daily behaviour for chimpanzees, where energy can be gained. For comparison reasons, this is kept the same.
Drinking		Following the rationale of Chapter 4: When investigating complete daily activity budgets for chimpanzees, drinking should be included as an important behaviour to obtain water, even though this is not often specified in the literature (see Chapter 2). For comparison reasons, this is kept the same.
Nesting		According the rationale of Chapter 4: When investigating chimpanzee behaviour over a 24-hour period, nesting should be included, as this is the only nighttime behaviour for chimpanzees (see Chapter 2). For comparison reasons, this is kept the same.
Resting		According the rationale of Chapter 4: Based on literature, resting can be regarded as an important daily behaviour for chimpanzees, and will make an individual lose fatigue. It can either be enforced due to, e.g., food processing, or ‘extra’ which can be used for other activities such as social behaviours (see Chapter 2). For comparison reasons, this is kept the same.
Travel		Following the rationale of Chapter 4: Based on literature, travel can be regarded as an important daily behaviour for chimpanzees, getting an individual from A to B. Travel is therefore often considered goal-directed (Chapter 2). Energy will be lost through travelling. For comparison reasons, this is kept the same.
Where		Results of Chapter 2 showed the important landscape-scale vegetation features and micro-climate characteristics for each modelled behaviour based on expert-based opinions.
• Feeding	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density between 4 – 84 food trees/patch, tree height between 1.5 – 29.5m, tree density between 72 – 172 trees/patch, temperature (day) between 22.3 – 24.4°C, and luminosity (day) between 1,012 – 8,113 Lux.	Issa field data, GMERC data, and literature data did not specify exact criteria for any of the environmental variables important for feeding. Criteria are therefore based on 2 assumptions (with respect to Chapter 4): 1) Chimpanzees should feed where there is enough fruit, at least enough to last them one time step, i.e. 3.5 fruits; 2) As GMERC data showed that forest vegetation types were preferred for feeding, tree density, food tree density, tree height, temperature day and luminosity day should fall within the ranges found in forest.
• Drinking	Amount water ≥ 50	Issa field data, GMERC data, and literature data did not

Parameter	Value	Justification
	(i.e. amount water drunk), temperature (day) between 22.3 – 24.4°C, and luminosity (day) between 1,012 – 8,113 Lux.	specify exact criteria for any of the environmental variables important for drinking. Criteria are therefore based on 2 assumptions (with respect to Chapter 4): 1) Chimpanzees should drink where there is enough water, at least enough to last them one time step, i.e. 50 hydrations; 2) As GMERC data showed that forest vegetation types were preferred for chimpanzee behaviours, temperature day and luminosity day should fall within the ranges found in forest.
- Nesting	Tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, tree density between 72 – 172 trees/patch, number fruit ≥ 3.5, understory density > 0%, food tree density between 4 – 84 trees/patch, amount water ≥ 50, temperature (night) between 16.8 – 20.1°C, and luminosity (night) between 0 – 9.	Literature data specified exact criteria for tree height, canopy cover and canopy connectivity for nesting. Criteria for all other environmental variables important for nesting were not specified exactly by literature data, Issa field data or GMERC data, and were therefore based on 2 assumptions (with respect to Chapter 4): 1) Chimpanzees should nest where there is enough food and water, at least enough to last them one time step (for the following morning), i.e. 50 hydrations and 3.5 fruits; 2) As GMERC data showed that forest vegetation types were preferred for nesting, temperature night, luminosity night, tree density, understory density, and food tree density should fall within the ranges found in forest.
- Resting	Temperature (day) between 22.3 – 24.4°C, luminosity (day) between 1,012 – 8,113 Lux, tree height ≥ 2m, canopy cover ≥ 5%, canopy connectivity ≥ 0%, understory density > 0%, tree density between 72 – 172 trees/patch, food tree density between 4 – 84 trees/patch, number fruit ≥ 3.5, and amount water ≥ 50.	Field data, GMERC data, and literature data did not specify exact criteria for any of the environmental variables important for resting. Criteria are therefore based on 3 assumptions (with respect to Chapter 4): 1) As similar locations to nesting can be expected for resting, tree height, canopy cover and canopy connectivity should follow the criteria specified for nesting; 2) Chimpanzees should rest where there is enough water and food, at least enough to last them one time step, i.e. 50 hydrations and 3.5 fruits (as feeding/ drinking is most likely the subsequent behaviour); 3) As GMERC data showed that forest vegetation types are preferred for resting, temperature day, luminosity day, tree density, understory density, and food tree density should fall within the ranges found in forest.
- Travel		Similar to Chapter 4 for comparison purposes, within the model, travel was assumed to be a goal-directed behaviour, based on findings from current literature (Chapter 2). No criteria were set as to where a chimpanzee could travel, as this would restrict individual decisions and enforce the model rules. Preferred vegetation features and micro-climate characteristics follow from the model results. In this way, only the 'goal activities' have strict 'where-criteria'. Within the travel procedure, individuals first check the vegetation features and micro-climate characteristics of their current patch and select this patch for their goal activity if the patch abides to all criteria. If not, individuals subsequently look at their neighbouring patches within 50m for a suitable patch, will then look at their surrounding patches within 100m for a suitable patch, or will 'jump' a random 3 – 6 patches (150 – 300m) to start a search there. Chimpanzees were expected to 'see' a maximum of 100m in all directions and were expected to travel a maximum of 300m within 10min (based on literature of average travel speed of 2.02km/hr: Bates and Byrne 2009).
- Relative importance		Similar to Chapter 4, no relative importance was included within the model. Vegetation features or micro-climate characteristics are either important for a specific behaviour, or they are not. An individual investigates the most

Parameter	**Value**	**Justification**
		important variables first, but all important variables are still included.
When		As no data exist for Issa on *when* chimpanzees perform their daily activities and the only other data found for chimpanzees at a savannah site (Fongoli) are consistent with the model design of Chapter 4, 'when' criteria followed the rationale of Chapter 4: Based on general knowledge assumptions (Chapter 2), it is specified for the model that chimpanzees must first assess whether it is dark/night. In this case, the only option for chimpanzees is to nest. During daytime, an individual must first decide whether the current weather conditions impair its daily activities. If so, an individual must rest. If not, it is expected that drinking is most important due to the importance of water, followed by feeding for gaining energy. This is however, relative, as an individual can be more hungry than thirsty, in which case it will feed. If no need for feeding or drinking, an individual can spend 'extra' time resting.
• Feeding	Energy ≤ 144 and energy < hydration.	Following Chapter 4, an individual should feed when it is hungry (and more hungry than thirsty). The feeding criterion is based on random variables and the assumption that individuals would like to maintain a neutral energy balance: in total 288 energy will be lost during a model run (see below), 144 of which will be lost during nighttime nesting. As long as an individual keeps its energy above 144 during daytime, it will be prepared for nesting.
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Following Chapter 4, an individual should drink when it is thirsty (and more thirsty than hungry). The drinking criterion is based on random variables and the assumption that individuals would like to maintain a neutral hydration (i.e. water) balance: in total 144 hydration will be lost during a model run (see below), 72 of which will be lost during nighttime nesting. As long as an individual keeps its hydration above 72 during daytime, it will be prepared for nesting.
• Nesting	Time steps > 72.	Following Chapter 4, an individual should nest when it is dark (i.e. after 12 hours, and thus after 72 time steps of 10 minutes). Nesting is the only option at nighttime.
• Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Following Chapter 4, chimpanzees should rest when it is too wet and/or rains too hard (put at > 25mm, as this is generally considered as a wet day), when it is too hot (put at > 29°C, as temperatures above this value are outside the thermoneutral range for chimpanzees), when they are too tired (it could be assumed that individuals would like to maintain a neutral fatigue balance: in total 144 fatigues will be gained during a model run (see below), of which only 72 will be lost during nighttime nesting. As long as an individual keeps its fatigue below 72 during daytime, it will be prepared for nesting), or when there is nothing else to do.
• Travel	-	Following Chapter 4, travel is incorporated within the behavioural procedures of feeding, drinking, nesting and resting, and is goal directed. Chimpanzees choose to travel when their current patch is not suitable for their selected activity.
How much		As is the case in Chapter 4, chimpanzees have internal variables for hydration, energy and fatigue. The model run starts off with initial levels of energy, hydration and fatigue for each individual. Individuals gain and lose energy, hydration and fatigue by performing their activities and simply by existing.
• Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	For comparison reasons and because there is no data present for Issa or any other savannah chimpanzee study sites, initial internal levels for energy, hydration and fatigue follow the rationale of Chapter 4: As there is no literature data (Chapter 2) on how much energy, hydration, and fatigue chimpanzees start off in the morning, these values are randomly set between 0 and 10, in order to keep it within the same order of magnitude of energy, hydration,

Parameter	**Value**	**Justification**
		and fatigue gained and lost each time step.
- Existing	Energy: -2; hydration: -1; fatigue: +1.	For comparison reasons and lack of data, internal levels for energy, hydration and fatigue for existing follow the rationale of Chapter 4: Based on general knowledge (Chapter 2), individuals lose energy and hydration, and gain fatigue simply by existing. The values are randomly set at 1 or 2 in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step and no data exist to inform this study otherwise.
- Feeding	Energy: +10.85 kCal (3.1kCal per fruit)	For comparison reasons and due to lack of data, internal levels for energy gains during feeding follow the rationale of Chapter 4: Based on literature data (Chapter 2), 1 gram of dry weight of fruits contains 3.1kCal of energy. On average, it is assumed that a fruit contains between 70 – 95% water, the remainder is called dry weight. Hourly energy intake rates are not specified for chimpanzees. In reality, individuals can lose a lot of energy every 10 minutes spend feeding due to mechanisms such as food processing. However, to keep the model simple, and the losses and gains in the same order of magnitude within the model, it is assumed that chimpanzees would be able to gain at least 3.1kCal per fruit eaten. Calibrating the model (in Ch4) resulted in 3.5 fruits eaten each time step, and thus gaining 10.85 kCal of energy net each time step spend feeding.
- Drinking	Hydration + 50	For comparison reasons and due to lack of data, internal levels for hydration for drinking follow the rationale of Chapter 4: As the amount of hydration while drinking is not specified in literature (see Chapter 2), it is assumed that an individual can gain a lot of hydration during each drinking bout. This is based on the observation that chimpanzees do not spent a lot of time drinking each day.
- Nesting	Fatigue: -2	For comparison reasons and due to lack of data, internal levels for fatigue for nesting follow the rationale of Chapter 4: No data are presented on the amount of fatigue lost while nesting (see Chapter 2). It is therefore assumed that individuals lose 1 fatigue each time step spent nesting.
- Resting	Fatigue: -2	For comparison reasons and due to lack of data, internal levels for fatigue for resting follow the rationale of Chapter 4: No data are presented on the amount of fatigue lost while resting (see Chapter 2). It is therefore assumed that individuals lose 1 fatigue each time step spent resting.
- Travel	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	For comparison reasons and due to lack of data, internal levels for energy, hydration and fatigue for travel follow the rationale of Chapter 4: Based on an average daily path length of 3.0km and average energy expenditure for travel of 207.3kCal/day, energy lost per 50m travelled equals about 3.5kCal (see Chapter 2). As chimpanzees can travel between 50 – 300m, energy loss due to travel is somewhere between -3.5kCal and -21kCal. For every extra 50m travelled (so when travelling between 100 – 300m) an additional hydration was lost, and an extra fatigue was gained, as an individual was travelling faster.
Output		
Feeding	+1 for each time step spent feeding.	To keep all output comparable to Chapter 4: Based on 144 time steps in the model, each time step spent on feeding will add +1 to the feeding column in the output table. This way, the amount of time spent feeding over a 24-hour period can easily be assessed.
Drinking	+1 for each time step spent drinking.	Based on 144 time steps in the model, each time step spent on drinking will add +1 to the drinking column in the output table.
Nesting	+1 for each time step spent resting.	Based on 144 time steps in the model, each time step spent on nesting will add +1 to the nesting column in the output table.
Resting	+1 for each time step spent nesting.	Based on 144 time steps in the model, each time step spent on resting will add +1 to the resting column in the output table.

Parameter	Value	Justification
Travel	+1 for each time step spent travelling.	Based on 144 time steps in the model, each time step spent on travel will add +1 to the travel column in the output table.
Forest	+1 for each time step spent in forest.	Based on 144 time steps in the model, each time step spent in forest will add +1 to the forest column in the output table.
Woodland	+1 for each time step spent in woodland.	Based on 144 time steps in the model, each time step spent in woodland will add +1 to the woodland column in the output table.
Savannah	+1 for each time step spent in savannah.	Based on 144 time steps in the model, each time step spent in savannah will add +1 to the savannah column in the output table.
Swamp.	+1 for each time step spent in swamp.	Based on 144 time steps in the model, each time step spent in swamp will add +1 to the swamp column in the output table.
Rocky Outcrop	+1 for each time step spent in rocky outcrop.	Based on 144 time steps in the model, each time step spent in rocky outcrops will add +1 to the rocky outcrop column in the output table.
Feed-forest	+1 for each time step spent on feeding in forest.	Based on 144 time steps in the model, each time step spent on feeding in forest will add +1 to the feed-forest column in the output table.
Feed-woodland	+1 for each time step spent on feeding in woodland.	Based on 144 time steps in the model, each time step spent on feeding in woodland will add +1 to the feed-woodland column in the output table.
Feed-savannah	+1 for each time step spent on feeding in savannah.	Based on 144 time steps in the model, each time step spent on feeding in savannah will add +1 to the feed-savannah column in the output table.
Feed-swamp	+1 for each time step spent on feeding in swamp.	Based on 144 time steps in the model, each time step spent on feeding in swamp will add +1 to the feed-swamp column in the output table.
Feed-rockyoutcrop	+1 for each time step spent on feeding in rocky outcrop.	Based on 144 time steps in the model, each time step spent on feeding in rocky outcrops will add +1 to the feed-rockyoutcrop column in the output table.
Drink-forest	+1 for each time step spent on drinking in forest.	Based on 144 time steps in the model, each time step spent on drinking in forest will add +1 to the drink-forest column in the output table.
Drink-woodland	+1 for each time step spent on drinking in woodland.	Based on 144 time steps in the model, each time step spent on drinking in woodland will add +1 to the drink-woodland column in the output table.
Drink-savannah	+1 for each time step spent on drinking in savannah.	Based on 144 time steps in the model, each time step spent on drinking in savannah will add +1 to the drink-savannah column in the output table. .
Drink-swamp	+1 for each time step spent on drinking in swamp.	Based on 144 time steps in the model, each time step spent on drinking in swamp will add +1 to the drink-swamp column in the output table.
Drink-rockyoutcrop	+1 for each time step spent on drinking in rocky outcrops.	Based on 144 time steps in the model, each time step spent on drinking in rocky outcrop will add +1 to the drink-rockyoutcrop column in the output table.
Nest-forest	+1 for each time step spent on nesting in forest.	Based on 144 time steps in the model, each time step spent on nesting in forest will add +1 to the nest-forest column in the output table.
Nest-woodland	+1 for each time step spent on nesting in woodland.	Based on 144 time steps in the model, each time step spent on nesting in woodland will add +1 to the nest -woodland column in the output table.
Nest-savannah	+1 for each time step spent on nesting in savannah.	Based on 144 time steps in the model, each time step spent on nesting in savannah will add +1 to the nest-savannah column in the output table.
Nest-swamp	+1 for each time step spent on nesting in swamp.	Based on 144 time steps in the model, each time step spent on nesting in swamp will add +1 to the nest-swamp column in the output table.

Parameter	Value	Justification
Nest-rockyoutcrop	+1 for each time step spent on nesting in rocky outcrops.	Based on 144 time steps in the model, each time step spent on nesting in rocky outcrop will add +1 to the nest - rockyoutcrop column in the output table.
Rest-forest	+1 for each time step spent on resting in forest.	Based on 144 time steps in the model, each time step spent on resting in forest will add +1 to the rest-forest column in the output table.
Rest-woodland	+1 for each time step spent on resting in woodland.	Based on 144 time steps in the model, each time step spent on resting in woodland will add +1 to the rest -woodland column in the output table.
Rest-savannah	+1 for each time step spent on resting in savannah.	Based on 144 time steps in the model, each time step spent on resting in savannah will add +1 to the rest-savannah column in the output table.
Rest-swamp	+1 for each time step spent on resting in swamp.	Based on 144 time steps in the model, each time step spent on resting in swamp will add +1 to the rest -swamp column in the output table.
Rest-rockyoutcrop	+1 for each time step spent on resting in rocky outcrops.	: Based on 144 time steps in the model, each time step spent on resting in rocky outcrop will add +1 to the rest - rockyoutcrop column in the output table.
Travel-forest	+1 for each time step spent on travelling in forest.	Based on 144 time steps in the model, each time step spent on travelling in forest will add +1 to the travel-forest column in the output table.
Travel-woodland	+1 for each time step spent on travelling in woodland.	Based on 144 time steps in the model, each time step spent on travelling in woodland will add +1 to the travel - woodland column in the output table.
Travel-savannah	+1 for each time step spent on travelling in savannah.	Based on 144 time steps in the model, each time step spent on travelling in savannah will add +1 to the travel -savannah column in the output table.
Travel-swamp	+1 for each time step spent on travelling in swamp.	Based on 144 time steps in the model, each time step spent on travelling in swamp will add +1 to the travel -swamp column in the output table.
Travel-rockyoutcrop	+1 for each time step spent on travelling in rocky outcrops.	Based on 144 time steps in the model, each time step spent on travelling in rocky outcrop will add +1 to the travel - rockyoutcrop column in the output table.
Daily path length	+50m for each patch travelled.	For each 50m travelled, 50m is added to the daily path length column in the output table.
Energy	Various	Each time energy is gained and/or lost (see above), this is updated in the energy column of the output table.
Hydration	Various	Each time hydration is gained and/or lost (see above), this is updated in the hydration column of the output table.
Fatigue	Various	Each time fatigue is gained and/or lost (see above), this is updated in the fatigue column of the output table.
Food intake	+ 3.5 for each feeding bout.	After each feeding bout, the amount of fruits eaten (see above) is updated in the food intake column in the output table.
Water intake	+ 50 for each drinking bout.	After each drinking bout, the amount of water drunk (see above) is updated in the water intake column in the output table.
Chimp land use		Output table (.csv) for further analyses.
Chimp activity		Output table (.csv) for further analyses.
Chimp site selection		Output table (.csv) for further analyses.

APPENDIX 5.7

Statistical comparisons of the structural vegetation features and micro-climates observed across vegetation types at Issa Valley, Tanzania

Vegetation plots (n = 24) and data loggers (n = 36) were measured to identify the structural vegetation features and micro-climate characteristics of different vegetation types at Issa Valley, Tanzania (Table A5.7.1). Kruskal-Wallis tests ($\alpha = 0.05$), *post hoc* Mann-Whitney U tests (Bonferroni correction: $\alpha = 0.05 / 6 = 0.008$), and Spearman rank correlation coefficients ($\alpha = 0.05$) were used to assess statistical differences and correlations. Statistical analyses were only carried out on variables that were measured on a continuous scale (e.g. tree height, tree density), and not on variables that were categorised in classes (e.g. canopy connectivity, understory density).

Table A5.7.1. Mean and range of vegetation features and micro-climates observed in forest, woodland, swamp and savannah grassland vegetation types at Issa Valley, Tanzania. Characteristics were measured using vegetation plots and micro-climate data loggers (Chapter 5 and Appendix 5.1). Note that this table is a partial replica of Table 5.2 (Chapter 5).

	Forest			**Woodland**			**Swamp**			**Savannah Grassland**		
	Mean	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*
Plot data												
# trees (DBH ≥10cm)[1]	32	18	43	15.2	12	19	6.2	0	25	7.8	1	21
# vines (diameter ≥ 10cm)	1.2	0	4	0	0	0	0	0	0	0	0	0
# feeding trees (DBH ≥10cm)[1]	11.5	1	21	7.2	5	11	3.8	0	20	0.5	0	2
% feeding trees (DBH ≥10cm)	36	5.6	75	47	35.7	69.2	62	0	100	6	0	40
% feeding trees (DBH ≥10cm) bearing fruit	4	0	23.8	27.9	0	54.5	4.2	0	25	8.3	0	50
# trees (DBH <10cm)	89	36	142	61	8	198	28	0	76	15.5	0	25
Altitude (m)	1516	1364	1619	1488	1249	1635	1641	1603	1690	1216	1150	1255
Slope[2]	-	-	-	-	-	-	-	-	-	-	-	-
Canopy cover (%)[3]	-	51	100	-	1	75	-	0	50	-	1	50
Canopy cover (%, Canopy Digi)[4]	68.8	55.4	78.3	44.0	19.4	57.1	14.2	0.0	35.7	19.0	2.4	42.3
Canopy connectivity (%)[3]	-	26	100	-	1	75	-	0	50	-	0	25
Understory (%)[3]	-	51	100	-	1	75	-	0	50	-	1	25
Grass (%)[3]	-	0	0	-	26	75	-	26	100	-	75	100
Bare land (%)[3]	-	76	100	-	26	50	-	0	50	-	0	25
THV (%)[3]	-	0	0	-	0	0	-	0	25	-	0	0
Water (%)	2.5	0	5	0	0	0	0	0	0	0	0	0
Ant nests (#)	0.5	0	2	0	0	0	0	0	0	0	0	0

	Forest			**Woodland**			**Swamp**			**Savannah Grassland**		
	Mean	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*
Termite mounts (#)	0	0	0	0.5	0	3	0	0	0	0	0	0
Chimp evidence (#)	0	0	0	0	0	0	0	0	0	0	0	0
Plot tree data (trees/vines ≥ 10cm DBH)												
Species[5]	-	-	-	-	-	-	-	-	-	-	-	-
Tree DBH (cm)	21.5	10	81	21,2	10.1	69.7	23.1	10.5	71.9	28.1	10	163.3
Tree LBH (m)	4.2	0	18.5	2.8	0	8.3	1.3	0	3.2	1.4	0	5.8
Tree height (m)	11.8	1.5	29.5	8.8	2.6	18.5	5.8	2.3	11.6	7.5	1.7	24.6
Crown width N (m)	2.2	0	13.6	2.2	0	7.9	1.9	0	5.3	2.9	0	12.4
Crown width S (m)	2.8	0	13.5	2.1	0	7	1.9	0	5.5	3.2	0	9.8
Crown width E (m)	2.1	0	7.7	1.7	0	7.2	1.9	0	5.5	2.7	0	8.5
Crown width W (m)	2.5	0	16.9	2.2	0	12.6	1.8	0	6.2	2.8	0	10.2
Crown height (m)	7.6	0.5	22.7	5.9	0	14.5	4.5	1.3	9.3	6.2	0.9	19.3
Crown shape[6]	-	-	-	-	-	-	-	-	-	-	-	-
Crown connectivity (%)[3]	-	0	100	-	0	100	-	0	100	-	0	75
Crown cover (%)[3]	-	0	100	-	0	100	-	1	100	-	0	100
Tree ripe chimp food coverage (%)[3]	-	0	25	-	0	50	-	0	25	-	0	25
Micro-climates												
Temperature day (average, °C)	23.3	22.3	24.4	26.6	23.9	29	25.8	23.8	28.9	29.8	28.5	31.7
Temperature night (average, °C)	18.5	16.8	20.1	18.6	16.7	20.4	15.7	14.8	16.2	21.1	20.7	21.8
Luminosity day (average, Lux)	3767	1012	8113	14440	6854	39578	19454	13059	29192	21968	10092	44272
Luminosity night (average, Lux)	3	0	9	8	3	18	30	11	76	23	10	50

[1]Number of (feeding) trees is equal to (feeding) tree density; [2]Slope cannot be explained with a mean, minimum or maximum, as it was only noted whether the slope of a plot was flat, mild, medium or steep. For forest, slopes were either flat or steep, for woodland slopes ranged from flat to steep, for swamp slopes were flat, and for grassland slopes ranged from flat to mild; [3]For canopy cover, canopy connectivity, understory, grass, bare land, THV, crown connectivity, crown cover, and tree ripe chimp food coverage, no mean can be presented as these variables were measured in categories (0 = 0%, 1: 1 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, 4 = 76 – 100%). Only minima and maxima are presented based on these categories; [4]Canopy cover measures are based on photograph analyses through CanopyDigi; [5]Various tree species are observed, including *Cola microcarpa* and *Brachystegia boehmii* for forest, *Brachystegia speciformis* and *Parinari curatelllifolia* for woodland, *Uapaca kirkiana* and *Erythrina excelsa* for swamp, and *Acacia polyacantha* and *Diplorhynchus condylocarpon* for savannah grassland; 6Crown shape cannot be explained with maxima, minima and means. For forest, all crown shapes were observed (see figure 5.2), and woodland, grassland and swamp had crown shapes 1, 2, 4 and 6.

Differences in structural vegetation features between vegetation types

Apart from the percentage of feeding trees and the percentage of feeding trees bearing fruit, Kruskal-Wallis tests showed that overall vegetation plot measurements were significantly different between forest, woodland, swamp and savannah grassland vegetation types (in all cases, $N_1 = 6$, $N_2 = 6$, $N_3 = 6$, $N_4 = 6$, $H \geq 7.9$, $df = 3$, $p \leq 0.048$). *Post-hoc* Mann-Whitney U tests showed that forest vegetation types had significantly more trees (DBH ≥ 10cm) than swamp and grassland, had significantly more feeding trees and small trees (DBH < 10cm) than grassland, was significantly higher in altitude than grassland, and had significantly more canopy cover than woodland, grassland and swamp (Table A5.7.2). Swamp vegetation types were significantly higher in altitude than forest and grassland vegetation types, and woodland had significantly more feeding trees than grassland (Table A5.7.2). All other pairwise comparisons were not significant (Table A5.7.2).

Plot tree data also differed significantly between forest, woodland, swamp and savannah grassland vegetation types (in all cases: $N_1 \geq 197$, $N_2 = 91$, $N_3 = 37$, $N_4 = 47$, $H \geq 8.3$, $df = 3$, $p \leq 0.040$); only DBH was not significantly different across different types of vegetation. *Post-hoc* Mann-Whitney U tests showed that forest vegetation types had significantly taller trees than woodland, swamp and grassland, had significantly higher LBHs than swamp and grassland, and had significantly larger canopy heights than woodland and swamp (Table A5.7.3). Woodland vegetation types had significantly higher LBHs and trees than swamp and grassland. Grassland vegetation types had significantly larger crown widths north than forest, significantly larger crown widths south than swamp, and significantly larger crown widths east than forest and woodland. Pairwise comparisons of other plot tree data were not significant (Table A5.7.3).

Differences in micro-climates between vegetation types

Micro-climate characteristics were significantly different between forest, woodland, swamp and savannah grassland vegetation types (in all cases, $N_1 = 9$, $N_2 = 9$, $N_3 = 7$, $N_4 = 9$, $H \geq 23.0$, $df = 3$, $p < 0.001$). Forest vegetation types had significantly lower average daytime temperatures and lower average daytime luminosities than all other types of vegetation (*post-hoc* Mann-Whitney U tests, Table A5.7.4). Average daytime temperatures were additionally significantly higher in grassland as compared to woodland and swamp. Savannah grassland vegetation types had significantly higher average nighttime temperatures than forest, woodland and swamp, and swamp average nighttime temperatures were significantly lower than forest and woodland. Average luminosity at nighttime was significantly higher for swamp and grassland vegetation as compared to forest and woodland vegetation types. All other pairwise comparisons of micro-climate characteristics between vegetation types were non-significant (Table A5.7.4).

Table A5.7.2. *Post-hoc* Mann-Whitney U test statistics for the comparisons of plot data between forest (F), woodland (W), swamp (S), and grassland (G) vegetation types at Issa Valley. Only significant differences specified., 'Not sign.' indicates not significant. In all cases, N = 6.

	Post-hoc **Mann-Whitney U tests** (in all cases, N = 6)					
	F vs W	**F vs S**	**F vs G**	**W vs S**	**W vs G**	**S vs G**
# trees (DBH ≥10cm)	Not sign.	F > S Z = -2.7 p = 0.004	F > G Z = -2.7 p = 0.004	Not sign.	Not sign.	Not sign.
# vines (diameter ≥10cm)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.
# feeding trees (DBH ≥10cm)	Not sign.	Not sign.	F > G Z = -2.7 p = 0.006	Not sign.	W > G Z = -2.9 p = 0.002	Not sign.
% feeding trees (DBH ≥10cm)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.
% fruiting trees (DBH ≥10cm)*	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.
# trees (DBH < 10cm)	Not sign.	Not sign.	F > G Z = -2.9 p = 0.002	Not sign.	Not sign.	Not sign.
Altitude (m)	Not sign.	S > F Z = -2.6 p = 0.006	F > G Z = -2.9 p = 0.002	Not sign.	Not sign.	S > G Z = -2.9 p = 0.002
Canopy cover (%, CanopyDigi)	F > W Z = -2.7 p = 0.004	F > S Z = -2.9 p = 0.002	F > G Z = -2.9 p = 0.002	Not sign.	Not sign.	Not sign.
Water (%)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.

* % fruiting trees is the percentage of feeding trees bearing fruit.

Correlations of vegetation features and micro-climates across vegetation types

Many vegetation features and micro-climate characteristics correlate with each other, and correlations were observed both within and between overall plot data, plot tree data and micro-climates (Table A5.7.5). For example, significant positive correlations were observed for number of trees and amount of water, number of trees and canopy cover, temperature day and temperature night, temperature day and luminosity day, tree height and DBH, tree height and LBH, DBH and crown height, DBH and crown width (north, east, south and west), tree height and number of trees, and canopy cover and tree height (Table A5.7.5). Significant negative correlations were observed between, for example, temperature day and altitude, temperature day and canopy cover, luminosity night and number of trees, temperature (day and night) and tree height, crown width (north, east, south and west) and altitude, and luminosity (day and night) and LBH (Table A5.7.5). Other correlations showed not to be significant (Table A5.7.5).

Table A5.7.3. *Post-hoc* Mann-Whitney U test statistics for the comparisons of plot tree data between forest (F), woodland (W), swamp (S), and grassland (G) vegetation at Issa Valley. Only significant differences specified.

	***Post-hoc* Mann-Whitney U tests**					
	F vs W	**F vs S**	**F vs G**	**W vs S**	**W vs G**	**S vs G**
Tree DBH (cm)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.
Tree LBH (m)	Not sign.	F > S $N_1 = 197$ $N_2 = 37$ $Z = -4.6$ $p < 0.001$	F > G $N_1 = 197$ $N_2 = 47$ $Z = -5.1$ $p < 0.001$	W > S $N_1 = 91$ $N_2 = 37$ $Z = -4.5$ $p < 0.001$	W > G $N_1 = 91$ $N_2 = 47$ $Z = -4.8$ $p < 0.001$	Not sign.
Tree height (m)	F > W $N_1 = 199$ $N_2 = 91$ $Z = -4.2$ $p < 0.001$	F > S $N_1 = 199$ $N_2 = 37$ $Z = -6.6$ $p < 0.001$	F > G $N_1 = 199$ $N_2 = 47$ $Z = -5.4$ $p < 0.001$	W > S $N_1 = 91$ $N_2 = 37$ $Z = -4.5$ $p < 0.001$	W > G $N_1 = 91$ $N_2 = 47$ $Z = -3.1$ $p = 0.002$	Not sign.
Crown width N (m)	Not sign.	Not sign.	G > F $N_1 = 199$ $N_2 = 47$ $Z = -3.0$ $p = 0.002$	Not sign.	Not sign.	Not sign.
Crown width S (m)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	G > S $N_1 = 37$ $N_2 = 47$ $Z = -2.7$ $p = 0.006$
Crown width E (m)	Not sign.	Not sign.	G > F $N_1 = 198$ $N_2 = 47$ $Z = -2,6$ $p = 0.008$	Not sign.	G > W $N_1 = 91$ $N_2 = 47$ $Z = -3.7$ $p < 0.001$	Not sign.
Crown width W (m)	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.
Crown height (m)	F > W $N_1 = 198$ $N_2 = 91$ $Z = -2.8$ $p = 0.005$	F > S $N_1 = 198$ $N_2 = 37$ $Z = -4.0$ $p < 0.001$	Not sign.	Not sign.	Not sign.	Not sign.

Table A5.7.4. *Post-hoc* Mann-Whitney U test statistics for the comparisons of micro-climate characteristics between forest (F), woodland (W), swamp (S), and grassland (G) vegetation at Issa Valley. Only significant differences specified. In all cases, N = 9 for forest, woodland and grassland, N = 7 for swamp.

	***Post-hoc* Mann-Whitney U tests** (N = 9 for F, W, G, and N = 7 for S)					
	F vs W	**F vs S**	**F vs G**	**W vs S**	**W vs G**	**S vs G**
Temperature day (mean, °C)	W > F $Z = -3.0$ $p = 0.001$	S > F $Z = -3.0$ $p = 0.001$	G > F $Z = -3.6$ $p < 0.001$	Not sign.	G > W $Z = -3.0$ $p = 0.001$	G > S $Z = -3.0$ $p = 0.001$
Temperature night (mean, °C)	Not sign.	F > S $Z = -3.3$ $p < 0.001$	G > F $Z = -3.6$ $p < 0.001$	W > S $Z = -3.3$ $p < 0.001$	G > W $Z = -3.6$ $p < 0.001$	G > S $Z = -3.3$ $p = 0.001$
Luminosity day (mean, Lux)	W > F $Z = -3.4$ $p < 0.001$	S > F $Z = -3.3$ $p < 0.001$	G > F $Z = -3.6$ $p < 0.001$	Not sign.	Not sign.	Not sign.
Luminosity night (mean, Lux)	Not sign.	S > F $Z = -3.3$ $p < 0.001$	G > F $Z = -3.6$ $p < 0.001$	S > W $Z = -2.8$ $p = 0.003$	G > W $Z = -2.9$ $p = 0.002$	Not sign.

Table A5.7.5. Spearman rank correlations of structural vegetation features and micro-climates across vegetation types at Issa Valley, Tanzania. Only significant correlations are specified. Note that correlations are performed regardless of vegetation type, i.e. data from all vegetation types are compiled and correlated. Within the table: '#trees' = # of trees ≥ 10cm DBH, '#ftrees' = # of feeding trees ≥ 10cm DBH, '#strees' = # of small trees < 10cm DBH, '#vines' = # of vines ≥ 10cm diameter, '%ftrees' = % feeding trees, '%frtrees' = % feeding trees in fruit, 'Alt' = altitude, 'CanCov' = canopy cover, 'Water' = % water, 'TH' = tree height, 'DBH' = diameter at breast height, 'LBH' = lowest branch height, 'CWN' = crown with north, 'CWS' = crown with south, 'CWE' = crown with east, 'CWW' = crown with west, 'T_{day}' = temperature at daytime, 'T_{night}' = temperature at nighttime, 'L_{day}' = luminosity at daytime, and 'L_{night}' = luminosity at nighttime. 'Not sign.' stands for no significant correlation observed.

	#trees	**#ftrees**	**#strees**	**#vines**	**%ftrees**	**%frtrees**	**Alt**	**CanCov**	**Water**	**TH**	**DBH**	**LBH**	**CWN**	**CWS**	**CWE**	**CWW**	**CH**	**T_{day}**	**T_{night}**	**L_{day}**	**L_{night}**
#trees	■																				
#ftrees	$\rho = 0.785$ $p < 0.001$ $n = 24$	■																			
#strees	$\rho = 0.429$ $p = 0.036$ $n = 24$	Not sign.	■																		
#vines	$\rho = 0.455$ $p = 0.026$ $n = 24$	Not sign.	Not sign.	■																	
%ftrees	$\rho = 0.441$ $p = 0.031$ $n = 24$	$\rho = 0.826$ $p < 0.001$ $n = 24$	Not sign.	Not sign.	■																
%frtrees	Not sign.	$\rho = 0.482$ $p = 0.017$ $n = 24$	Not sign.	Not sign.	$\rho = 0.548$ $p = 0.006$ $n = 24$	■															
Alt	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	■														
CanCov	$\rho = 0.801$ $p < 0.001$ $n = 24$	$\rho = 0.708$ $p < 0.001$ $n = 24$	$\rho = 0.407$ $p = 0.049$ $n = 24$	$\rho = 0.524$ $p = 0.009$ $n = 24$	$\rho = 0.497$ $p = 0.013$ $n = 24$	Not sign.	Not sign.	■													
Water	$\rho = 0.556$ $p = 0.005$ $n = 24$	Not sign.	$\rho = 0.483$ $p = 0.017$ $n = 24$	$\rho = 0.477$ $p = 0.018$ $n = 24$	Not sign.	Not sign.	Not sign.	$\rho = 0.537$ $p = 0.007$ $n = 24$	■												
TH	$\rho = 0.396$ $p < 0.001$ $n = 374$	$\rho = 0.397$ $p < 0.001$ $n = 374$	$\rho = 0.282$ $p < 0.001$ $n = 374$	$\rho = 0.160$ $p = 0.002$ $n = 374$	$\rho = 0.203$ $p < 0.001$ $n = 374$	Not sign.	$\rho = 0.108$ $p = 0.037$ $n = 374$	$\rho = 0.482$ $p < 0.001$ $n = 374$	$\rho = 0.381$ $p < 0.001$ $n = 374$	■											
DBH	Not sign.	Not sign.	$\rho = -0.195$ $p < 0.001$ $n = 374$	Not sign.	Not sign.	$\rho = 0.111$ $p = 0.032$ $n = 374$	Not sign.	Not sign.	Not sign.	$\rho = 0.433$ $p < 0.001$ $n = 374$	■										
LBH	$\rho = 0.294$ $p < 0.001$ $n = 372$	$\rho = 0.469$ $p < 0.001$ $n = 372$	$\rho = 0.267$ $p < 0.00$ $n = 372$	Not sign.	$\rho = 0.301$ $p < 0.001$ $n = 372$	Not sign.	Not sign.	$\rho = 0.364$ $p < 0.001$ $n = 372$	$\rho = 0.275$ $p < 0.001$ $n = 372$	$\rho = 0.611$ $p < 0.001$ $n = 372$	Not sign.	■									
CWN	$\rho = -0.209$ $p < 0.001$ $n = 374$	Not sign.	$\rho = -0.174$ $p = 0.001$ $n = 374$	Not sign.	Not sign.	$\rho = 0.105$ $p = 0.041$ $n = 374$	$\rho = -0.201$ $p < 0.001$ $n = 374$	$\rho = -0.151$ $p = 0.003$ $n = 374$	$\rho = -0.210$ $p < 0.001$ $n = 374$	$\rho = 0.181$ $p < 0.001$ $n = 374$	$\rho = 0.364$ $p < 0.001$ $n = 374$	Not sign.	■								
CWS	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = -0.109$ $p = 0.034$ $n = 374$	Not sign.	Not sign.	$\rho = 0.259$ $p < 0.001$ $n = 374$	$\rho = 0.345$ $p < 0.001$ $n = 374$	Not sign.	Not sign.	■							

	#trees	**#ftrees**	**#strees**	**#vines**	**%ftrees**	**%frtrees**	**Alt**	**CanCov**	**Water**	**TH**	**DBH**	**LBH**	**CWN**	**CWS**	**CWE**	**CWW**	**CH**	**T_{day}**	**T_{night}**	**L_{day}**	**L_{night}**
CWE	$\rho = -0.120$ $p = 0.020$ $n = 373$	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = -0.150$ $p = 0.004$ $n = 373$	Not sign.	Not sign.	Not sign.	$\rho = 0.248$ $p < 0.001$ $n = 373$	$\rho = -0.11$ $p = 0.035$ $n = 373$	$\rho = 0.311$ $p < 0.001$ $n = 373$	$\rho = 0.358$ $p < 0.001$ $n = 373$							
CWW	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = -0.129$ $p = 0.013$ $n = 374$	$\rho = -0.193$ $p = 0.004$ $n = 374$	Not sign.	Not sign.	$\rho = 0.301$ $p < 0.001$ $n = 374$	$\rho = 0.316$ $p < 0.001$ $n = 374$	$\rho = 0.118$ $p = 0.023$ $n = 372$	$\rho = 0.356$ $p < 0.001$ $n = 374$	$\rho = 0.293$ $p < 0.001$ $n = 374$	$\rho = 0.179$ $p = 0.001$ $n = 373$						
CH	$\rho = 0.223$ $p < 0.001$ $n = 373$	$\rho = 0.115$ $p = 0.027$ $n = 373$	$\rho = 0.103$ $p = 0.047$ $n = 373$	$\rho = 0.134$ $p = 0.009$ $n = 373$	Not sign.	Not sign.	$\rho = 0.110$ $p = 0.034$ $n = 373$	$\rho = 0.281$ $p < 0.001$ $n = 373$	$\rho = 0.180$ $p < 0.001$ $n = 373$	$\rho = 0.750$ $p < 0.001$ $n = 373$	$\rho = 0.509$ $p < 0.001$ $n = 373$	Not sign.	$\rho = 0.213$ $p < 0.001$ $n = 373$	$\rho = 0.298$ $p < 0.001$ $n = 373$	$\rho = 0.206$ $p < 0.001$ $n = 372$	$\rho = 0.286$ $p < 0.001$ $n = 373$					
T_{day}	Not sign.	Not sign.	Not sign.	$\rho = -0.732$ $p = 0.007$ $n = 12$	Not sign.	Not sign.	$\rho = -0.622$ $p = 0.031$ $n = 12$	$\rho = -0.608$ $p = 0.036$ $n = 12$	Not sign.	$\rho = -0.46$ $p < 0.001$ $n = 169$	Not sign.	$\rho = -0.46$ $p < 0.001$ $n = 168$	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.				
T_{night}	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = -0.783$ $p = 0.003$ $n = 12$	Not sign.	Not sign.	$\rho = -0.29$ $p < 0.001$ $n = 169$	Not sign.	$\rho = -0.31$ $p < 0.001$ $n = 168$	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = 0.519$ $p = 0.002$ $n = 34$			
L_{day}	Not sign.	Not sign.	$\rho = -0.641$ $p = 0.025$ $n = 12$	$\rho = 0.746$ $p = 0.005$ $n = 12$	Not sign.	Not sign.	Not sign.	$\rho = -0.671$ $p = 0.017$ $n = 12$	Not sign.	$\rho = -0.23$ $p = 0.003$ $n = 169$	Not sign.	$\rho = -0.33$ $p < 0.001$ $n = 168$	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = 0.532$ $p = 0.001$ $n = 34$	Not sign.		
L_{night}	$\rho = -0.692$ $p = 0.013$ $n = 12$	$\rho = -0.621$ $p = 0.031$ $n = 12$	$\rho = -0.585$ $p = 0.046$ $n = 12$	$\rho = 0.732$ $p = 0.007$ $n = 12$	Not sign.	Not sign.	Not sign.	$\rho = -0.762$ $p = 0.004$ $n = 12$	Not sign.	$\rho = -0.42$ $p < 0.001$ $n = 169$	Not sign.	$\rho = -0.49$ $p < 0.001$ $n = 168$	Not sign.	Not sign.	Not sign.	Not sign.	Not sign.	$\rho = 0.486$ $p = 0.004$ $n = 34$	Not sign.	$\rho = 0.889$ $p < 0.001$ $n = 34$	

APPENDIX 6.1

Input parameters for the *Ardipithecus ramidus* landscape use model of Chapter 6

The input parameters for the *Ardipithecus ramidus* landscape use model presented in Chapter 6 are outlined in Table A6.1.1 below. The table details the baseline parameter values, the source of the parameter values, and which parameters were included for the sensitivity analysis. Parameter values were selected based upon empirical data, or based on general knowledge considerations. Appendix 6.5 outlines the rationale behind the specified input parameter values.

Table A6.1.1. Model parameters for the *Ardipithecus ramidus* landscape use model presented in Chapter 6. 'Data source' indicates whether a parameter value is based upon empirical data or general knowledge-based considerations, 'Output' indicates that a parameter value was selected to produce model output, 'Sensitivity analysis' indicates whether a parameter was used to assess the model's robustness, 'F' stands for dense forests, 'M' for forest mosaics, and 'S' for savannah environments. When a parameter value is specified as, for example, 0 – 21, this indicates that a random value was chosen between 0 and 21 at the onset of each model run for each individual or patch as appropriate.

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
home range size	36km2	Empirical data	No
patch size	50mx50m	General knowledge	No
% forest cover	80% (F), 45% (M), 10% (S)	Empirical data	No
% woodland cover	10% (F), 40% (M), 55%(S)	Empirical data	No
% savannah cover	10% (F), 15% (M), 35%(S)	Empirical data	No
fragmentation	0.05	General knowledge	No
temperature	25	General knowledge	No
rainfall	0	General knowledge	No
tree height forest	10 - 50m	Empirical data	No
tree height woodland	8 - 20m	Empirical data	No
tree height savannah	3 - 15m	Empirical data	No
canopy cover forest	75 – 100%	Empirical data	No
canopy cover woodland	25 – 75%	Empirical data	No
canopy cover savannah	0 – 25%	Empirical data	No
canopy connectivity forest	75 – 100%	Empirical data	No
canopy connectivity woodland	25 – 75%	Empirical data	No
canopy connectivity savannah	0 – 25%	Empirical data	No
understory density forest	0 – 25%	Empirical data	No
understory density woodland	25 – 75%	Empirical data	No
understory density savannah	75 – 100%	Empirical data	No
tree density forest	75 – 100%	Empirical data	No
tree density woodland	25 – 75%	Empirical data	No
tree density savannah	0 – 25%	Empirical data	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
food tree density forest	75 – 100%	Empirical data	No
food tree density woodland	25 – 75%	Empirical data	No
food tree density savannah	0 – 25%	Empirical data	No
number of fruit forest	0 - 21	General knowledge	Yes
number of fruit woodland	0 - 14	General knowledge	Yes
number of fruit savannah	0 - 7	General knowledge	Yes
amount USOs forest	0 - 7	General knowledge	Yes
amount USOs woodland	0 - 14	General knowledge	Yes
amount USOs savannah	0 - 21	General knowledge	Yes
amount of water forest	0 - 100	General knowledge	Yes
amount of water woodland	0 - 75	General knowledge	Yes
amount of water savannah	0 - 50	General knowledge	Yes
temperature-day forest	0 – 25 (scaled)	Empirical data	No
temperature-day woodland	25 – 75 (scaled)	Empirical data	No
temperature-day savannah	75 – 100 (scaled)	Empirical data	No
temperature-night forest	75 – 100 (scaled)	Empirical data	No
temperature-night woodland	25 – 75 (scaled)	Empirical data	No
temperature-night savannah	0 – 25 (scaled)	Empirical data	No
luminosity-day forest	0 – 25 (scaled)	Empirical data	No
luminosity-day woodland	25 – 75 (scaled)	Empirical data	No
luminosity-day savannah	75 – 100 (scaled)	Empirical data	No
luminosity-night forest	0 – 25 (scaled)	Empirical data	No
luminosity-night woodland	0 – 25 (scaled)	Empirical data	No
luminosity-night savannah	0 – 25 (scaled)	Empirical data	No
number of *Ardipithecus*	60	Empirical data	No
where - canopy cover criterion	>0%	Empirical data	No
where - canopy connectivity criterion	>0%	Empirical data	No
where - understory density criterion	≤50%	General knowledge	Yes
where - tree density criterion	≥50%	General knowledge	Yes
where - food tree density criterion	≥50%	General knowledge	Yes
where - tree height criterion	≥1m	Empirical data	No
where - local temperature criterion	≤50 (scaled)	General knowledge	Yes
where - local luminosity criterion	≤50 (scaled)	General knowledge	Yes
where - understory feeding criterion	≥50 (scaled)	General knowledge	Yes
where - temperature feeding criterion	≤ 81.25 (scaled)	General knowledge	Yes
where - luminosity feeding criterion	≤ 81.25 (scaled)	General knowledge	Yes
where - number of fruits	3.5 fruits	General knowledge	No
where - amount USOs	3.5 USOs	General knowledge	No
where - amount water	50 hydrations	General knowledge	No
where - feeding fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	Empirical data	No
where - feeding USOs	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	General knowledge	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
where -drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Empirical data	No
where - nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Empirical data	No
where - resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Empirical data	No
where - travel	None	General knowledge	No
when - feeding criterion	energy <= 144, and energy < hydration	General knowledge	Yes
when - drinking criterion	hydration <= 72, and hydration < energy	General knowledge	Yes
when - resting criterion	fatigue >= 73	General knowledge	Yes
when - nesting criterion	time > 72 steps	Empirical data	No
when - temperature criterion	temperature > 29	Empirical data	No
when - rainfall criterion	rainfall > 25	Empirical data	No
Initial - energy	0 – 10kCal	General knowledge	Yes
Initial - hydration	0 – 10 hydrations	General knowledge	Yes
Initial - fatigue	0 – 10 fatigues	General knowledge	Yes
Step - energy	-2kCal	General knowledge	Yes
Step - hydration	-1 hydrations	General knowledge	Yes
Step - fatigue	+1 fatigues	General knowledge	Yes
Feeding fruit - energy	+10.85kCal 3.1kCal per gram	Empirical data	No
Feeding fruit - energy per fruit	3.1kCal (per gram)	Empirical data	No
Feeding fruit - number fruits eaten	3.5 fruits	General knowledge	Yes
Feeding USOs - energy	+7.49kCal 2.14kCal per gram	Empirical data	No
Feeding USOs - energy per USO	2.14kCal per gram	Empirical data	No
Feeding USOs - amount USOs eaten	3.5 USOs	General knowledge	Yes
Drinking - hydration	50 hydrations	General knowledge	No
Drinking - amount water drunk	50 hydrations	General knowledge	Yes
Resting - fatigue	-2 fatigues	General knowledge	Yes
Nesting - fatigue	-2 fatigues	General knowledge	Yes
Travel - energy	3.2kCal per 50m	Empirical data	No
Travel - hydration	-0.9 hydrations for every extra 50m	General knowledge	Yes
Travel - fatigue	+0.9 fatigues for every extra 50m	General knowledge	Yes
Travel - daily path length	50m per patch travelled	Empirical data	No
Travel - number of patches	in order: 0, 1, 2, 3 - 6 (jump)	General knowledge	No
Feed-fruit-forest	+1 for every step in this activity/veg type	Output	No
Feed-fruit-woodland	+1 for every step in this activity/veg type	Output	No
Feed-fruit-savannah	+1 for every step in this activity/veg type	Output	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
Feed-USOs-forest	+1 for every step in this activity/veg type	Output	No
Feed-USOs-woodland	+1 for every step in this activity/veg type	Output	No
Feed-USOs-savannah	+1 for every step in this activity/veg type	Output	No
Drink-forest	+1 for every step in this activity/veg type	Output	No
Drink-woodland	+1 for every step in this activity/veg type	Output	No
Drink-savannah	+1 for every step in this activity/veg type	Output	No
Rest-forest	+1 for every step in this activity/veg type	Output	No
Rest-woodland	+1 for every step in this activity/veg type	Output	No
Rest-savannah	+1 for every step in this activity/veg type	Output	No
Nest-forest	+1 for every step in this activity/veg type	Output	No
Nest-woodland	+1 for every step in this activity/veg type	Output	No
Nest-savannah	+1 for every step in this activity/veg type	Output	No
Travel-forest	+1 for every step in this activity/veg type	Output	No
Travel-woodland	+1 for every step in this activity/veg type	Output	No
Travel-savannah	+1 for every step in this activity/veg type	Output	No
Daily-path-length	+50m for every patch travelled	Output	No
Energy	variable depending on behaviour	Output	No
Hydration	variable depending on behaviour	Output	No
Fatigue	variable depending on behaviour	Output	No
Fruit intake	+3.5 for each time step feeding fruit	Output	No
USO intake	+3.5 for each time step feeding USOs	Output	No
Water intake	+50 for each time step drinking	Output	No
Current activity	variable depending on behaviour	Output	No
Tick	1 per time step	Output	No

APPENDIX 6.2

Model code of the *Ardipithecus ramidus* landscape use model of Chapter 6

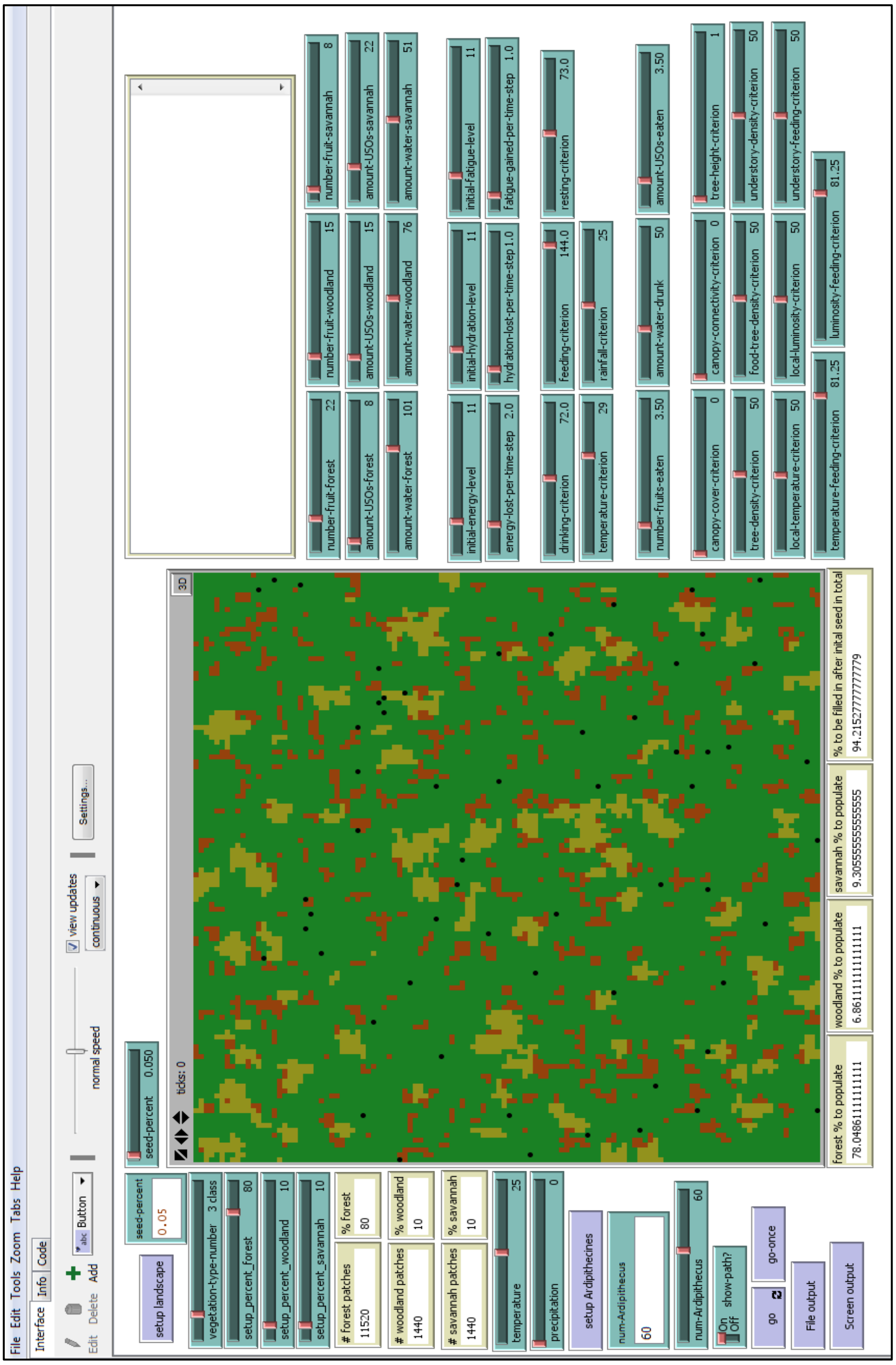
The code of the individual-based model on *Ardipithecus* landscape use presented in Chapter 6 can be accessed online using the specifics outlined below. The *Ardipithecus* model was created using NetLogo software (version 5.2.1; Willensky 1999) and was adapted from the generic chimpanzee landscape use model presented in Chapter 4 to suit the behaviour, characteristics and habitats of *Ardipithecus ramidus*. Exact adaptations to create the *Ardipithecus* model from the generic chimpanzee model are outlined in Appendix 6.4. Within the model code online, italics denote code explanations. The rationale behind the model code, development and design is outlined in Appendix 6.5.

Webpage: http://kellyvanleeuwen.com/thesis/
Username: klvanleeuwen
Password: please contact the author

APPENDIX 6.3

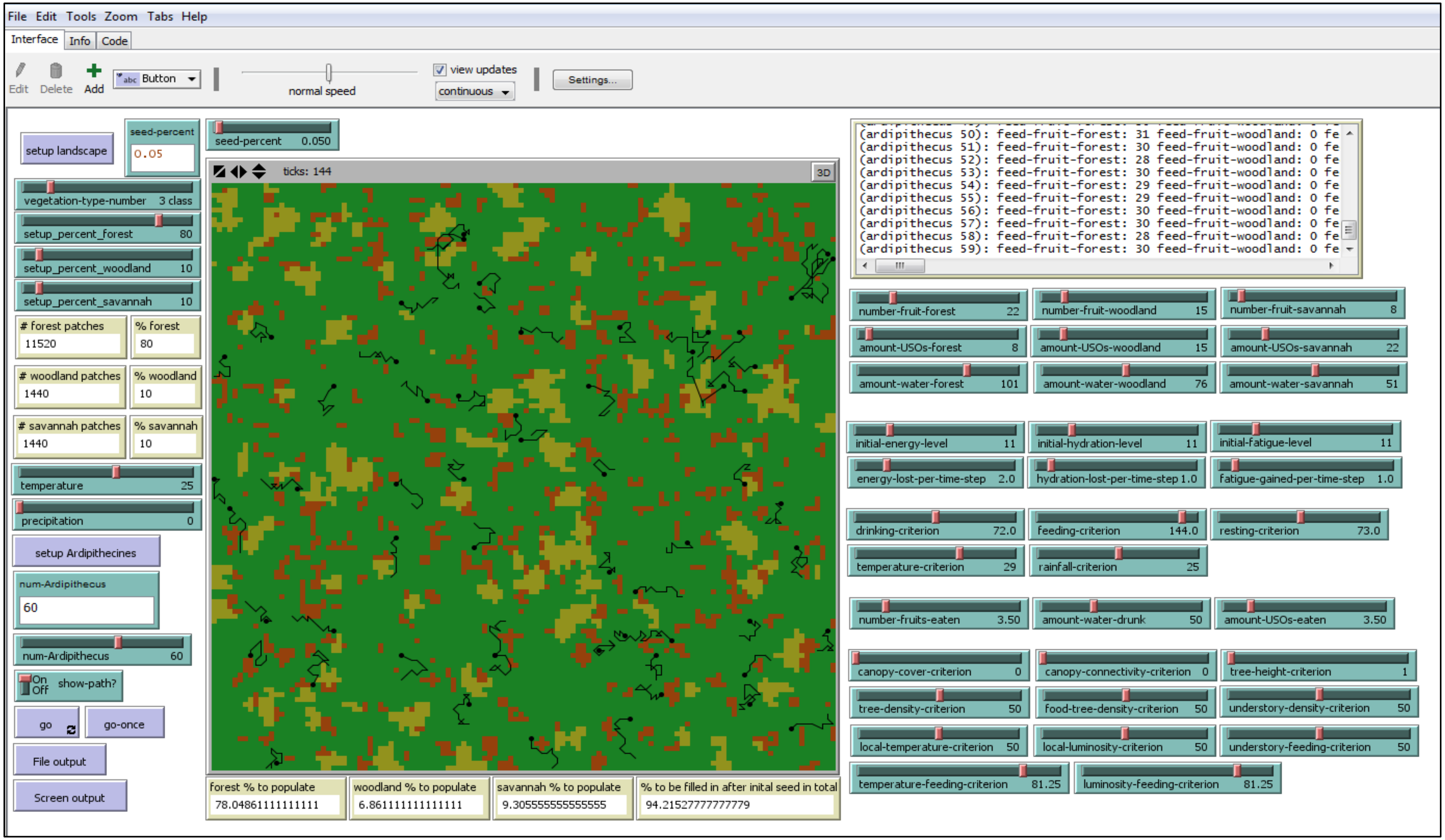
Model interface of the *Ardipithecus ramidus* landscape use model of Chapter 6

Figure A6.3.1 and A6.3.2 outline the interface of the *Ardipithecus ramidus* landscape use model presented in Chapter 6. Whereas the former figure presents the model at the onset of a model run, the latter figure presents the model interface after a model run. The rationales behind specific model parameter settings on the interface tab are outlined in Appendix 6.5.



seed-percent 0.05
seed-percent 0.050
vegetation-type-number 3 class
setup_percent_forest 80
setup_percent_woodland 10
setup_percent_savannah 10
% forest 80
# forest patches 11520
% woodland 10
# woodland patches 1440
% savannah 10
# savannah patches 1440
temperature 25
precipitation 0
num-Ardipithecus 60
num-Ardipithecus 60
show-path? On Off
ticks: 0
forest % to populate 78.0486111111111
woodland % to populate 6.86111111111111
savannah % to populate 9.30555555555555
% to be filled in after inital seed in total 94.2152777777779
number-fruit-forest 22
number-fruit-woodland 15
number-fruit-savannah 8
amount-USOs-forest 8
amount-USOs-woodland 15
amount-USOs-savannah 22
amount-water-forest 101
amount-water-woodland 76
amount-water-savannah 51
initial-energy-level 11
initial-hydration-level 11
initial-fatigue-level 11
energy-lost-per-time-step 2.0
hydration-lost-per-time-step 1.0
fatigue-gained-per-time-step 1.0
drinking-criterion 72.0
feeding-criterion 144.0
resting-criterion 73.0
temperature-criterion 29
rainfall-criterion 25
number-fruits-eaten 3.50
amount-water-drunk 50
amount-USOs-eaten 3.50
canopy-cover-criterion 0
canopy-connectivity-criterion 0
tree-height-criterion 1
tree-density-criterion 50
food-tree-density-criterion 50
understory-density-criterion 50
local-temperature-criterion 50
local-luminosity-criterion 50
understory-feeding-criterion 50
temperature-feeding-criterion 81.25
luminosity-feeding-criterion 81.25

Figure A6.3.1. Model interface of the *Ardipithecus* model at the onset of a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).



seed-percent 0.05

seed-percent 0.050

vegetation-type-number 3 class

setup_percent_forest 80

setup_percent_woodland 10

setup_percent_savannah 10

forest patches 11520

% forest 80

woodland patches 1440

% woodland 10

savannah patches 1440

% savannah 10

temperature 25

precipitation 0

num-Ardipithecus 60

num-Ardipithecus 60

On Off show-path?

forest % to populate 78.0486111111111

woodland % to populate 6.861111111111111

savannah % to populate 9.305555555555555

% to be filled in after inital seed in total 94.21527777777779

```
(ardipithecus 51): feed-fruit-forest: 30 feed-fruit-woodland: 0 fe
(ardipithecus 52): feed-fruit-forest: 28 feed-fruit-woodland: 0 fe
(ardipithecus 53): feed-fruit-forest: 30 feed-fruit-woodland: 0 fe
(ardipithecus 54): feed-fruit-forest: 29 feed-fruit-woodland: 0 fe
(ardipithecus 55): feed-fruit-forest: 29 feed-fruit-woodland: 0 fe
(ardipithecus 56): feed-fruit-forest: 30 feed-fruit-woodland: 0 fe
(ardipithecus 57): feed-fruit-forest: 30 feed-fruit-woodland: 0 fe
(ardipithecus 58): feed-fruit-forest: 28 feed-fruit-woodland: 0 fe
(ardipithecus 59): feed-fruit-forest: 30 feed-fruit-woodland: 0 fe
```

number-fruit-forest 22

number-fruit-woodland 15

number-fruit-savannah 8

amount-USOs-forest 8

amount-USOs-woodland 15

amount-USOs-savannah 22

amount-water-forest 101

amount-water-woodland 76

amount-water-savannah 51

initial-energy-level 11

initial-hydration-level 11

initial-fatigue-level 11

energy-lost-per-time-step 2.0

hydration-lost-per-time-step 1.0

fatigue-gained-per-time-step 1.0

drinking-criterion 72.0

feeding-criterion 144.0

resting-criterion 73.0

temperature-criterion 29

rainfall-criterion 25

number-fruits-eaten 3.50

amount-water-drunk 50

amount-USOs-eaten 3.50

canopy-cover-criterion 0

canopy-connectivity-criterion 0

tree-height-criterion 1

tree-density-criterion 50

food-tree-density-criterion 50

understory-density-criterion 50

local-temperature-criterion 50

local-luminosity-criterion 50

understory-feeding-criterion 50

temperature-feeding-criterion 81.25

luminosity-feeding-criterion 81.25

Figure A6.3.2. Model interface of the *Ardipithecus* model after a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).

APPENDIX 6.4

Model code adaptations to create the *Ardipithecus* model of Chapter 6 from the chimpanzee model of Chapter 4

To create the *Ardipithecus ramidus* landscape use model presented in Chapter 6, the generic chimpanzee landscape use model of Chapter 4 was adapted to suit the behaviour, habitat and characteristics of early hominins. Table A6.4.1 outlines the specific model code adaptations to create the *Ardipithecus* model from the generic chimpanzee model. See Appendix 6.5 for the rationale behind the model code.

Table A6.4.1. Model code adaptations to create the *Ardipithecus ramidus* landscape use model of Chapter 6 from the generic chimpanzee landscape use model presented in Chapter 4. The 'Data source' column highlights the source of the *Ardipithecus* model code or adaptation. The rationale behind model rules is outlined in Appendix 6.5.

Parameter	**Generic model (Ch4)**	***Ardipithecus* model (Ch6)**	**Data source**
Global			
Model size/ Home range	36km^2	36km^2	Chimpanzee data (Ch4)
Patch size	50m x 50m 120 x 120 patches	50m x 50m 120 x 120 patches	Chimpanzee data (Ch4)
Model run (time)	24 hours	24 hours	Chimpanzee data (Ch4)
Time step (time)	10 minutes	10 minutes	Chimpanzee data (Ch4)
Landscape			
Vegetation types	3	3	Chimpanzee data (Ch4)
Vegetation cover	Dense forest: Forest (F) = 80%, woodland (W) = 10%, savannah grassland (S) = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	Dense forest: Forest (F) = 80%, woodland (W) = 10%, savannah grassland (S) = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	Chimpanzee data (Ch4)
Fragmentation	0.05	0.05	Chimpanzee data (Ch4)
Temperature	25^{0}C	25^{0}C	Chimpanzee data (Ch4)
Precipitation	0mm	0mm	Chimpanzee data (Ch4)
GIS map or random	Random	Random	Chimpanzee data (Ch4)
Vegetation features			
• Tree height	F: 10-50m; W: 8-20m; G: 3-15m.	F: 10-50m; W: 8-20m; G: 3-15m.	Chimpanzee data (Ch4)
• Canopy cover	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Canopy connectivity	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Understory density	F: 0-25%; W: 25-75%, G: 75-100%.	F: 0-25%; W: 25-75%, G: 75-100%.	Chimpanzee data (Ch4)
• Tree density	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Food tree density	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Number fruit	F: 0-21; W: 0-14; G: 0-7.	F: 0-21; W: 0-14; G: 0-7.	Chimpanzee data (Ch4)
• Amount water	F: 0-100; W: 0-75; G: 0-50.	F: 0-100; W: 0-75; G: 0-50.	Chimpanzee data (Ch4)
• Amount USOs	-	F: 0-7, W: 0-14, S: 0-21	Hominin literature data and assumptions

Parameter	**Generic model (Ch4)**	***Ardipithecus* model (Ch6)**	**Data source**
Micro-climate characteristics			
• Temperature (day)	F: 0-25, W: 25-75; G: 75-100.	F: 0-25, W: 25-75; G: 75-100.	Chimpanzee data (Ch4)
• Temperature (night)	F: 75-100; W: 25-75; G: 0-25.	F: 75-100; W: 25-75; G: 0-25.	Chimpanzee data (Ch4)
• Luminosity (day)	F: 0-25, W: 25-75; G: 75-100.	F: 0-25, W: 25-75; G: 75-100.	Chimpanzee data (Ch4)
• Luminosity (night)	F: 0 -25; W: 0-25, G: 0-25.	F: 0 -25; W: 0-25, G: 0-25.	Chimpanzee data (Ch4)
Chimpanzees/ Ardipithecus			
Community size	60	60	Chimpanzee data (Ch4)
Internal states	3	3	Chimpanzee data (Ch4)
Behaviour			
Feeding	√	√	Chimpanzee data (Ch4)
Drinking	√	√	Chimpanzee data (Ch4)
Nesting	√	√	Chimpanzee data (Ch4)
Resting	√	√	Chimpanzee data (Ch4)
Travel	√	√	Chimpanzee data (Ch4)
Where			
• Feeding-fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	Hominin literature data and assumptions.
• Feeding-USOs	-	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	Hominin literature data and assumptions.
• Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Chimpanzee data (Ch4)
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Chimpanzee data (Ch4)
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Chimpanzee data (Ch4)
• Travel	-	-	Chimpanzee data (Ch4)
• Relative importance	-	-	Chimpanzee data (Ch4)
When			
• Feeding	Energy ≤ 144 and energy < hydration.	Energy ≤ 144 and energy < hydration.	Chimpanzee data (Ch4)
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Hydration ≤ 72 and hydration ≤ energy.	Chimpanzee data (Ch4)

Parameter	**Generic model (Ch4)**	***Ardipithecus* model (Ch6)**	**Data source**
• Nesting	Time steps > 72.	Time steps > 72.	Chimpanzee data (Ch4)
• Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Chimpanzee data (Ch4)
• Travel	-	-	Chimpanzee data (Ch4)
How much			
• Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Chimpanzee data (Ch4)
• Existing	Energy: -2; hydration: -1; fatigue: +1.	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Chimpanzee data (Ch4)
• Feeding-fruit	Energy: +10.85kCal (3.1kCal per fruit)	Energy: +10.85kCal (3.1kCal per fruit)	Chimpanzee data (Ch4)
• Feeding-USOs	-	Energy: + 7.49kCal (2.14kCal per USO)	Hominin literature data and calculations
• Drinking	Hydration + 50	Hydration + 50	Chimpanzee data (Ch4)
• Nesting	Fatigue: -2	Fatigue: -2	Chimpanzee data (Ch4)
• Resting	Fatigue: -2	Fatigue: -2	Chimpanzee data (Ch4)
• Travel	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	Energy: - 3.2kCal per 50m. Travelling more than 50m: lose 0.9 extra hydrations and gain 0.9 extra fatigues for every extra 50m travelled.	Calculations based on Ch4 in combination with findings of Pontzer et al. (2009).
Output			
Feeding-fruit	-	+1 for each time step spent feeding on fruit.	-
Feeding-USOs	-	+1 for each time step spent feeding on USOs.	-
Drinking	+1 for each time step spent drinking.	+1 for each time step spent drinking.	Chimpanzee data (Ch4)
Nesting	+1 for each time step spent resting.	+1 for each time step spent resting.	Chimpanzee data (Ch4)
Resting	+1 for each time step spent nesting.	+1 for each time step spent nesting.	Chimpanzee data (Ch4)
Travel	+1 for each time step spent travelling.	+1 for each time step spent travelling.	Chimpanzee data (Ch4)
Forest	+1 for each time step spent in forest.	+1 for each time step spent in forest.	Chimpanzee data (Ch4)
Woodland	+1 for each time step spent in woodland.	+1 for each time step spent in woodland.	Chimpanzee data (Ch4)
Savannah	+1 for each time step spent in savannah.	+1 for each time step spent in savannah.	Chimpanzee data (Ch4)
Feed-fruit-forest	-	+1 for each time step spent on feeding on fruit in forest.	-
Feed-fruit-woodland	-	+1 for each time step spent on feeding on fruit in woodland.	-
Feed-fruit-savannah	-	+1 for each time step spent on feeding on fruit in savannah.	-
Feed-USOs-forest	-	+1 for each time step spent on feeding on USOs in forest.	-
Feed-USOs-woodland	-	+1 for each time step spent on feeding on USOs in woodland.	-
Feed-USOs-savannah	-	+1 for each time step spent on feeding on USOs in savannah.	-
Drink-forest	+1 for each time step spent on drinking in forest.	+1 for each time step spent on drinking in forest.	Chimpanzee data (Ch4)
Drink-woodland	+1 for each time step spent on drinking in woodland.	+1 for each time step spent on drinking in woodland.	Chimpanzee data (Ch4)

Parameter	**Generic model (Ch4)**	***Ardipithecus* model (Ch6)**	**Data source**
Drink-savannah	+1 for each time step spent on drinking in savannah.	+1 for each time step spent on drinking in savannah.	Chimpanzee data (Ch4)
Nest-forest	+1 for each time step spent on nesting in forest.	+1 for each time step spent on nesting in forest.	Chimpanzee data (Ch4)
Nest-woodland	+1 for each time step spent on nesting in woodland.	+1 for each time step spent on nesting in woodland.	Chimpanzee data (Ch4)
Nest-savannah	+1 for each time step spent on nesting in savannah.	+1 for each time step spent on nesting in savannah.	Chimpanzee data (Ch4)
Rest-forest	+1 for each time step spent on resting in forest.	+1 for each time step spent on resting in forest.	Chimpanzee data (Ch4)
Rest-woodland	+1 for each time step spent on resting in woodland.	+1 for each time step spent on resting in woodland.	Chimpanzee data (Ch4)
Rest-savannah	+1 for each time step spent on resting in savannah.	+1 for each time step spent on resting in savannah.	Chimpanzee data (Ch4)
Travel-forest	+1 for each time step spent on travelling in forest.	+1 for each time step spent on travelling in forest.	Chimpanzee data (Ch4)
Travel-woodland	+1 for each time step spent on travelling in woodland.	+1 for each time step spent on travelling in woodland.	Chimpanzee data (Ch4)
Travel-savannah	+1 for each time step spent on travelling in savannah.	+1 for each time step spent on travelling in savannah.	Chimpanzee data (Ch4)
Daily path length	+50m for each patch travelled.	+50m for each patch travelled.	Chimpanzee data (Ch4)
Energy	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Hydration	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Fatigue	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Fruit intake	+ 3.5 for each feeding bout feeding on fruit.	+ 3.5 for each feeding bout feeding on fruit.	Chimpanzee data (Ch4)
USO intake	-	+ 3.5 for each feeding bout feeding on USOs.	Hominin literature and assumptions.
Water intake	+ 50 for each drinking bout.	+ 50 for each drinking bout.	Chimpanzee data (Ch4)
Chimp/ *Ardipithecus* land use	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)
Chimp/ *Ardipithecus* activity	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)
Chimp/ *Ardipithecus* site selection	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)

APPENDIX 6.5

Model code rationale of the *Ardipithecus ramidus* landscape use model (Chapter 6)

Table A6.5.1 presents the rationale behind the model code, decisions and design of the *Ardipithecus ramidus* landscape use model outlined in Chapter 6. As the model was adapted from the generic chimpanzee landscape use model presented in Chapter 4, model codes are either based on published hominin literature on *Ardipithecus ramidus*, or follow the rationale of the generic model (Appendix 4.5).

Table A6.5.1. Rationale behind model code, decisions and design for the *Ardipithecus ramidus* landscape use model presented in Chapter 6.

Parameter	**Value**	**Justification**
Global		
Model size/ Home range	36km^2	As no data exists on early hominin home-ranges, it is assumed that home-range sizes are similar to those of chimpanzees (Chapter 6). In Chapter 4, the average home-range size for chimpanzee communities across sites was 36km^2.
Patch size	50m x 50m 120 x 120 patches	Similar to Ch4, a patch of 50m x 50 m is small enough to contain the necessary detail for each vegetation type, but not too small to affect processing power and difficulty.
Model run (time)	24 hours	As the model simulated daily activity budgets, path lengths, and vegetation type usage of *Ardipithecus ramidus*, a run of 24 hours was chosen, which is in line with the generic model of Ch4.
Time step (time)	10 minutes	Following Ch4, a time step of 10min is small enough to capture the necessary behavioural details, but not too small to affect processing power.
Landscape		
Overall landscapes	3	Descriptions of the environments at *Ardipithecus ramidus* fossil localities do not encompass the necessary detail to develop specific model environments, i.e. no data are given on the vegetation cover, spatial vegetation arrangement, temperature and rainfall at typical *Ardipithecus ramidus* sites (Chapter 6). This lack of available data also makes it difficult to assess how *Ardipithecus ramidus* landscapes fit with the environments outlined for chimpanzees in Chapter 3. However, when carefully reading the environmental reconstructions of *Ardipithecus ramidus* fossil localities (Chapter 6), some reconstructions indicate forested environments (which could be linked to typical chimpanzee FOREST landscapes), others imply open environments dominated by grassland (which could be linked to typical chimpanzee SAVANNAH landscapes), and again others point to woodland environments (which could be linked to either typical chimpanzee MOSAIC or SAVANNAH landscapes, depending on the coverage of other vegetation types). As such, it seems best to simulate *Ardipithecus ramidus* in all typical chimpanzee landscapes (i.e. FOREST, SAVANNAH, and MOSAIC), and investigate how differently or similarly they would have behaved given their species-specific behavioural rules. With regards to vegetation features and micro-climates, the given data for *Ardipithecus ramidus* are not based on actual reconstructions of paleoenvironments, but based on present-day measurements and classifications. As these have already been studied in detail for Chapter 3 (including much more,

Parameter	Value	Justification
		and partially overlapping, references, Chapter 6), the micro-climates presented in this chapter were used.
Landscape implementation	Random	As no data on the exact vegetation cover and spatial arrangement of *Ardipithecus ramidus* environments are known, landscapes are set up randomly with respect to the assumed vegetation coverage for each typical landscape as outlined in Ch4 for chimpanzees.
Vegetation types	3	As data for *Ardipithecus ramidus* include various different environments which do not allow efficient modelling, modelled vegetation types follow the rationale of chimpanzee landscapes outlined in Ch4: Results of Chapter 3 indicated that every chimpanzee study site contained the vegetation type forest (F). Furthermore, results showed that woodland (W) and savannah grassland (S) is available at each site classified as a savannah landscape. The presence of all other vegetation types is variable. It was therefore chosen to only use the three vegetation types above in order to be consistent.
Vegetation cover	Dense forest: F = 80%, W = 10%, S = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	Modelled *Ardipithecus ramidus* landscapes followed the rationale of chimpanzee landscapes outlined in Ch4: Forest cover is the main driver of landscape-based classifications of chimpanzees and their environments and therefore, the amount of forest cover was specified first, so that it nicely fits within the definitions outlined in Chapter 3 and is evenly spaced between landscapes. The remaining percentage of cover was then filled with woodland and savannah grassland in a way that is roughly similar to the woodland and grassland cover averages within the different environments.
Fragmentation	0.05	As no data exist on the fragmentation of *Ardipithecus ramidus* landscapes, fragmentation is kept equal to Ch4 and set to 0.05. This value is allocated randomly.
Temperature	25°C	As no data exist on the overall temperature of *Ardipithecus ramidus* landscapes, overall temperature is kept equal to Ch4 and set to 25°C. This nicely falls within the thermoneutral zone for chimpanzees (20 - 29°C). This value is allocated randomly.
Precipitation	0mm	Data on average rainfall of *Ardipithecus ramidus* landscapes remains absent, and precipitation is kept equal to Ch4 and set to 0mm, indicating that it was a 'dry' day and there was no interference of precipitation. This value is allocated randomly.
Vegetation features		Following the generic chimpanzee landscape use model of Ch4, only landscape-scale environmental variables that are assumed important for chimpanzee behaviours (and therefore also assumed important for early hominin behaviours) were included in the model: tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, amount food, and amount water. Other variables are not included because they are too small-scale and/or correlated with the other variables. Slope and altitude were not be included as there is no consistency between sites, which would impair the model rules.
• Tree height	F: 10-50m; W: 8-20m; S: 3-15m.	As no explicit data are presented for *Ardipithecus ramidus* environments, vegetation features followed the rationale outlined for the chimpanzee model of Ch4: Chapter 3 showed that current literature specified tree height as either high, medium or low in forest, woodland and savannah grassland, with the exact heights specified as high = 10-50m, medium = 8-20m, and low = 3-15m.
• Canopy cover	F: 75-100%; W: 25-75%, S: 0-25%.	Following Ch4 for *Ardipithecus ramidus* environments, canopy cover was specified as either high, medium or low for forest, woodland and grassland. Exact values are scaled to high being 75-100%, medium 25-75%, and low 0-25% of canopy cover. Values were allocated randomly.
• Canopy connectivity	F: 75-100%; W: 25-75%, S: 0-25%.	Similar to Ch4, for *Ardipithecus ramidus* environments, canopy connectivity was scaled to high (75-100%), medium (25-75%), or low (0-25%). Values were allocated randomly.
• Understory density	F: 0-25%; W: 25-	Understory density for *Ardipithecus ramidus* environments,

Parameter	Value	Justification
	75%, S: 75-100%.	followed the rationale outlined for the chimpanzee model of Ch4 and was specified (i.e. scaled) as either high (75-100%), medium (25-75%), or low (0-25%). Values were allocated randomly.
• Tree density	F: 75-100%; W: 25-75%, S: 0-25%.	As no explicit data are presented for *Ardipithecus ramidus* environments, tree density estimates followed the generic chimpanzee model of Ch4 and was outlined as either high (75 – 100%), medium (25 – 75%) or low (0-25%). Values were allocated randomly.
• Food tree density	F: 75-100%; W: 25-75%, S: 0-25%.	Food tree density for *Ardipithecus ramidus* environments followed the rationale outlined for the chimpanzee model of Ch4: Food tree density was specified as either high, medium or low, without exact percentages specified. It was therefore scaled for the model to 0-100%, with high being 75-100%, medium 25-75%, and low 0-25%. Values were allocated randomly.
• Number fruit	F: 0-21; W: 0-14; S: 0-7.	As no explicit data are presented for *Ardipithecus ramidus* environments, based on a knowledge-based assumption and similar to Ch4, forest was assumed to have more fruit than woodland, and woodland had more fruit than savannah. With respect to the amount of fruit eaten per time step (see below), it was specified that individuals could eat occasionally in savannah grasslands, sometimes in woodland, and regularly in forest. A maximum feeding time of 1 hour is assumed per patch, i.e. individuals could never eat more than six time steps in a row within the same patch.
• Amount water	F: 0-100; W: 0-75; S: 0-50.	Similar to Ch4, as no explicit data are presented for *Ardipithecus ramidus* environments, forest was assumed to have more water available than woodland, and woodland had more water than savannah, based on a general knowledge-based assumptions. With respect to the amount of water drunk per time step (see below), it was specified that individuals could rarely drink in savannah, occasionally in woodland, and sometimes in forest.
• Amount USOs	F: 0-7, W: 0-14, S: 0-21	For the distribution of USOs, it has been found that USOs were found regularly in savannah grassland, and occasionally in forest (Chapter 6). Woodland is assumed to be intermediate between these two vegetation types. As USOs are considered fallback foods, and with respect to the amount of USOs eaten each time step, it was assumed that the amount of USOs present are equally available to fruits at minimum. Numbers for amount USOs per vegetation type were therefore set as similar quantities as fruits, with respect to the assigned vegetation type and above info. Similar to feeding on fruit, the assumption is made that individuals can eat a maximum of one hour within a single patch.
Micro-climate characteristics		
Temperature (day)	F: 0-25, W: 25-75; S: 75-100.	As no explicit data are presented for *Ardipithecus ramidus* environments, micro-climates follow the rationale outlined for the chimpanzee model of Ch4: Chapter 3 showed that literature specified daytime temperature as either hot, medium, or cold, but no exact values have been specified. It was therefore scaled for the model to 0-100, with hot (i.e. high temperatures) being 75-100, medium 25-75, and cool (i.e. low temperatures) 0-25. Values were allocated randomly.
Temperature (night)	F: 75-100; W: 25-75; S: 0-25.	Nighttime temperature for *Ardipithecus ramidus* environments followed Ch4 and were scaled to hot (75-100), medium (25-75), and (cool 0-25). Values were allocated randomly.
Luminosity (day)	F: 0-25, W: 25-75; S: 75-100.	As no explicit data are presented for *Ardipithecus ramidus* environments, micro-climates follow the rationale outlined for the chimpanzee model of Ch4: Chapter 3 showed that current literature specified daytime luminosity as either high, medium, or low, but no exact values are specified. It was therefore scaled for the model to 0-100, with light being 75-100 (i.e. high luminosity), medium 25-75, and dark 0-25 (i.e. low luminosity). Values were allocated randomly.

Parameter	**Value**	**Justification**
Luminosity (night)	F: 0 -25; W: 0-25, S: 0-25.	Following Ch4, nighttime luminosity for *Ardipithecus ramidus* environments were scaled to light (75-100), medium (25-75), and dark (0-25). Values were allocated randomly.
Ardipithecines		
Community size	60	Australopithecines and chimpanzees have been assumed to have equal population sizes (Chapter 6). As *Ardipithecus ramidus* is in the middle between these two species, it can be assumed that this species would have a similar population size as well. Ch4 calculated average population size of chimpanzee communities across sites to 60 individuals. Individuals were placed randomly within the model environment at realistic nesting locations to start the day.
Internal states	3	Similar to Ch4, based on simplifications of general knowledge, it was decided that model behaviours were driven by internal states for energy, hydration, and fatigue.
Behaviour		
Feeding		Just as is the case for chimpanzees as outlined in Ch4, for *Ardipithecus ramidus* feeding is assumed to be an important daily behaviour, where energy can be gained.
Drinking		Following Ch4, for *Ardipithecus ramidus*, drinking should be included as an important behaviour to obtain water.
Nesting		For *Ardipithecus ramidus*, nesting should be included, as this is the only assumed nighttime behaviour (similar to Ch4).
Resting		Just as is the case for chimpanzees outlined in Ch4, for *Ardipithecus ramidus*, resting is assumed to be an important daily behaviour for chimpanzees, where fatigue can be lost. It can either be enforced due to, e.g., food processing and/or climatic conditions, or 'extra' which can be used for other activities such as social behaviours.
Travel		For *Ardipithecus ramidus*, following Ch4, travel is assumed to be an important daily behaviour, getting an individual from A to B. Travel is therefore often considered goal-directed. Energy and hydration are lost during travelling, and fatigue is gained.
Where		As no explicit data are presented for where *Ardipithecus ramidus* perform their daily activities, where-rules follow the rationale outlined for the chimpanzee model of Ch4: Results of Chapter 2 showed the important landscape-scale vegetation features and micro-climate characteristics for each modelled behaviour based on expert-based opinions.
• Feeding-fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	*Where* to feed on fruit is kept similar to chimpanzees, apart from temperature and luminosity. Similar locations to chimpanzees are expected, as *Ardipithecus ramidus* still prefers to eat fruit, and a combination of number-fruits, (food) tree density and tree height defines whether a patch is suitable for feeding. Following Ch4: As exact criteria of any of the important environmental variables remain absent, criteria are chosen randomly for the model, based on general knowledge assumptions: Individuals should feed where there is enough fruit, at least enough to last them one time step, i.e. 3.5 fruits (see below). Individuals should furthermore prefer locations with higher tree and food tree densities (high densities 50-100, low densities 0-50), taller trees (higher trees have larger DBHs and should contain more food, but also short trees can have food), and lower temperatures and luminosities (high temperature /light 50-100, low temperature /dark 0-50). Due to the increased thermoregulatory advantage (i.e. higher tolerance to open areas), bipedality, and the subsequently wider access to food sources, temperature and luminosity criteria are relaxed to include a part of the savannah patches as well (>75), but extreme conditions are still avoided (>87.5). To make a distinction between *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*, criteria for the

Parameter	Value	Justification
		former are set to ≤ 81.25.
• Feeding-USOs	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 81.25, and luminosity (day) ≤ 81.25.	Where to feed on USOs is based on a combination of amount USOs (i.e. at least enough to last them one time step) and understory density (similar to food tree density, a minimal amount of understory is needed to be able to feed on USOs, as tubers come from herbaceous plants), as well as temperature and luminosity. Similar to the above, due to the increased thermoregulatory advantage (i.e. higher tolerance to open areas) bipedality, and the subsequently wider access to food sources, temperature and luminosity criteria are relaxed to include a part of the savannah patches as well (>75), but extreme conditions are still avoided (>87.5). To make a distinction between *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*, criteria for the former are set to ≤ 81.25.
• Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	For drinking, no actual quantitative data have been specified to set out specific drinking rules for the *Ardipithecus ramidus* model. As *Ardipithecus ramidus* was equally water dependent as chimpanzees, it is likely that drinking patterns would have been similar as well. As such, it is considered best to leave the drinking rules as they are and specify that *Ardipithecus ramidus* loses the same amount of hydration as chimpanzees simply by existing at each time step, has a drinking *when*-criterion similar to that of chimpanzees, gains an equal amount of hydrations from drinking at each time step as chimpanzees, and selects similar drinking locations as chimpanzees. Following Ch4, results of Ch2 did not specify exact criteria of any of these environmental variables. Criteria were therefore chosen randomly for the model, based on general knowledge-based assumptions: Individuals should drink where there is enough water, at least enough to last them one time step, i.e. 50 hydrations. Individuals should furthermore prefer locations where it is not too hot or too light (high temperature /light 50-100, low temperature /dark 0-50). Even though *Ardipithecus ramidus* have a thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Similar sleeping, and thus nesting patterns, to chimpanzees are expected for *Ardipithecus ramidus*. As no further information has been specified, it is considered best to keep the nesting rules for the *Ardipithecus ramidus* model the same as the rules specified for the Ch4 chimpanzee model. This implies that, similar to chimpanzees, *Ardipithecus ramidus* would gain the same amount of fatigues simply by existing at each time step, would lose an equal amount of fatigue while nesting each time step, and would have similar *where*- and *when*-criteria for nesting. Following Ch4, results of Ch2 did specify exact criteria for tree height, canopy cover, and canopy connectivity for nesting, but did not specify exact criteria of any of the other environmental variables. The criteria set out for these variables for the model are therefore based on general knowledge-based assumptions: Individuals would prefer to nest at locations with high tree and food tree densities and low understory densities, at locations where there is enough food (i.e. more than 3.5 fruits) and water (i.e. more than 50 hydrations), and at locations where it is not too hot or too light. It should be noted that, even though *Ardipithecus ramidus* eats more than fruit and has been parameterised to also include USOs in its diet, nesting locations only assess the presence of fruits. This is because fruit is the preferred food source, and nesting locations are therefore selected to be in close proximity to their preferred food source. Additionally, only temperature/ luminosity day are included in selecting a location (as opposed to night). In this case, individuals select locations that are not too hot or light during daytime, with respect to nest building in the evening and leaving the nest in the morning. Even though *Ardipithecus ramidus* have a

Parameter	**Value**	**Justification**
		thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	As quantitative data on *Ardipithecus ramidus* resting patterns are lacking, it is considered best to keep resting patterns similar to the specified resting patterns for chimpanzees in Ch4 and also in line with the *Ardipithecus ramidus* nesting patterns. As such, similar to chimpanzees, *Ardipithecus ramidus* would gain the same amount of fatigues simply by existing at each time step, would lose an equal amount of fatigue while resting each time step, and would have similar *where*- and *when*-criteria for resting. Following Ch4, results of Ch2 did not specify exact criteria of any of the environmental variables important for resting. Criteria are therefore chosen randomly for the model, based on knowledge-based assumptions: Individuals would prefer to rest at cooler and shadier locations, and at locations with higher trees (use the same criterion as for nesting and feeding, as similar locations can be expected), higher canopy cover and connectivities (use the same criterion as for nesting as similar locations can be expected), lower understory densities and higher tree and food tree densities, and with enough fruit (i.e. more than 3.5 fruits) and water (i.e. more than 50 hydrations) available. It should be noted that, even though *Ardipithecus ramidus* eats more than fruit and has been parameterised to also include USOs in its diet, resting locations only assess the presence of fruits. This is because fruit is the preferred food source, and resting locations are therefore selected to be in close proximity to their preferred food source. Even though *Ardipithecus ramidus* have a thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Travel	-	Within the model, travel is assumed to be a goal-directed behaviour, based on findings from current literature on chimpanzees. No criteria are set as to where *Ardipithecus ramidus* can or cannot travel, as this would restrict individual decisions and enforce the model rules. Preferred vegetation features and micro-climate characteristics will follow from the model results. In this way, only the ‘goal activities’ will have strict ‘where-criteria’. Within the travel procedure, individuals will first check the vegetation features and micro-climate characteristics of their current patch and select this patch for their goal activity if the patch abides to all criteria. If not, individuals will subsequently look at its neighbouring patches within 50m for a suitable patch, will then look at its surrounding patches within 100m for a suitable patch, or will ‘jump’ a random 3 – 6 patches (150 – 300m) to start a search there. Based on findings from chimpanzees and the hominin model of Griffith et al. (2010), *Ardipithecus ramidus* is expected to ‘see’ a maximum of 100m in all directions, and is expected to travel a maximum of 300m within 10min following chimpanzee literature findings (Bates & Byrne 2009).
• Relative importance		Similar to Ch4, no relative importance is included within the model. Vegetation features or micro-climate characteristics are either important for a specific behaviour, or they are not. An individual investigates the most important variables first, but all important variables are still included.
When		As no explicit data are presented for when *Ardipithecus ramidus* perform their daily activities, when-rules follow the rationale outlined for the chimpanzee model of Ch4: Based on general knowledge assumptions, overall for the model, it is specified that individuals must first assess whether it is dark/night. In this case, the only option for individuals is to nest. During daytime, an individual must first decide whether the current weather conditions impair its daily activities. If so, an individual must rest. If not, it is expected that drinking is most important due to the importance of water, followed by feeding for gaining energy. This is

Parameter	Value	Justification
		however, relative, as an individual can be more hungry than thirsty, in which case it will feed. If no need for feeding or drinking, an individual can spend 'extra' time resting.
• Feeding	Energy ≤ 144 and energy < hydration.	Following the rationale of Ch4: An individual should feed when it is hungry (and more hungry than thirsty). The feeding criterion is based on random variables and the assumption that individuals would like to maintain a neutral energy balance: in total 288 energy will be lost during a model run (see below), 144 of which will be lost during nighttime nesting. As long as an individual keeps its energy above 144 during daytime, it will be prepared for nesting.
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Similar to Ch4: An individual should drink when it is thirsty (and more thirsty than hungry). The drinking criterion is based on random variables and the assumption that individuals would like to maintain a neutral hydration (i.e. water) balance: in total 144 hydration will be lost during a model run (see below), 72 of which will be lost during nighttime nesting. As long as an individual keeps its hydration above 72 during daytime, it will be prepared for nesting.
• Nesting	Time steps > 72.	Following Ch4: An individual should nest when it is dark (i.e. after 12 hours, and thus after 72 time steps of 10 minutes). Nesting is the only option at nighttime.
• Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Similar to Ch4: Individuals should rest when it is too wet and/or rains too hard (put at > 25mm, as this is generally considered as a wet day), when it is too hot (put at > 29°C, as temperatures above this value are outside the thermoneutral range for chimpanzees), when they are too tired (it could be assumed that individuals would like to maintain a neutral fatigue balance: in total 144 fatigues will be gained during a model run (see below), of which only 72 will be lost during nighttime nesting. As long as an individual keeps its fatigue below 72 during daytime, it will be prepared for nesting), or when there is nothing else to do.
• Travel	-	Following the rationale of Ch4: Travel is incorporated within the behavioural procedures of feeding, drinking, nesting and resting, and is goal directed. Individuals will choose to travel if their current patch is not suitable for their selected activity.
How much		
• Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	As no data are presented on initial energy, hydration, and fatigue levels for *Ardipithecus ramidus*, initial levels follow the rationale outlined in Ch4 for chimpanzees and were randomly set between 0 and 10, in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step. It is assumed that individuals start off their day with feeding and/or drinking, similar to chimpanzees (Chapter 2).
• Existing	Energy: -2; hydration: -1; fatigue: +1.	Following Ch4, *Ardipithecus ramidus* energy and hydration losses, and fatigue gains are randomly set at 1 or 2 in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step and no data exist to inform this study otherwise.
• Feeding-fruit	Energy: +10.85 kCal (3.1kCal per fruit)	Similar to Ch4, *Ardipithecus ramidus* fruit intake has been specified as follows: based on literature data for chimpanzees (Chapter 4), 1 gram of dry weight of fruits contains 3.1kCal of energy (including fig fruit and non-fig fruit). Hourly energy intake rates are not specified for chimpanzees (or *Ar. ramidus*). In reality, individuals would lose a lot of energy every 10 minutes due to mechanisms such as food processing. However, in order to keep the model simple and losses and gains in the same order of magnitude, it is assumed, after model calibration, that chimpanzees (and *Ar. ramidus*) would be able to gain at least 10.85 kCal of net energy each time step, i.e. eating 3.5 fruits (after calibration calculations). On average, it is assumed that a fruit contains between 70 – 95% water, the remainder is called dry weight. Even though this may seem

Parameter	**Value**	**Justification**
		a small energy gain per 10min (i.e. a limited amount of fruits eaten per time step), this is a simplification to keep all internal states gains and losses within a similar order of magnitude.
• Feeding-USOs	Energy: + 7.49kCal (2.14kCal per USO)	For USOs, it has been specified that 1 gram of edible dry weight tuber, contains 2.14kCal of energy. As USOs are fallback foods, similar intake rates to fruit can be expected, i.e. if an individual cannot obtain its 3.5 gram dry weight of fruit, it will be looking for 3.5 gram dry weight of another food source.
• Drinking	Hydration + 50	As no data are presented on hydration gains while drinking for *Ardipithecus ramidus*, hydration gains follow the rationale outlined in Ch4 for chimpanzees and specify that an individual can gain a lot of hydration during each drinking bout. This is based on the observation that chimpanzees do not spent a lot of time drinking each day.
• Nesting	Fatigue - 2	As no data are presented on fatigue loss while nesting for *Ardipithecus ramidus*, fatigue losses follow Ch4 and assume that individuals lose 1 fatigue each time step spent nesting.
• Resting	Fatigue – 2	Similar to Ch4, *Ardipithecus ramidus* fatigue losses are assumed to be 1 fatigue for each time step spent resting.
• Travel	Energy: - 3.2kCal per 50m. Travelling more than 50m: lose 0.9 extra hydrations and gain 0.9 extra fatigues for every extra 50m travelled.	For Ch4, chimpanzee energy and hydration loss, and fatigue gained through travel was calculated as follows: Based on an average daily path length of 3.0km and an average energy expenditure for travel of 207.3kCal/day, energy lost per 50m travelled equals about 3.5kCal. As chimpanzees can travel between 50 – 300m, energy loss due to travel is somewhere between -3.5kCal and -21kCal. For every extra 50m travelled (so when travelling between 100 – 300m) an additional hydration will be lost, and an extra fatigue will be gained, as an individual is travelling faster. Pontzer et al. (2009) specified human, chimpanzee, and *Australopithecus afarensis* walking costs to 0.08 O_2/kg/m, 0.17 O_2/kg/m, and 0.14 O_2/kg/m respectively. Even though this is not the same unit over measurement as used for the model, it can be used for scaling. If 0.17 O_2/kg/m equals 3.5 kCal for every 50m in chimpanzees, 0.14 O_2/kg/m equals 2.9 kCal for every 50m in *Australopithecus afarensis*. Similarly, if 0.17 O_2/kg/m equals 1 hydration lost and 1 fatigue gained for every extra 50m in chimps, 0.14 O_2/kg/m would equal 0.8 hydrations lost and 0.8 fatigues gained for every extra 50m in *Australopithecus afarensis*. As can be read in the tables of Ch6, *Ardipithecus ramidus* is morphologically intermediate between chimpanzees and *Australopithecus anamensis/ afarensis*. As such, it can be assumed that also its travel costs are intermediate between the three species. This would indicate 3.2kCal lost for every 50m of travel, and 0.9 hydrations lost and 0.9 fatigues gained for every extra 50m of travel.
Output		Output ‘rules’ follow similar outlines as specified for Ch4 for comparison reasons.
Feeding-fruit	+1 for each time step spent feeding on fruit.	Based on 144 time steps in the model, each time step spent on feeding-fruit will add +1 to the feeding-fruit column in the output table. This way, the amount of time spent feeding and feeding-fruit over a 24-hour period can easily be assessed.
Feeding-USOs	+1 for each time step spent feeding on USOs.	Based on 144 time steps in the model, each time step spent on feeding-USOs will add +1 to the feeding-USOs column in the output table.
Drinking	+1 for each time step spent drinking.	Based on 144 time steps in the model, each time step spent on drinking will add +1 to the drinking column in the output table.
Nesting	+1 for each time step spent resting.	Based on 144 time steps in the model, each time step spent on nesting will add +1 to the nesting column in the output table.
Resting	+1 for each time step spent nesting.	Based on 144 time steps in the model, each time step spent on resting will add +1 to the resting column in the output

Parameter	Value	Justification
		table.
Travel	+1 for each time step spent travelling.	Based on 144 time steps in the model, each time step spent on travelling will add +1 to the travel column in the output table.
Forest	+1 for each time step spent in forest.	Based on 144 time steps in the model, each time step spent in forest will add +1 to the forest column in the output table.
Woodland	+1 for each time step spent in woodland.	Based on 144 time steps in the model, each time step spent in woodland will add +1 to the woodland column in the output table.
Savannah	+1 for each time step spent in savannah.	Based on 144 time steps in the model, each time step spent in savannah will add +1 to the savannah column in the output table. .
Feed-fruit-forest	+1 for each time step spent on feeding on fruit in forest.	Based on 144 time steps in the model, each time step spent on feeding-fruit in forest will add +1 to the feeding-fruit-forest column in the output table.
Feed-fruit-woodland	+1 for each time step spent on feeding on fruit in woodland.	Based on 144 time steps in the model, each time step spent on feeding-fruit in woodland will add +1 to the feeding-fruit-woodland column in the output table.
Feed-fruit-savannah	+1 for each time step spent on feeding on fruit in savannah.	Based on 144 time steps in the model, each time step spent on feeding-fruit in savannah will add +1 to the feeding-fruit-savannah column in the output table.
Feed-USOs-forest	+1 for each time step spent on feeding on USOs in forest.	Based on 144 time steps in the model, each time step spent on feeding-USOs in forest will add +1 to the feeding-USOs-forest column in the output table.
Feed-USOs-woodland	+1 for each time step spent on feeding on USOs in woodland.	Based on 144 time steps in the model, each time step spent on feeding-USOs in woodland will add +1 to the feeding-USOs-woodland column in the output table.
Feed-USOs-savannah	+1 for each time step spent on feeding on USOs in savannah.	Based on 144 time steps in the model, each time step spent on feeding-USOs in savannah will add +1 to the feeding-USOs-savannah column in the output table.
Drink-forest	+1 for each time step spent on drinking in forest.	Based on 144 time steps in the model, each time step spent on drinking in forest will add +1 to the drink-forest column in the output table.
Drink-woodland	+1 for each time step spent on drinking in woodland.	Based on 144 time steps in the model, each time step spent on drinking in woodland will add +1 to the drink-woodland column in the output table.
Drink-savannah	+1 for each time step spent on drinking in savannah.	Based on 144 time steps in the model, each time step spent on drinking in savannah will add +1 to the drink-savannah column in the output table. .
Nest-forest	+1 for each time step spent on nesting in forest.	Based on 144 time steps in the model, each time step spent on nesting in forest will add +1 to the nest-forest column in the output table.
Nest-woodland	+1 for each time step spent on nesting in woodland.	Based on 144 time steps in the model, each time step spent on nesting in woodland will add +1 to the nest -woodland column in the output table.
Nest-savannah	+1 for each time step spent on nesting in savannah.	Based on 144 time steps in the model, each time step spent on nesting in savannah will add +1 to the nest-savannah column in the output table.
Rest-forest	+1 for each time step spent on resting in forest.	Based on 144 time steps in the model, each time step spent on resting in forest will add +1 to the rest-forest column in the output table.
Rest-woodland	+1 for each time step spent on resting in woodland.	Based on 144 time steps in the model, each time step spent on resting in woodland will add +1 to the rest -woodland column in the output table.
Rest-savannah	+1 for each time step spent on	Based on 144 time steps in the model, each time step spent on resting in savannah will add +1 to the rest-savannah

Parameter	Value	Justification
	resting in savannah.	column in the output table.
Travel-forest	+1 for each time step spent on travelling in forest.	Based on 144 time steps in the model, each time step spent on travelling in forest will add +1 to the travel-forest column in the output table.
Travel-woodland	+1 for each time step spent on travelling in woodland.	Based on 144 time steps in the model, each time step spent on travelling in woodland will add +1 to the travel - woodland column in the output table.
Travel-savannah	+1 for each time step spent on travelling in savannah.	Based on 144 time steps in the model, each time step spent on travelling in savannah will add +1 to the travel -savannah column in the output table. .
Daily path length	+50m for each patch travelled.	For each 50m travelled, 50m is added to the daily path length column in the output table.
Energy	Various	Each time energy is gained and/or lost, this is updated in the energy column of the output table.
Hydration	Various	Each time hydration is gained and/or lost, this is updated in the hydration column of the output table.
Fatigue	Various	Each time fatigue is gained and/or lost, this is updated in the fatigue column of the output table.
Fruit intake	+ 3.5 for each feeding bout feeding fruit.	After each feeding bout, the amount of fruits eaten is updated in the fruit intake column in the output table.
USO intake	+ 3.5 for each feeding bout feeding USOs.	After each feeding bout, the amount of fruits eaten is updated in the USO intake column in the output table.
Water intake	+ 50 for each drinking bout.	After each drinking bout, the amount of water drunk is updated in the water intake column in the output table.
Ardipithecus land use	-	Output table (.csv) for further analyses.
Ardipithecus activity	-	Output table (.csv) for further analyses.
Ardipithecus site selection	-	Output table (.csv) for further analyses.

APPENDIX 6.6

Model input parameters for the *Australopithecus anamensis/ afarensis* landscape use model of Chapter 6

Table A6.6.1 below outlines the input parameters for the *Australopithecus anamensis/ afarensis* landscape use model presented in Chapter 6. The table presents detailed information on the initial parameter values, the source of these parameter values (i.e. empirical data or knowledge-based considerations), and whether parameters were used for the local sensitivity analysis of the model. The rationales behind each of the parameter values are outlined in Appendix 6.10.

Table A6.6.1. Model parameters for the *Australopithecus anamensis/ afarensis* landscape use model of Chapter 6. Within the model, 'Data source' indicates whether a parameter value is based upon empirical data or general knowledge-based considerations, 'Output' indicates that a parameter value was selected to produce model output, 'Sensitivity analysis' indicates whether a parameter was used to assess the model's robustness, 'F' stands for dense forests, 'M' for forest mosaics, and 'S' for savannah environments. When a parameter value is specified as, for example, 0 – 21, this indicates that a random value was chosen between 0 and 21 at the onset of each model run for each individual or patch as appropriate.

Model parameter	Value	Data source	Sensitivity analysis
home range size	36km2	Empirical data	No
patch size	50mx50m	General knowledge	No
% forest cover	80% (F), 45% (M), 10% (S)	Empirical data	No
% woodland cover	10% (F), 40% (M), 55%(S)	Empirical data	No
% savannah cover	10% (F), 15% (M), 35%(S)	Empirical data	No
fragmentation	0.05	General knowledge	No
temperature	25°C	General knowledge	No
rainfall	0mm	General knowledge	No
tree height forest	10 - 50m	Empirical data	No
tree height woodland	8 - 20m	Empirical data	No
tree height savannah	3 - 15m	Empirical data	No
canopy cover forest	75 – 100%	Empirical data	No
canopy cover woodland	25 – 75%	Empirical data	No
canopy cover savannah	0 – 25%	Empirical data	No
canopy connectivity forest	75 – 100%	Empirical data	No
canopy connectivity woodland	25 – 75%	Empirical data	No
canopy connectivity savannah	0 – 25%	Empirical data	No
understory density forest	0 – 25%	Empirical data	No
understory density woodland	25 – 75%	Empirical data	No
understory density savannah	75 – 100%	Empirical data	No
tree density forest	75 – 100%	Empirical data	No
tree density woodland	25 – 75%	Empirical data	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
tree density savannah	0 – 25%	Empirical data	No
food tree density forest	75 – 100%	Empirical data	No
food tree density woodland	25 – 75%	Empirical data	No
food tree density savannah	0 – 25%	Empirical data	No
number of fruit forest	0 - 21	General knowledge	Yes
number of fruit woodland	0 - 14	General knowledge	Yes
number of fruit savannah	0 - 7	General knowledge	Yes
amount USOs forest	0 - 7	General knowledge	Yes
amount USOs woodland	0 - 14	General knowledge	Yes
amount USOs savannah	0 - 21	General knowledge	Yes
amount of water forest	0 - 100	General knowledge	Yes
amount of water woodland	0 - 75	General knowledge	Yes
amount of water savannah	0 - 50	General knowledge	Yes
carcass probability forest/woodland	6%	Empirical data	No
carcass probability grassland	18%	Empirical data	No
amount meat	0 - 21	General knowledge	Yes
temperature-day forest	0 – 25 (scaled)	Empirical data	No
temperature-day woodland	25 – 75 (scaled)	Empirical data	No
temperature-day savannah	75 – 100 (scaled)	Empirical data	No
temperature-night forest	75 – 100 (scaled)	Empirical data	No
temperature-night woodland	25 – 75 (scaled)	Empirical data	No
temperature-night savannah	0 – 25 (scaled)	Empirical data	No
luminosity-day forest	0 – 25 (scaled)	Empirical data	No
luminosity-day woodland	25 – 75 (scaled)	Empirical data	No
luminosity-day savannah	75 – 100 (scaled)	Empirical data	No
luminosity-night forest	0 – 25 (scaled)	Empirical data	No
luminosity-night woodland	0 – 25 (scaled)	Empirical data	No
luminosity-night savannah	0 – 25 (scaled)	Empirical data	No
number of *Australopithecus*	60	Empirical data	No
where - canopy cover criterion	>0%	Empirical data	No
where - canopy connectivity criterion	>0%	Empirical data	No
where - understory density criterion	≤50%	General knowledge	Yes
where - tree density criterion	≥50%	General knowledge	Yes
where - food tree density criterion	≥50%	General knowledge	Yes
where - tree height criterion	≥1m	Empirical data	No
where - local temperature criterion	≤50 (scaled)	General knowledge	Yes
where - local luminosity criterion	≤50 (scaled)	General knowledge	Yes
where - understory feeding criterion	≥50 (scaled)	General knowledge	Yes
where - temperature feeding criterion	< 87.5 (scaled)	General knowledge	Yes
where - luminosity feeding criterion	< 87.5 (scaled)	General knowledge	Yes
where - number of fruits	3.5 fruits	General knowledge	No
where - amount USOs	3.5 USOs	General knowledge	No
where - amount meat	3.5 grams of meat	General knowledge	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
where - amount water	50 hydrations	General knowledge	No
where - feeding fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Empirical data	No
where - feeding USOs	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	General knowledge	No
where - feeding meat	Amount meat ≥ 3.5 (i.e. amount meat (grams) eaten), temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	General knowledge	No
where -drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Empirical data	No
where - nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Empirical data	No
where - resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Empirical data	No
where - travel	None	General knowledge	No
when - feeding criterion	energy <= 144, and energy < hydration	General knowledge	Yes
when - drinking criterion	hydration <= 72, and hydration < energy	General knowledge	Yes
when - resting criterion	fatigue >= 73	General knowledge	Yes
when - nesting criterion	time > 72 steps	Empirical data	No
when - temperature criterion	temperature > 29°C	Empirical data	No
when - rainfall criterion	rainfall > 25mm	Empirical data	No
Initial - energy	0 – 10kCal	General knowledge	Yes
Initial - hydration	0 – 10 hydrations	General knowledge	Yes
Initial - fatigue	0 – 10 fatigues	General knowledge	Yes
Step - energy	-2kCal	General knowledge	Yes
Step - hydration	-1 hydrations	General knowledge	Yes
Step - fatigue	+1 fatigues	General knowledge	Yes
Feeding fruit - energy	+10.85kCal 3.1kCal per gram	Empirical data	No
Feeding fruit - energy per fruit	3.1kCal (per gram)	Empirical data	No
Feeding fruit - number fruits eaten	3.5 fruits	General knowledge	Yes
Feeding USOs - energy	+7.49kCal 2.14kCal per gram	Empirical data	No
Feeding USOs - energy per USO	2.14kCal per gram	Empirical data	No
Feeding USOs - amount USOs eaten	3.5 USOs	General knowledge	Yes
Feeding meat - energy	18.305kCal 5.23kCal per gram	Empirical data	No
Feeding meat - energy per gram	5.23kCal per 100gram	Empirical data	No
Feeding meat - amount meat eaten	3.5 grams of meat	General knowledge	Yes
Drinking - hydration	50 hydrations	General knowledge	No

Model parameter	**Value**	**Data source**	**Sensitivity analysis**
Drinking - amount water drunk	50 hydrations	General knowledge	Yes
Resting - fatigue	-2 fatigues	General knowledge	Yes
Nesting - fatigue	-2 fatigues	General knowledge	Yes
Travel - energy	2.9kCal per 50m	Empirical data	No
Travel - hydration	-0.8 hydrations for every extra 50m	General knowledge	Yes
Travel - fatigue	+0.8 fatigues for every extra 50m	General knowledge	Yes
Travel - daily path length	50m per patch travelled	Empirical data	No
Travel - number of patches	in order: 0, 1, 2, 3 - 6 (jump)	General knowledge	No
Feed-fruit-forest	+1 for every step in this activity/veg type	Output	No
Feed-fruit-woodland	+1 for every step in this activity/veg type	Output	No
Feed-fruit-savannah	+1 for every step in this activity/veg type	Output	No
Feed-USOs-forest	+1 for every step in this activity/veg type	Output	No
Feed-USOs-woodland	+1 for every step in this activity/veg type	Output	No
Feed-USOs-savannah	+1 for every step in this activity/veg type	Output	No
Feed-meat-forest	+1 for every step in this activity/veg type	Output	No
Feed-meat-woodland	+1 for every step in this activity/veg type	Output	No
Feed-meat-savannah	+1 for every step in this activity/veg type	Output	No
Drink-forest	+1 for every step in this activity/veg type	Output	No
Drink-woodland	+1 for every step in this activity/veg type	Output	No
Drink-savannah	+1 for every step in this activity/veg type	Output	No
Rest-forest	+1 for every step in this activity/veg type	Output	No
Rest-woodland	+1 for every step in this activity/veg type	Output	No
Rest-savannah	+1 for every step in this activity/veg type	Output	No
Nest-forest	+1 for every step in this activity/veg type	Output	No
Nest-woodland	+1 for every step in this activity/veg type	Output	No
Nest-savannah	+1 for every step in this activity/veg type	Output	No
Travel-forest	+1 for every step in this activity/veg type	Output	No
Travel-woodland	+1 for every step in this activity/veg type	Output	No
Travel-savannah	+1 for every step in this activity/veg type	Output	No
Daily-path-length	+50m for every patch travelled	Output	No
Energy	variable depending on behaviour	Output	No
Hydration	variable depending on behaviour	Output	No
Fatigue	variable depending on behaviour	Output	No
Fruit intake	+3.5 for each time step feeding fruit	Output	No
USO intake	+3.5 for each time step feeding USOs	Output	No
Meat intake	+3.5 for each time step feeding meat	Output	No
Water intake	+50 for each time step drinking	Output	No

Model parameter	Value	Data source	Sensitivity analysis
Current activity	variable depending on behaviour	Output	No
Tick	1 per time step	Output	No

APPENDIX 6.7

Model code of the *Australopithecus anamensis/ afarensis* landscape use model of Chapter 6

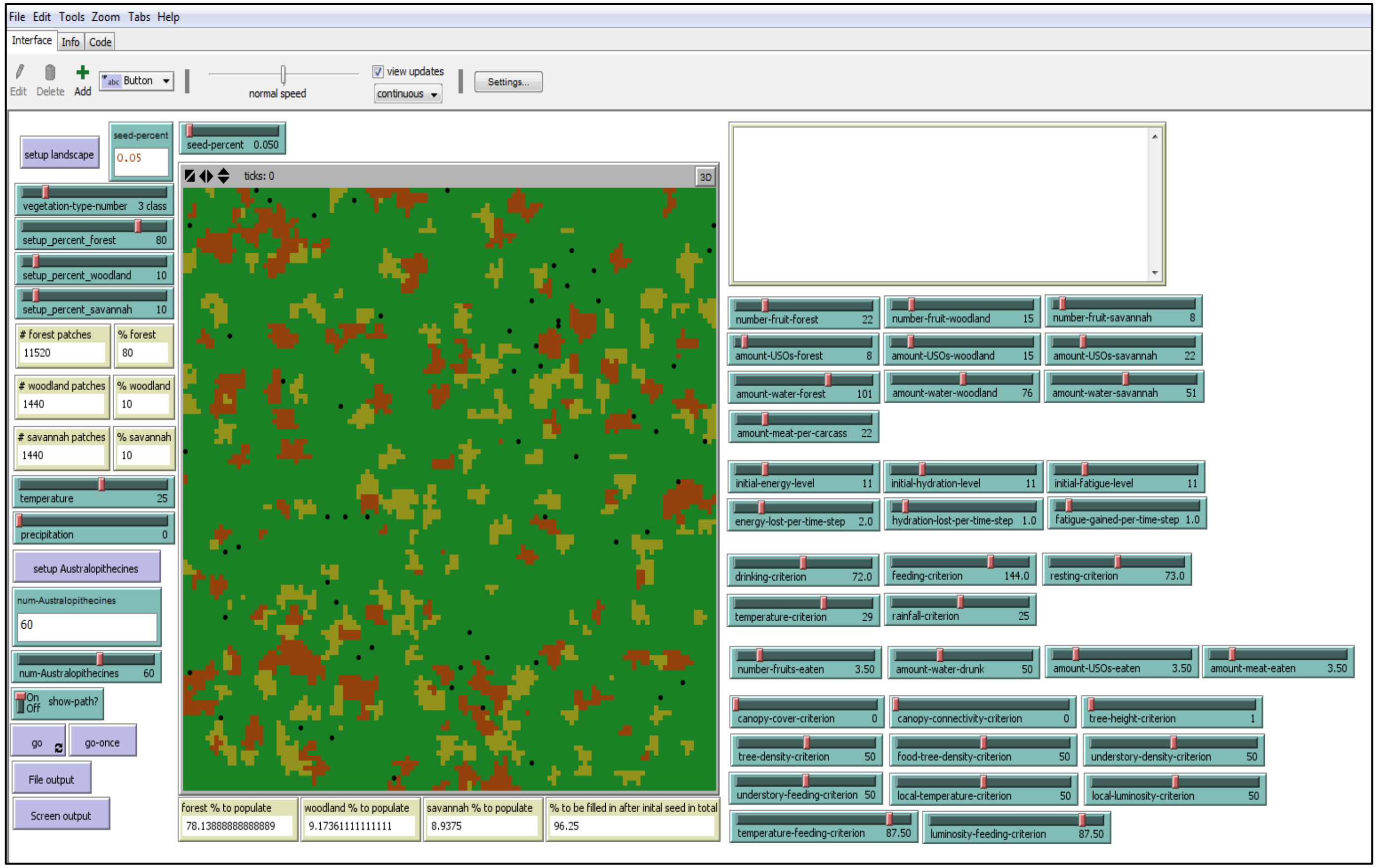
The *Australopithecus anamensis*/ *afarensis* landscape use model presented in Chapter 6 was developed using NetLogo software (version 5.2.1; Willensky 1999). Model code of the *Australopithecus* landscape use model is presented online, and can be accessed using the specifics outlined below. Italics in the code outline code explanations. The *Australopithecus* model was adapted from the generic chimpanzee landscape use model of Chapter 4 to suit the behaviour, habitats and characteristics of *Australopithecus afarensis* and *Australopithecus anamensis*, and specific adaptations are outlined in Appendix 6.9. Rationale behind the model code is presented in Appendix 6.10.

Webpage: http://kellyvanleeuwen.com/thesis/
Username: klvanleeuwen
Password: please contact the author

APPENDIX 6.8

Model interface of the *Australopithecus anamensis/ afarensis* landscape use model of Chapter 6

The interface tab, or front screen, of the *Australopithecus anamensis/ afarensis* landscape use model of in Chapter 6 is outlined below. Figure A6.8.1 presents the interface tab before the model has been run, and Figure 6.8.2 outlines the model interface tab after a model run. The rationales behind the input parameters on the interface tab are presented in Appendix 6.10.



seed-percent 0.05

seed-percent 0.050

vegetation-type-number 3 class

setup_percent_forest 80

setup_percent_woodland 10

setup_percent_savannah 10

forest patches 11520

% forest 80

woodland patches 1440

% woodland 10

savannah patches 1440

% savannah 10

temperature 25

precipitation 0

num-Australopithecines 60

num-Australopithecines 60

show-path?

forest % to populate 78.13888888888889

woodland % to populate 9.17361111111111

savannah % to populate 8.9375

% to be filled in after inital seed in total 96.25

number-fruit-forest 22

number-fruit-woodland 15

number-fruit-savannah 8

amount-USOs-forest 8

amount-USOs-woodland 15

amount-USOs-savannah 22

amount-water-forest 101

amount-water-woodland 76

amount-water-savannah 51

amount-meat-per-carcass 22

initial-energy-level 11

initial-hydration-level 11

initial-fatigue-level 11

energy-lost-per-time-step 2.0

hydration-lost-per-time-step 1.0

fatigue-gained-per-time-step 1.0

drinking-criterion 72.0

feeding-criterion 144.0

resting-criterion 73.0

temperature-criterion 29

rainfall-criterion 25

number-fruits-eaten 3.50

amount-water-drunk 50

amount-USOs-eaten 3.50

amount-meat-eaten 3.50

canopy-cover-criterion 0

canopy-connectivity-criterion 0

tree-height-criterion 1

tree-density-criterion 50

food-tree-density-criterion 50

understory-density-criterion 50

understory-feeding-criterion 50

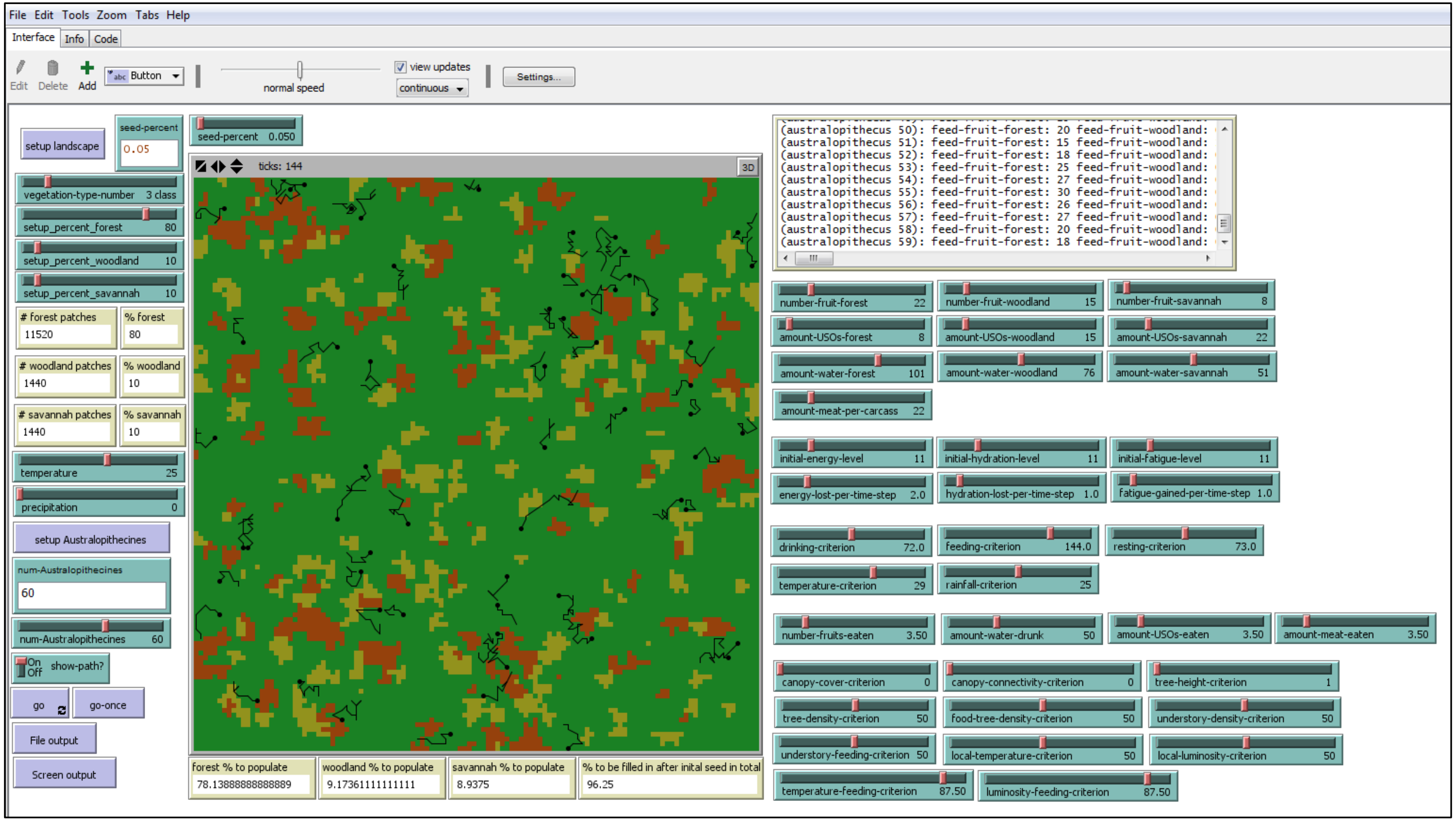
local-temperature-criterion 50

local-luminosity-criterion 50

temperature-feeding-criterion 87.50

luminosity-feeding-criterion 87.50

Figure A6.8.1. Model interface of the *Australopithecus* model at the onset of a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).



seed-percent 0.05

seed-percent 0.050

ticks: 144

vegetation-type-number 3 class

setup_percent_forest 80

setup_percent_woodland 10

setup_percent_savannah 10

forest patches 11520

% forest 80

woodland patches 1440

% woodland 10

savannah patches 1440

% savannah 10

temperature 25

precipitation 0

num-Australopithecines 60

num-Australopithecines 60

On Off show-path?

forest % to populate 78.13888888888889

woodland % to populate 9.17361111111111

savannah % to populate 8.9375

% to be filled in after inital seed in total 96.25

```
(australopithecus 50): feed-fruit-forest: 20 feed-fruit-woodland:
(australopithecus 51): feed-fruit-forest: 15 feed-fruit-woodland:
(australopithecus 52): feed-fruit-forest: 18 feed-fruit-woodland:
(australopithecus 53): feed-fruit-forest: 25 feed-fruit-woodland:
(australopithecus 54): feed-fruit-forest: 27 feed-fruit-woodland:
(australopithecus 55): feed-fruit-forest: 30 feed-fruit-woodland:
(australopithecus 56): feed-fruit-forest: 26 feed-fruit-woodland:
(australopithecus 57): feed-fruit-forest: 27 feed-fruit-woodland:
(australopithecus 58): feed-fruit-forest: 20 feed-fruit-woodland:
(australopithecus 59): feed-fruit-forest: 18 feed-fruit-woodland:
```

number-fruit-forest 22

number-fruit-woodland 15

number-fruit-savannah 8

amount-USOs-forest 8

amount-USOs-woodland 15

amount-USOs-savannah 22

amount-water-forest 101

amount-water-woodland 76

amount-water-savannah 51

amount-meat-per-carcass 22

initial-energy-level 11

initial-hydration-level 11

initial-fatigue-level 11

energy-lost-per-time-step 2.0

hydration-lost-per-time-step 1.0

fatigue-gained-per-time-step 1.0

drinking-criterion 72.0

feeding-criterion 144.0

resting-criterion 73.0

temperature-criterion 29

rainfall-criterion 25

number-fruits-eaten 3.50

amount-water-drunk 50

amount-USOs-eaten 3.50

amount-meat-eaten 3.50

canopy-cover-criterion 0

canopy-connectivity-criterion 0

tree-height-criterion 1

tree-density-criterion 50

food-tree-density-criterion 50

understory-density-criterion 50

understory-feeding-criterion 50

local-temperature-criterion 50

local-luminosity-criterion 50

temperature-feeding-criterion 87.50

luminosity-feeding-criterion 87.50

Figure A6.8.2. Model interface of the *Australopithecus* model after a model run. A forest environment is simulated, with 80% forest (green), 10% woodland (orange) and 10% grassland (yellow).

APPENDIX 6.9

Model code adaptations to create the *Australopithecus* model of Chapter 6 from the chimpanzee model of Chapter 4

The *Australopithecus anamensis*/ *afarensis* landscape use model of Chapter 6 was adapted from the generic chimpanzee landscape use model of Chapter 4 to suit the characteristics, behaviour and habitat of *Australopithecus anamensis* and *Australopithecus afarensis*. Table A6.9.1 outlines the specific model adaptations, and thus the differences and similarities, between the two models. The rationale behind the presented model rules is outlined in Appendix 6.10.

Table A6.9.1. Model code adaptations to create the *Australopithecus* model (Chapter 6) from the generic chimpanzee landscape use model (Chapter 4). The column 'Data source' indicates the source of the model code. See Appendix 6.10 for the rationale behind the model code.

Parameter	**Generic model (Ch4)**	***Australopithecus* model (Ch6)**	**Data source**
Global			
Model size/ Home-range	$36km^2$	$36km^2$	Chimpanzee data (Ch4)
Patch size	50m x 50m	50m x 50m 120 x 120 patches	Chimpanzee data (Ch4)
Model run (time)	24 hours	24 hours	Chimpanzee data (Ch4)
Time step (time)	10 minutes	10 minutes	Chimpanzee data (Ch4)
Landscape			
Vegetation types	3	3	Chimpanzee data (Ch4)
Vegetation cover	Dense forest: Forest (F) = 80%, woodland (W) = 10%, savannah grassland (S) = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	Dense forest: Forest (F) = 80%, woodland (W) = 10%, savannah grassland (S) = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	Chimpanzee data (Ch4)
Fragmentation	0.05	0.05	Chimpanzee data (Ch4)
Temperature	25^0C	25^0C	Chimpanzee data (Ch4)
Precipitation	0mm	0mm	Chimpanzee data (Ch4)
GIS map or random	Random	Random	Chimpanzee data (Ch4)
Vegetation features			Chimpanzee data (Ch4)
• Tree height	F: 10-50m; W: 8-20m; G: 3-15m.	F: 10-50m; W: 8-20m; G: 3-15m.	Chimpanzee data (Ch4)
• Canopy cover	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Canopy connectivity	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Understory density	F: 0-25%; W: 25-75%, G: 75-100%.	F: 0-25%; W: 25-75%, G: 75-100%.	Chimpanzee data (Ch4)
• Tree density	F: 75-100%; W: 25-	F: 75-100%; W: 25-75%, G: 0-	Chimpanzee data

Parameter	**Generic model (Ch4)**	***Australopithecus* model (Ch6)**	**Data source**
	75%, G: 0-25%.	25%.	(Ch4)
• Food tree density	F: 75-100%; W: 25-75%, G: 0-25%.	F: 75-100%; W: 25-75%, G: 0-25%.	Chimpanzee data (Ch4)
• Number fruit	F: 0-21; W: 0-14; G: 0-7.	F: 0-21; W: 0-14; G: 0-7.	Chimpanzee data (Ch4)
• Amount water	F: 0-100; W: 0-75; G: 0-50.	F: 0-100; W: 0-75; G: 0-50.	Chimpanzee data (Ch4)
• Amount USOs	-	F: 0-7, W: 0-14, S: 0-21	Hominin literature data and assumptions
• Amount meat	-	F: 6% probability of a carcass per patch, W: 6% probability of a carcass per patch, S: 18% probability of a carcass per patch. Carcasses contain between 0 – 21 grams of edible dry weight.	Hominin literature data and assumptions
Micro-climate characteristics			
• Temperature (day)	F: 0-25, W: 25-75; G: 75-100.	F: 0-25, W: 25-75; G: 75-100.	Chimpanzee data (Ch4)
• Temperature (night)	F: 75-100; W: 25-75; G: 0-25.	F: 75-100; W: 25-75; G: 0-25.	Chimpanzee data (Ch4)
• Luminosity (day)	F: 0-25, W: 25-75; G: 75-100.	F: 0-25, W: 25-75; G: 75-100.	Chimpanzee data (Ch4)
• Luminosity (night)	F: 0 -25; W: 0-25, G: 0-25.	F: 0 -25; W: 0-25, G: 0-25.	Chimpanzee data (Ch4)
Chimpanzees/ Australopithecus			
Community size	60	60	Chimpanzee data (Ch4)
Internal states	3	3	Chimpanzee data (Ch4)
Behaviour			
Feeding	√	√	Chimpanzee data (Ch4)
Drinking	√	√	Chimpanzee data (Ch4)
Nesting	√	√	Chimpanzee data (Ch4)
Resting	√	√	Chimpanzee data (Ch4)
Travel	√	√	Chimpanzee data (Ch4)
Where			
• Feeding-fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Hominin literature data and assumptions
• Feeding-USOs	-	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Hominin literature data and assumptions
• Feeding-meat	-	Amount meat ≥ 3.5 (i.e. amount meat (grams) eaten), temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Hominin literature data and assumptions
• Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Chimpanzee data (Ch4)

Parameter	**Generic model (Ch4)**	***Australopithecus* model (Ch6)**	**Data source**
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Chimpanzee data (Ch4)
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Chimpanzee data (Ch4)
• Travel	-	-	Chimpanzee data (Ch4)
• Relative importance	-	-	Chimpanzee data (Ch4)
When			Chimpanzee data (Ch4)
• Feeding	Energy ≤ 144 and energy < hydration.	Energy ≤ 144 and energy < hydration.	Chimpanzee data (Ch4)
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Hydration ≤ 72 and hydration ≤ energy.	Chimpanzee data (Ch4)
• Nesting	Time steps > 72.	Time steps > 72.	Chimpanzee data (Ch4)
• Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	Chimpanzee data (Ch4)
• Travel	-	-	Chimpanzee data (Ch4)
How much			
• Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Chimpanzee data (Ch4)
• Existing	Energy: -2; hydration: -1; fatigue: +1.	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	Chimpanzee data (Ch4)
• Feeding-fruit	Energy: +10.85 kCal (3.1kCal per fruit)	Energy: +10.85 kCal (3.1kCal per fruit)	Chimpanzee data (Ch4)
• Feeding-USOs	-	Energy: + 7.49kCal (2.14kCal per USO)	Hominin literature data and assumptions
• Feeding-meat	-	Energy + 18.305 kCal (5.23 kCal per gram meat dry weight).	Hominin literature data and assumptions
• Drinking	Hydration + 50	Hydration + 50	Chimpanzee data (Ch4)
• Nesting	Fatigue: -2	Fatigue: -2	Chimpanzee data (Ch4)
• Resting	Fatigue: -2	Fatigue: -2	Chimpanzee data (Ch4)
• Travel	Energy: -3.5kCal per 50m. Travelling more than 50m: lose an extra hydration and gain an extra fatigue for each 50m travelled.	Energy: -2.9 kCal per 50m. Travelling more than 50m: lose 0.8 extra hydrations and gain 0.8 extra fatigues for each extra 50m travelled.	Calculations based on chimpanzee data (Ch4) and Pontzer et al. (2009)
Output			
Feeding-fruit	-	+1 for each time step spent feeding on fruit.	-

Parameter	**Generic model (Ch4)**	***Australopithecus* model (Ch6)**	**Data source**
Feeding-USOs	-	+1 for each time step spent feeding on USOs.	-
Feeding-meat	-	+1 for each time step spent feeding on meat	-
Drinking	+1 for each time step spent drinking.	+1 for each time step spent drinking.	Chimpanzee data (Ch4)
Nesting	+1 for each time step spent resting.	+1 for each time step spent resting.	Chimpanzee data (Ch4)
Resting	+1 for each time step spent nesting.	+1 for each time step spent nesting.	Chimpanzee data (Ch4)
Travel	+1 for each time step spent travelling.	+1 for each time step spent travelling.	Chimpanzee data (Ch4)
Forest	+1 for each time step spent in forest.	+1 for each time step spent in forest.	Chimpanzee data (Ch4)
Woodland	+1 for each time step spent in woodland.	+1 for each time step spent in woodland.	Chimpanzee data (Ch4)
Savannah	+1 for each time step spent in savannah.	+1 for each time step spent in savannah.	Chimpanzee data (Ch4)
Feed-fruit-forest	-	+1 for each time step spent on feeding on fruit in forest.	-
Feed-fruit-woodland	-	+1 for each time step spent on feeding on fruit in woodland.	-
Feed-fruit-savannah	-	+1 for each time step spent on feeding on fruit in savannah.	-
Feed-USOs-forest	-	+1 for each time step spent on feeding on USOs in forest.	-
Feed-USOs-woodland	-	+1 for each time step spent on feeding on USOs in woodland.	-
Feed-USOs-savannah	-	+1 for each time step spent on feeding on USOs in savannah.	-
Feed-meat-forest	-	+1 for each time step spent on feeding on meat in forest.	-
Feed-meat-woodland	-	+1 for each time step spent on feeding on meat in woodland.	-
Feed-meat-savannah	-	+1 for each time step spent on feeding on meat in savannah.	-
Drink-forest	+1 for each time step spent on drinking in forest.	+1 for each time step spent on drinking in forest.	Chimpanzee data (Ch4)
Drink-woodland	+1 for each time step spent on drinking in woodland.	+1 for each time step spent on drinking in woodland.	Chimpanzee data (Ch4)
Drink-savannah	+1 for each time step spent on drinking in savannah.	+1 for each time step spent on drinking in savannah.	Chimpanzee data (Ch4)
Nest-forest	+1 for each time step spent on nesting in forest.	+1 for each time step spent on nesting in forest.	Chimpanzee data (Ch4)
Nest-woodland	+1 for each time step spent on nesting in woodland.	+1 for each time step spent on nesting in woodland.	Chimpanzee data (Ch4)
Nest-savannah	+1 for each time step spent on nesting in savannah.	+1 for each time step spent on nesting in savannah.	Chimpanzee data (Ch4)
Rest-forest	+1 for each time step spent on resting in forest.	+1 for each time step spent on resting in forest.	Chimpanzee data (Ch4)
Rest-woodland	+1 for each time step spent on resting in woodland.	+1 for each time step spent on resting in woodland.	Chimpanzee data (Ch4)
Rest-savannah	+1 for each time step spent on resting in savannah.	+1 for each time step spent on resting in savannah.	Chimpanzee data (Ch4)
Travel-forest	+1 for each time step spent on travelling in forest.	+1 for each time step spent on travelling in forest.	Chimpanzee data (Ch4)
Travel-woodland	+1 for each time step	+1 for each time step spent on	Chimpanzee data

Parameter	**Generic model (Ch4)**	***Australopithecus* model (Ch6)**	**Data source**
	spent on travelling in woodland.	travelling in woodland.	(Ch4)
Travel-savannah	+1 for each time step spent on travelling in savannah.	+1 for each time step spent on travelling in savannah.	Chimpanzee data (Ch4)
Daily path length	+50m for each patch travelled.	+50m for each patch travelled.	Chimpanzee data (Ch4)
Energy	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Hydration	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Fatigue	Various, depending on behaviour/ time step.	Various, depending on behaviour/ time step.	Chimpanzee data (Ch4)
Fruit intake	+ 3.5 for each feeding bout feeding on fruit	+ 3.5 for each feeding bout feeding on fruit	Chimpanzee data (Ch4)
USO intake	-	+ 3.5 for each feeding bout feeding on USOs	Following chimpanzee data (Ch4)
Meat intake	-	+ 3.5 for each feeding bout feeding on meat	Following chimpanzee data (Ch4)
Water intake	+ 50 for each drinking bout.	+ 50 for each drinking bout.	Chimpanzee data (Ch4)
Chimp land use	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)
Chimp activity	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)
Chimp site selection	Output file, calculations	Output file, calculations	Chimpanzee data (Ch4)

APPENDIX 6.10

Model code rationale for the *Australopithecus anamensis/ afarensis* landscape use model of Chapter 6

The rationale behind the model code, decisions and design of the *Australopithecus anamensis*/ *afarensis* landscape use model presented in Chapter 6 is outlined in Table A6.10.1. The *Australopithecus* model is based upon the generic chimpanzee landscape use model of Chapter 4. The outlined rationale therefore either follows the justification of the generic model (Appendix 4.5), or is based upon published hominin literature on *Australopithecus anamensis* and *Australopithecus afarensis*.

Table A6.10.1. The rationales behind model codes, decisions and design of the *Australopithecus anamensis/ afarensis* landscape use model presented in Chapter 6.

Parameter	**Value**	**Justification**
Global		
Model size/ Home range	36km^2	As no data exist on early hominin home-ranges, it is assumed that home-range sizes are similar to those of chimpanzees (Chapter 6). In Chapter 4, the average home-range size for chimpanzee communities across sites was 36km^2.
Patch size	50m x 50m 120 x 120 patches	Similar to Ch4, a patch of 50m x 50 m is small enough to contain the necessary detail for each vegetation type, but not too small to affect processing power and difficulty.
Model run (time)	24 hours	As the model simulated daily activity budgets, path lengths, and vegetation type usage of *Australopithecus anamensis/ afarensis*, a run of 24 hours was chosen, which is similar to Ch4.
Time step (time)	10 minutes	Following Ch4 time step of 10min is small enough to capture the necessary behavioural details, but not too small to affect processing power.
Landscape		
Overall landscapes	3	Descriptions of the environments at *Australopithecus anamensis/ afarensis* fossil localities do not encompass the necessary detail to develop specific model environments, i.e. no data are given on the vegetation cover, spatial vegetation arrangement, temperature and rainfall at typical *Australopithecus anamensis/ afarensis* sites (Chapter 6). This lack of available data also makes it difficult to assess how *Australopithecus anamensis/ afarensis* landscapes fit with the environments outlined for chimpanzees in Chapter 3. However, when carefully reading the environmental reconstructions of *Australopithecus anamensis/ afarensis* fossil localities (Chapter 6), some reconstructions indicate mosaic environments of various vegetation types (which could be linked to typical chimpanzee MOSAIC landscapes), other imply dry grasslands and open environments (which could be linked to typical chimpanzee SAVANNAH landscapes), again others point to woodland/ wooded environments (which could be linked to either typical chimpanzee MOSAIC or SAVANNAH landscapes, depending on the cover of other vegetation types), and last, reconstructions also specify densely wooded environments with permanent water (which could be linked to typical chimpanzee FOREST environments). As such, it may be best to simulate *Australopithecus anamensis/ afarensis* in all typical

Parameter	**Value**	**Justification**
		chimpanzee landscapes (i.e. SAVANNAH, MOSAIC, and FOREST), and investigate how differently or similarly they would have behaved given their species-specific behavioural rules. With regards to vegetation features and micro-climates, the given data for *Australopithecus anamensis/ afarensis* are not based on actual reconstructions of paleoenvironments but based on present-day measurements and classifications. As these have already been studied in detail for Chapter 3 (including much more, and partially overlapping, references to the above), the micro-climates presented in this chapter were used.
Landscape implementation	Random	As no data on the exact vegetation coverage and spatial arrangement of *Australopithecus anamensis/ afarensis* environments are known, landscapes were set up randomly with respect to an assumed vegetation coverage for each typical landscape as outlined in Ch4 for chimpanzees.
Vegetation types	3	Data for *Australopithecus anamensis/ afarensis* include various different environments which do not allow efficient modelling, modelled vegetation types follow the rationale of chimpanzee landscapes outlined in Ch4: Results of Chapter 3 indicated that every chimpanzee study site contained the vegetation type forest (F). Furthermore, results showed that woodland (W) and savannah grassland (S) is available at each site classified as a savannah landscape. The presence of all other vegetation types is variable. It was therefore chosen to only use the three vegetation types above in order to be consistent.
Vegetation cover	Dense forest: F = 80%, W = 10%, S = 10%; Forest mosaic: F = 45%, W = 40%, S = 15%; Savannah: F = 10%, W = 55%, S = 35%.	As no data exist on the vegetation cover of *Australopithecus anamensis/ afarensis* landscapes, modelled vegetation cover followed the rationale of chimpanzee landscapes outlined in Ch4: Forest cover is the main driver of landscape-based classifications of chimpanzees and their environments and therefore, the amount of forest cover was specified first, so that it nicely fits within the definitions outlined in Chapter 3 and is evenly spaced between landscapes. The remaining percentage of cover was then filled with woodland and savannah grassland in a way that is roughly similar to the woodland and grassland cover averages within the different environments.
Fragmentation	0.05	Fragmentation of *Australopithecus anamensis/ afarensis* landscapes was kept equal to Ch4 and was set to 0.05. This value was allocated randomly.
Temperature	25°C	Overall temperature of *Australopithecus anamensis/ afarensis* landscapes was set to 25°C, which follows Ch4 and nicely falls within the thermoneutral zone for chimpanzees (20 - 29°C). This value was allocated randomly.
Precipitation	0mm	Overall rainfall of *Australopithecus anamensis/ afarensis* landscapes, precipitation was kept equal to Ch4 and specified to 0mm, i.e. a 'dry' day. This value was allocated randomly.
Vegetation features		Following the generic chimpanzee landscape use model of Ch4, only landscape-scale environmental variables that are assumed important for chimpanzee behaviours (and therefore also assumed important for early hominin behaviours) were included in the model: tree height, canopy cover, canopy connectivity, understory density, tree density, food tree density, amount food, and amount water. Other variables are not included because they are too small-scale and/or correlated with the other variables. Slope and altitude were not be included as there is no consistency between sites, which would impair the model rules.
• Tree height	F: 10-50m; W: 8-20m; S: 3-15m.	As no explicit data are presented for *Australopithecus anamensis/ afarensis* environments, vegetation features

Parameter	Value	Justification
		follow the rationale outlined for the chimpanzee model of Ch4: Chapter 3 showed that current literature specified tree height as either high, medium or low, with the exact heights specified as high = 10-50m, medium = 8-20m, and low = 3-15m.
• Canopy cover	F: 75-100%; W: 25-75%, S: 0-25%.	Canopy cover for *Australopithecus anamensis/ afarensis* environments followed Ch4 and scaled canopy cover to either high (75-100%), medium (25 – 75%) or low (0 – 25%). Values were allocated randomly.
• Canopy connectivity	F: 75-100%; W: 25-75%, S: 0-25%.	*Australopithecus anamensis/ afarensis* environments had a canopy connectivity scaled to high (75-100%), medium (25 – 75%) or low (0 – 25%), following Ch4. Values were allocated randomly.
• Understory density	F: 0-25%; W: 25-75%, S: 75-100%.	As no explicit data are presented for *Australopithecus anamensis/ afarensis* environments, understory density was scaled to high (75-100%), medium (25 – 75%) or low (0 – 25%) depending on vegetation type (similar to Ch4). Values were allocated randomly.
• Tree density	F: 75-100%; W: 25-75%, S: 0-25%.	Tree density for *Australopithecus anamensis/ afarensis* environments followed Ch4 and were scaled to high (75-100%), medium (25 – 75%) or low (0 – 25%). Values were allocated randomly.
• Food tree density	F: 75-100%; W: 25-75%, S: 0-25%.	Similarly, also food tree density for *Australopithecus anamensis/ afarensis* environments was scaled to high (75-100%), medium (25 – 75%) or low (0 – 25%) following Ch4. Values were allocated randomly.
• Number fruit	F: 0-21; W: 0-14; S: 0-7.	Similar to Ch4, number of fruit per patch for *Australopithecus anamensis/ afarensis* environments was based on a knowledge-based assumption: forest has more fruit than woodland, and woodland has more fruit than savannah. With respect to the amount of fruit eaten per time step (see below), it was specified that individuals could eat occasionally in savannah grasslands, sometimes in woodland, and regularly in forest. It is assumed that individuals can feed no longer than one hour on the same food source in the same patch, i.e. maximum 6 time steps eating on a single food item per patch.
• Amount water	F: 0-100; W: 0-75; S: 0-50.	As no explicit data is presented for *Australopithecus anamensis/ afarensis* environments, vegetation features follow the rationale outlined for the chimpanzee model of Ch4: Based on a general knowledge assumption, forest has more water available than woodland, and woodland has more water than savannah. With respect to the amount of water drunk per time step (see below), it was specified that individuals could rarely drink in savannah, occasionally in woodland, and sometimes in forest.
• Amount USOs	F: 0-7, W: 0-14, S: 0-21	For the distribution of USOs, it was found that USOs can be found regularly in savannah grassland, and occasionally in forest (Chapter 6). Woodland is assumed to be intermediate between these two vegetation types. As USOs are considered fallback foods, and with respect to the amount of USOs eaten each time step (see below), it was assumed that the amount of USOs present would show similar availability to fruits. Numbers for amount USOs per vegetation type are therefore set to similar quantities as fruits, with respect to the assigned vegetation type. Similar to feeding fruit, the assumption is made that individuals can eat a maximum of one hour on USOs in a single patch.
• Amount meat	F: 6% probability of a carcass per patch, W: 6% probability of a carcass per patch, S: 18% probability of a carcass per patch. Carcasses contain between 0 – 21 grams of	Based on a general knowledge assumption, savannah vegetation types have more herbivores, and thus more carcasses, than any other type of vegetation. Leonard & Robertson (1997) specified herbivore productivity as 10.1kCal/m^2/year for savannah and 3.6kCal/m^2/year for forest/woodland. This means a 64.4% reduction in productivity, i.e. productivity in forest/woodland is about a third of that in savannah grassland. Griffith et al. (2010) specified that only small carcasses can be consumed by single individuals. Their modelling paper stated a (small)

Parameter	**Value**	**Justification**
	edible dry weight.	carcass probability as 0.183 on average, i.e. 18% per cell /patch across land cover types (note: Griffith et al. (2010) land cover types include flooded, unflooded and channel areas and are referred to as topographical zones, which are not compatible with the vegetation types in the current model). If assumed that the carcass probability of 18% is for each patch in a savannah vegetation type, the carcass probability for forest/woodland should be 6% per patch. Size of a carcass is specified to between 0 – 21 edible grams dry weight at random, with regards to the amount-meat-eaten per time step and for consistency reasons of feeding on fruit and USOs (see below). Similar to feeding on USOs and fruit, the assumption is made that feeding meat can be done for a maximum of 6 time steps at the same patch.
Micro-climate characteristics		
• Temperature (day)	F: 0-25, W: 25-75; S: 75-100.	As no explicit data are presented for *Australopithecus anamensis/ afarensis* environments, micro-climates follow the rationale outlined for the chimpanzee model of Ch4 and daytime temperatures were scaled to hot (75-100), medium (25 – 75) or cold (0 – 25). Values were allocated randomly.
• Temperature (night)	F: 75-100; W: 25-75; S: 0-25.	Nighttime temperatures for *Australopithecus anamensis/ afarensis* environments, were also scaled to hot (75-100), medium (25 – 75) or cold (0 – 25) following Ch4. Values were allocated randomly.
• Luminosity (day)	F: 0-25, W: 25-75; S: 75-100.	Daytime luminosity levels for *Australopithecus anamensis/ afarensis* environments were scaled to light (75-100), medium (25 – 75) or dark (0 – 25), similar to Ch4. Values were allocated randomly.
• Luminosity (night)	F: 0 -25; W: 0-25, S: 0-25.	Nighttime luminosity for *Australopithecus anamensis/ afarensis* environments also followed Ch4 and were scaled similarly to light (75-100), medium (25 – 75) or dark (0 – 25). Values were allocated randomly.
Australopithecines		
Community size	60	Australopithecines and chimpanzees have been assumed to have similar population sizes. Ch4 calculated average population size of chimpanzee communities across sites as 60 individuals. Individuals are placed randomly within the model environment at realistic nesting locations to start the day.
Internal states	3	Similar to Ch4, based on simplifications of general knowledge, it was decided that model behaviours are driven by internal states for energy, hydration, and fatigue.
Behaviour		
Feeding		Just as is the case for chimpanzees outlined in Ch4, for *Australopithecus anamensis/ afarensis* feeding is assumed to be an important daily behaviour, where energy can be gained.
Drinking		For *Australopithecus anamensis/ afarensis*, drinking should be included as an important behaviour to obtain water/ hydration.
Nesting		Following Ch4, for *Australopithecus anamensis/ afarensis*, nesting should be included, as this is the only assumed nighttime behaviour.
Resting		Resting is assumed to be an important daily behaviour for *Australopithecus anamensis/ afarensis*, just like for chimpanzees (Ch4), where fatigue can be lost. It can either be enforced due to, for example, food processing, or 'extra' which can be used for other activities such as social behaviours.
Travel		Similar to Ch4, for *Australopithecus anamensis/ afarensis*, travel is assumed to be an important daily behaviour, getting an individual from A to B. Travel is therefore often considered goal-directed. Energy will be lost while travelling.

Parameter	Value	Justification
Where		As no explicit data are presented for where *Australopithecus anamensis/ afarensis* perform their daily activities, where-rules follow the rationale outlined for the chimpanzee model of Ch4: Results of Chapter 2 showed the important landscape-scale vegetation features and micro-climate characteristics for each modelled behaviour based on expert-based opinions.
- Feeding-fruit	Number fruit ≥ 3.5 (i.e. amount fruit eaten), food tree density ≥ 50, tree height ≥ 1, tree density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Where to feed on fruit is kept similar to chimpanzees, apart from temperature and luminosity. Similar locations to chimpanzees are expected, as *Australopithecus anamensis/ afarensis* still prefer to eat fruit, and a combination of number-fruits, (food) tree density and tree height concludes whether a patch is suitable for feeding. Following Ch4, as exact criteria of any of the environmental variables remain absent, these criteria are therefore chosen randomly for the model, based on general knowledge assumptions: Individuals should feed where there is enough fruit, at least enough to last them one time step, i.e. 3.5 fruits (see below). Individuals should furthermore prefer locations with higher tree and food tree densities (high densities 50-100, low densities 0-50), taller trees (higher trees have larger DBHs and should contain more food, but also short trees can have food), and lower temperatures and luminosities (high temperature /light 50-100, low temperature /dark 0-50). Due to the increased thermoregulatory advantage (i.e. higher tolerance to open areas), bipedality and the subsequently wider access to food sources, temperature and luminosity criteria are relaxed to include a part of the savannah patches as well (>75), but extreme conditions are still avoided (>87.5). To make a distinction between *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*, criteria for the latter are set to ≤ 87.5.
- Feeding-USOs	Amount USOs ≥ 3.5 (i.e. amount USOs (grams) eaten), understory density ≥ 50, temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	Where to feed on USOs is based on a combination of amount USOs (at least enough to last them one time step) and understory density (similar to food tree density, a minimal amount of understory is needed to be able to feed on USOs, as tubers come from herbaceous plants), as well as temperature and luminosity. Similar to the above, due to the increased thermoregulatory advantage (i.e. higher tolerance to open areas), bipedality and the subsequently wider access to food sources, temperature and luminosity criteria are relaxed to include a part of the savannah patches as well (>75), but extreme conditions are still avoided (>87.5). To make a distinction between *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis*, criteria for the latter are set to ≤ 87.5.
- Feeding-meat	Amount meat ≥ 3.5 (i.e. amount meat (grams) eaten), temperature (day) ≤ 87.5, and luminosity (day) ≤ 87.5.	As meat is a rare but preferred food item with high caloric gains, it is assumed that individuals will eat from a carcass wherever there are enough scavengable edible grams. Temperature and luminosity criteria are included to keep the model consistent.
- Drinking	Amount water ≥ 50 (i.e. amount water drunk), temperature (day) ≤ 50, and luminosity (day) ≤ 50.	For drinking, no actual quantitative data have been specified to set out specific drinking rules for the *Australopithecus anamensis/ afarensis* model. As *Australopithecus anamensis/ afarensis* was equally water dependent as chimpanzees, it is likely that drinking patterns would have been similar as well. As such, it was specified that *Australopithecus anamensis/ afarensis* lost the same amount of hydration as chimpanzees simply by existing at each time step, had a drinking *when*-criterion similar to that of chimpanzees, gained an equal amount of hydrations from drinking at each time step as chimpanzees, and selected similar drinking locations as chimpanzees. Following Ch4, criteria on where to drink were chosen randomly for the model, based on knowledge-

Parameter	Value	Justification
		based assumptions: Individuals should drink where there is enough water, at least enough to last them one time step, i.e. 50 hydrations. Individuals should furthermore prefer locations where it is not too hot or too light. Even though individuals have a thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Nesting	Tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, tree density ≥ 50, number fruit ≥ 3.5, understory density ≤ 50, food tree density ≥ 50, amount water ≥ 50, temperature (day) ≤ 50, and luminosity (day) ≤ 50.	Similar sleeping, and thus nesting patterns, to chimpanzees are expected for *Australopithecus anamensis/ afarensis*. As no further information has been specified, this indicates that it is best to keep the nesting rules for the *Australopithecus anamensis/ afarensis* model the same as the rules specified for the Ch4 chimpanzee model. This implies that, similar to chimpanzees, *Australopithecus anamensis/ afarensis* would gain the same amount of fatigues simply by existing at each time step, would lose an equal amount of fatigue while nesting each time step, and would have similar *where*- and *when*-criteria for nesting. Following Ch4, results of Ch2 did specify exact criteria for tree height, canopy cover, and canopy connectivity for nesting, but did not specify exact criteria of any of the other environmental variables. The criteria set out for these variables for the model were therefore based on general knowledge assumptions: Individuals would prefer to nest at locations with high tree and food tree densities and low understory densities (high densities 50-100, low densities 0-50), at locations where there is enough food (i.e. more than 3.5 fruits) and water (i.e. more than 50 hydrations), and at locations where it is not too hot or too light. It should be noted that, even though *Australopithecus anamensis/ afarensis* eats more than fruit and has been parameterised to also include USOs and meat in its diet, nesting locations only assess the presence of fruits. This is because fruit is the preferred food, and nesting locations are therefore selected to be in close proximity to their preferred food source. Meat is preferred over fruit, but this is an opportunistic food source, individuals only scan their immediate surrounding for meat, and do not actively search for it. Additionally, only temperature/ luminosity day are included in selecting a location (as opposed to night). In this case, individuals select locations that are not too hot or light during daytime, with respect to nest building in the evening and leaving the nest in the morning. Even though individuals have a thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Resting	Temperature (day) ≤ 50, luminosity (day) ≤ 50, tree height ≥ 1, canopy cover ≥ 0, canopy connectivity ≥ 0, understory density ≤ 50, tree density ≥ 50, food tree density ≥ 50, number fruit ≥ 3.5, and amount water ≥ 50.	Rules on where to nest for *Australopithecus anamensis/ afarensis* followed the specified resting patterns for chimpanzees in Ch4 and were also in line with the *Australopithecus anamensis/ afarensis* nesting patterns. As such, similar to chimpanzees, *Australopithecus anamensis/ afarensis* would gain the same amount of fatigues simply by existing at each time step, would lose an equal amount of fatigue while resting each time step, and would have similar where- and when-criteria for nesting. Exact data for any of the environmental variables important for resting were not specified, and criteria were therefore chosen randomly for the model, based on knowledge-based assumptions: Individuals would prefer to rest at cooler and shadier locations and at locations with higher trees (use the same criterion as for nesting and feeding, as similar locations can be expected), higher canopy cover and connectivities (use the same criterion as for nesting as similar locations can be expected), lower understory densities and higher tree and food tree densities, and with enough fruit (i.e. more than 3.5 fruits) and water (i.e. more than 50 hydrations) available. It should be noted that, even though *Australopithecus anamensis/ afarensis* eats more than fruit and has been parameterised to also include USOs

Parameter	Value	Justification
		and meat in its diet, nesting locations only assess the presence of fruits. This is because fruit is the preferred food, and nesting locations are therefore selected to be in close proximity to their preferred food source. Meat is preferred over fruit, but this is an opportunistic food source, individuals only scan their immediate surrounding for meat, and do not actively search for it. Even though individuals have a thermoregulatory advantage, shadier, cooler areas are still assumed to be preferred.
• Travel	-	Within the model, travel is assumed to be a goal-directed behaviour, based on findings from current literature based on findings from chimpanzees. No criteria are set as to where *Australopithecus anamensis/ afarensis* can or cannot travel, as this would restrict individual decisions and enforce the model rules. Preferred vegetation features and micro-climate characteristics will follow from the model results. In this way, only the 'goal activities' will have strict 'where-criteria'. Within the travel procedure, individuals will first check the vegetation features and micro-climate characteristics of their current patch and select this patch for their goal activity if the patch abides to all criteria. If not, individuals will subsequently look at its neighbouring patches within 50m for a suitable patch, will then look at its surrounding patches within 100m for a suitable patch, or will 'jump' a random 3 – 6 patches (150 – 300m) to start a search there. Based on findings from chimpanzees and the hominin model of Griffith et al. (2010), *Australopithecus anamensis/ afarensis* is expected to 'see' a maximum of 100m in all directions, and is expected to travel a maximum of 300m within 10min (chimp literature: Bates & Byrne 2009).
• Relative importance		Similar to Ch4, no relative importance is included within the model. Vegetation features or micro-climate characteristics are either important for a specific behaviour, or they are not. An individual investigates the most important variables first, but all important variables are still included.
When		As no explicit data are presented for when *Australopithecus anamensis/ afarensis* perform their daily activities, when-rules follow the rationale outlined for the chimpanzee model of Ch4: Based on general knowledge assumptions, overall for the model, it is specified that individuals must first assess whether it is dark/night. In this case, the only option for individuals is to nest. During daytime, an individual must first decide whether the current weather conditions impair its daily activities. If so, an individual must rest. If not, it is expected that drinking is most important due to the importance of water, followed by feeding for gaining energy. This is, however, relative, as an individual can be more hungry than thirsty, in which case it will feed. If no need for feeding or drinking, an individual will rest.
• Feeding	Energy ≤ 144 and energy < hydration.	Following the rationale of Ch4: An individual should feed when it is hungry (and more hungry than thirsty). The feeding criterion is based on random variables and the assumption that individuals would like to maintain a neutral energy balance: in total 288 energy will be lost during a model run (see below), 144 of which will be lost during nighttime nesting. As long as an individual keeps its energy above 144 during daytime, it will be prepared for nesting.
• Drinking	Hydration ≤ 72 and hydration ≤ energy.	Following Ch4, an individual should drink when it is thirsty (and more thirsty than hungry). The drinking criterion is based on random variables and the assumption that individuals would like to maintain a neutral hydration (i.e. water) balance: in total 144 hydration will be lost during a model run (see below), 72 of which will be lost during nighttime nesting. As long as an individual keeps

Parameter	Value	Justification
		its hydration above 72 during daytime, it will be prepared for nesting.
- Nesting	Time steps > 72.	Individual should nest when it is dark (i.e. after 12 hours, and thus after 72 time steps of 10 minutes). Nesting is the only option at nighttime, similar to Ch4.
- Resting	Rainfall > 25, or temperature > 29, or fatigue ≥ 73, or energy ≥ 144 and hydration ≥ 73.	As outlined in Ch4, individuals should rest when it is too wet and/or rains too hard (put at > 25mm, as this is generally considered as a wet day), when it is too hot (put at > 29°C, as temperatures above this value are outside the thermoneutral range for chimpanzees), when they are too tired (it could be assumed that individuals would like to maintain a neutral fatigue balance: in total 144 fatigues will be gained during a model run (see below), of which only 72 will be lost during nighttime nesting. As long as an individual keeps its fatigue below 72 during daytime, it will be prepared for nesting), or when there is nothing else to do.
- Travel	-	Following the rationale of Ch4: Travel is incorporated within the behavioural procedures of feeding, drinking, nesting and resting, and is goal directed. Individuals will choose to travel if their current patch is not suitable for their selected activity.
How much		
- Initial	Energy: 0-10, hydration: 0-10, fatigue: 0-10.0	As no data are presented on initial energy, hydration, and fatigue levels for *Australopithecus anamensis/ afarensis*, initial levels follow the rationale outlined in Ch4 for chimpanzees: As there is no literature data (see Chapter 2) on how much energy, hydration, and fatigue individuals start off with in the morning, these values are randomly set between 0 and 10, in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step. Similar to chimps, hominins start off their day by feeding and/or drinking (Ch2).
- Existing	Energy: -2; hydration: -1; fatigue: +1.	Following Ch4, *Australopithecus anamensis/ afarensis* lost 2 energies, lost 1 hydration and gained 1 fatigue simply by existing in order to keep it within the same order of magnitude of energy, hydration, and fatigue gained and lost each time step and no data exist to inform this study otherwise.
- Feeding-fruit	Energy: +10.85 kCal (3.1kCal per fruit)	Similar to Ch4, *Australopithecus anamensis/ afarensis* fruit intake has been specified as follows: based on chimpanzee literature data (Chapter 2), 1 gram of dry weight of fruits contains 3.1kCal of energy (including fig fruit and non-fig fruit). Hourly energy intake rates are not specified for chimpanzees or *Au. anamensis/ afarensis*. In reality, individuals would lose a lot of energy every 10 minutes due to mechanisms such as food processing. However, in order to keep the model simple and losses and gains in the same order of magnitude, it is assumed, after model calibration, that individuals would be able to gain at least 10.85 kCal of energy net each time step, i.e. eating 3.5 fruits (after calibration calculations). On average, it is assumed that a fruit contains between 70 – 95% water, the remainder is called dry weight. Even though this may seem a small energy gain per 10min (i.e. a limited amount of fruits eaten per time step), this is a simplification to keep all internal states gains and losses within a similar order of magnitude.
- Feeding-USOs	Energy: + 7.49kCal (2.14kCal per USO)	For USOs, it has been specified that 1 gram of edible dry weight tuber, contains 2.14kCal of energy. As USOs are fallback foods, similar intake rates to fruit can be expected, i.e. if an individual cannot obtain its 3.5 gram dry weight of fruit, it will be looking for 3.5 gram dry weight of another food source.
- Feeding-meat	Energy + 18.305 kCal (5.23 kCal per gram meat dry weight).	Following the modelling paper of Griffith et al. (2010), meat contains 1.57kCal in energy per gram wet weight. When conferring this to dry weight, it is specified that meat consists of about 70% water and the remaining 30%

Parameter	Value	Justification
		is dry weight, this can be set at 1.57kCal/ 0.3grams of dry weight meat. To keep the model consistent and energy gains and losses within the same order of magnitude, it is assumed that 3.5 grams of meat dry weight can be eaten each time step. This is necessarily low due to consistency and simplification reasons of the model. Per feeding bout 18.305 kCal can thus be gained, making meat the preferred food item.
• Drinking	Hydration + 50	As no data are presented on hydration gain while drinking for *Australopithecus anamensis/ afarensis*, hydration gains follow the rationale outlined in Ch4 for chimpanzees, and it was assumed that individuals could gain a lot of hydration during each drinking bout. This is based on the observation that chimpanzees do not spent a lot of time drinking each day.
• Nesting	+2 fatigues	As no data are presented on fatigue loss while nesting for *Australopithecus anamensis/ afarensis*, fatigue losses follow the rationale outlined in Ch4 and it is specified that individuals lose 1 fatigue each time step spent nesting.
• Resting	+2 fatigues	Similarly for *Australopithecus anamensis/ afarensis*, fatigue losses while resting are specified to 1 fatigue per time step nesting (following Ch4).
• Travel	Energy: -2.9 kCal per 50m. Travelling more than 50m: lose 0.8 extra hydrations and gain 0.8 extra fatigues for each extra 50m travelled.	For Ch4, chimpanzee energy and hydration loss, and fatigue gained for travel was calculated as follows: Based on an average daily path length of 3.0km and an average energy expenditure for travel of 207.3kCal/day, energy lost per 50m travelled equals about 3.5kCal. As chimpanzees can travel between 50 – 300m, energy loss due to travel is somewhere between -3.5kCal and -21kCal. For every extra 50m travelled (so when travelling between 100 – 300m) an additional hydration will be lost, and an extra fatigue will be gained, as an individual is travelling faster. Pontzer et al. (2009) specified human, chimp, and *Australopithecus afarensis* walking costs to 0.08 O_2/kg/m, 0.17 O_2/kg/m, and 0.14 O_2/kg/m respectively. Even though this is not the same unit over measurement as used for the model, it can be used for scaling. If 0.17 O_2/kg/m equals 3.5 kCal for every 50m in chimpanzees, 0.14 O_2/kg/m equals 2.9 kCal for every 50m in *Australopithecus afarensis*. Similarly, if 0.17 O_2/kg/m equals 1 hydration lost and 1 fatigue gained for every extra 50m in chimps, 0.14 O_2/kg/m would equal 0.8 hydrations lost and 0.8 fatigues gained for every extra 50m in *Australopithecus afarensis*. These values will be used for travel in the model.
Output		Output was kept similar to the generic model presented in Chapter 4 for comparison reasons.
Feeding-fruit	+1 for each time step spent feeding on fruit.	Based on 144 time steps in the model, each time step spent on feeding-fruit will add +1 to the feeding-fruit column in the output table. This way, the amount of time spent feeding and feeding-fruit over a 24-hour period can easily be assessed.
Feeding-USOs	+1 for each time step spent feeding on USOs.	Based on 144 time steps in the model, each time step spent on feeding-USOs will add +1 to the feeding-USOs column in the output table.
Feeding-meat	+1 for each time step spent feeding on meat	Based on 144 time steps in the model, each time step spent on feeding-meat will add +1 to the feeding-meat column in the output table. .
Drinking	+1 for each time step spent drinking.	Based on 144 time steps in the model, each time step spent on drinking will add +1 to the drinking column in the output table.
Nesting	+1 for each time step spent nesting.	Based on 144 time steps in the model, each time step spent on nesting will add +1 to the nesting column in the output table.
Resting	+1 for each time step spent resting.	Based on 144 time steps in the model, each time step spent on resting will add +1 to the resting column in the output table.

Parameter	Value	Justification
Travel	+1 for each time step spent travelling.	Based on 144 time steps in the model, each time step spent on travelling will add +1 to the resting column in the output table.
Forest	+1 for each time step spent in forest.	Based on 144 time steps in the model, each time step spent in forest will add +1 to the forest column in the output table.
Woodland	+1 for each time step spent in woodland.	Based on 144 time steps in the model, each time step spent in woodland will add +1 to the woodland column in the output table.
Savannah	+1 for each time step spent in savannah.	Based on 144 time steps in the model, each time step spent in savannah will add +1 to the savannah column in the output table.
Feed-fruit-forest	+1 for each time step spent on feeding on fruit in forest.	Based on 144 time steps in the model, each time step spent on feeding-fruit in forest will add +1 to the feeding-fruit-forest column in the output table.
Feed-fruit-woodland	+1 for each time step spent on feeding on fruit in woodland.	Based on 144 time steps in the model, each time step spent on feeding-fruit in woodland will add +1 to the feeding-fruit-woodland column in the output table.
Feed-fruit-savannah	+1 for each time step spent on feeding on fruit in savannah.	Based on 144 time steps in the model, each time step spent on feeding-fruit in savannah will add +1 to the feeding-fruit-savannah column in the output table.
Feed-USOs-forest	+1 for each time step spent on feeding on USOs in forest.	Based on 144 time steps in the model, each time step spent on feeding-USOs in forest will add +1 to the feeding-USOs-forest column in the output table.
Feed-USOs-woodland	+1 for each time step spent on feeding on USOs in woodland.	Based on 144 time steps in the model, each time step spent on feeding-USOs in woodland will add +1 to the feeding-USOs-woodland column in the output table.
Feed-USOs-savannah	+1 for each time step spent on feeding on USOs in savannah.	Based on 144 time steps in the model, each time step spent on feeding-USOs in savannah will add +1 to the feeding-USOs-savannah column in the output table.
Feed-meat-forest	+1 for each time step spent on feeding on meat in forest.	Based on 144 time steps in the model, each time step spent on feeding-meat in forest will add +1 to the feeding-meat-forest column in the output table.
Feed-meat-woodland	+1 for each time step spent on feeding on meat in woodland.	Based on 144 time steps in the model, each time step spent on feeding-meat in woodland will add +1 to the feeding-meat-woodland column in the output table.
Feed-meat-savannah	+1 for each time step spent on feeding on meat in savannah.	Based on 144 time steps in the model, each time step spent on feeding-meat in savannah will add +1 to the feeding-meat-savannah column in the output table.
Drink-forest	+1 for each time step spent on drinking in forest.	Based on 144 time steps in the model, each time step spent on drinking in forest will add +1 to the drink-forest column in the output table.
Drink-woodland	+1 for each time step spent on drinking in woodland.	Based on 144 time steps in the model, each time step spent on drinking in woodland will add +1 to the drink-woodland column in the output table.
Drink-savannah	+1 for each time step spent on drinking in savannah.	Based on 144 time steps in the model, each time step spent on drinking in savannah will add +1 to the drink-savannah column in the output table.
Nest-forest	+1 for each time step spent on nesting in forest.	Based on 144 time steps in the model, each time step spent on nesting in forest will add +1 to the nest-forest column in the output table.
Nest-woodland	+1 for each time step spent on nesting in woodland.	Based on 144 time steps in the model, each time step spent on nesting in woodland will add +1 to the nest -woodland column in the output table.
Nest-savannah	+1 for each time	Based on 144 time steps in the model, each time step spent

Parameter	**Value**	**Justification**
	step spent on nesting in savannah.	on nesting in savannah will add +1 to the nest-savannah column in the output table.
Rest-forest	+1 for each time step spent on resting in forest.	Based on 144 time steps in the model, each time step spent on resting in forest will add +1 to the rest-forest column in the output table.
Rest-woodland	+1 for each time step spent on resting in woodland.	Based on 144 time steps in the model, each time step spent on resting in woodland will add +1 to the rest -woodland column in the output table.
Rest-savannah	+1 for each time step spent on resting in savannah.	Based on 144 time steps in the model, each time step spent on resting in savannah will add +1 to the rest-savannah column in the output table.
Travel-forest	+1 for each time step spent on travelling in forest.	Based on 144 time steps in the model, each time step spent on travelling in forest will add +1 to the travel-forest column in the output table.
Travel-woodland	+1 for each time step spent on travelling in woodland.	Based on 144 time steps in the model, each time step spent on travelling in woodland will add +1 to the travel - woodland column in the output table.
Travel-savannah	+1 for each time step spent on travelling in savannah.	Based on 144 time steps in the model, each time step spent on travelling in savannah will add +1 to the travel - savannah column in the output table.
Daily path length	+50m for each patch travelled.	For each 50m travelled, 50m is added to the daily path length column in the output table.
Energy	Various	Each time energy is gained and/or lost, this is updated in the energy column of the output table.
Hydration	Various	Each time hydration is gained and/or lost, this is updated in the hydration column of the output table.
Fatigue	Various	Each time fatigue is gained and/or lost, this is updated in the fatigue column of the output table.
Fruit intake	+ 3.5 for each feeding bout feeding on fruit.	After each feeding bout feeding on fruit, the amount of fruits eaten is updated with +3.5 in the fruit intake column in the output table.
USO intake	+ 3.5 for each feeding bout feeding on fruit.	After each feeding bout feeding on USOs, the amount of USOs eaten is updated with +3.5 in the USO intake column in the output table.
Meat intake	+ 3.5 for each feeding bout feeding on fruit.	After each feeding bout feeding on meat, the amount of meat eaten is updated with +3.5 in the meat intake column in the output table.
Water intake	+ 50 for each drinking bout.	After each drinking bout, the amount of water drunk is updated in the water intake column in the output table.
Chimp land use	-	Output table (.csv) for further analyses.
Chimp activity	-	Output table (.csv) for further analyses.
Chimp site selection	-	Output table (.csv) for further analyses.

APPENDIX 6.11

Additional test statistics for the *Ardipithecus* and *Australopithecus* models presented in Chapter 6

Statistical analyses additional to the ones presented in Chapter 6 are outlined below to assess how time spent on different activities in different vegetation types differed between landscapes and between hominid species. Kruskal-Wallis tests ($\alpha = 0.05$) were used to assess overall differences. In case of significant differences, *post-hoc* Mann-Whitney U tests were used to evaluate where this difference occurred; the Bonferroni correction ($\alpha = 0.05 / 3 = 0.0167$) was used to control for multiple comparisons. Time spent feeding on USOs was only compared for *Ardipithecus* and *Australopithecus*, and time spent feeding on meat was only tested for *Australopithecus*. Note that the findings for chimpanzees are a replica of those presented in Chapter 4; findings are included here only for hominid model comparisons. Time spent on different activities in different vegetation types for chimpanzees, *Ardipithecus* and *Australopithecus* is outlined in Figures A6.11.1 – A6.11.3.

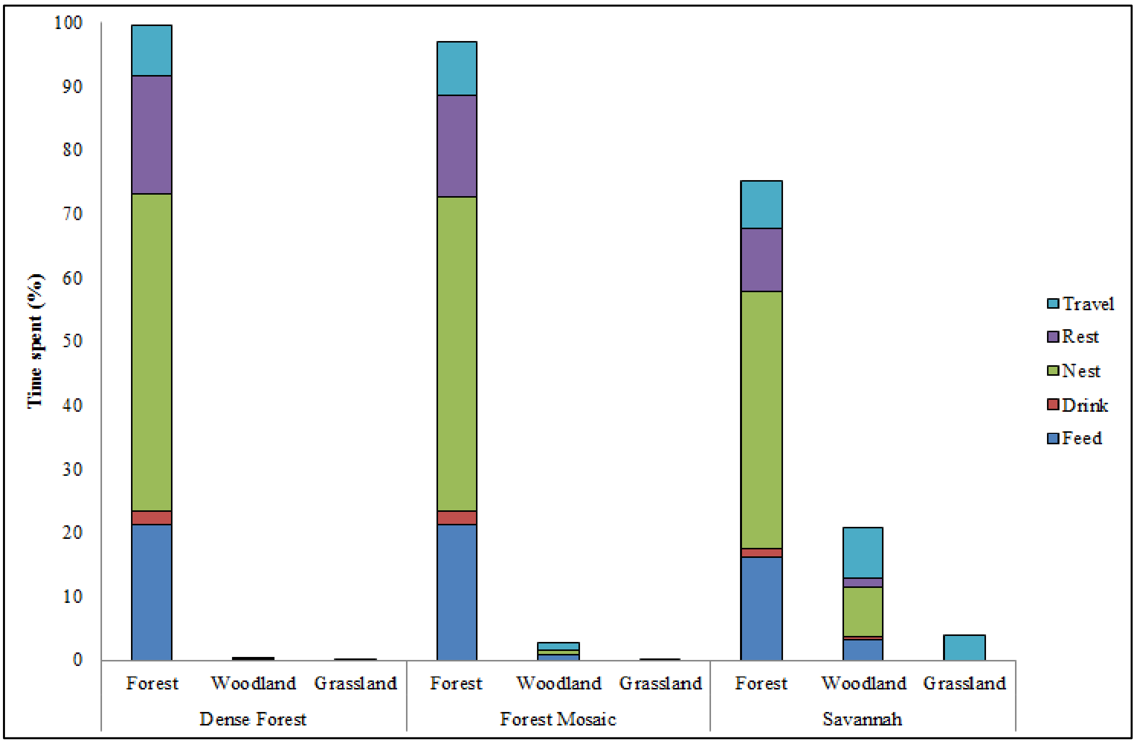


Figure A6.11.1. Model output for time spent on different activities (i.e. feeding, drinking, nesting, resting and travelling) in different vegetation types (i.e. forest, woodland, and grassland) for chimpanzees in dense forest, forest mosaic and savannah environments (Chapter 4). Note that this figure is a replica of the figure presented in Chapter 4 (Figure 4.12). For chimpanzees, feeding time is spent only on fruit.

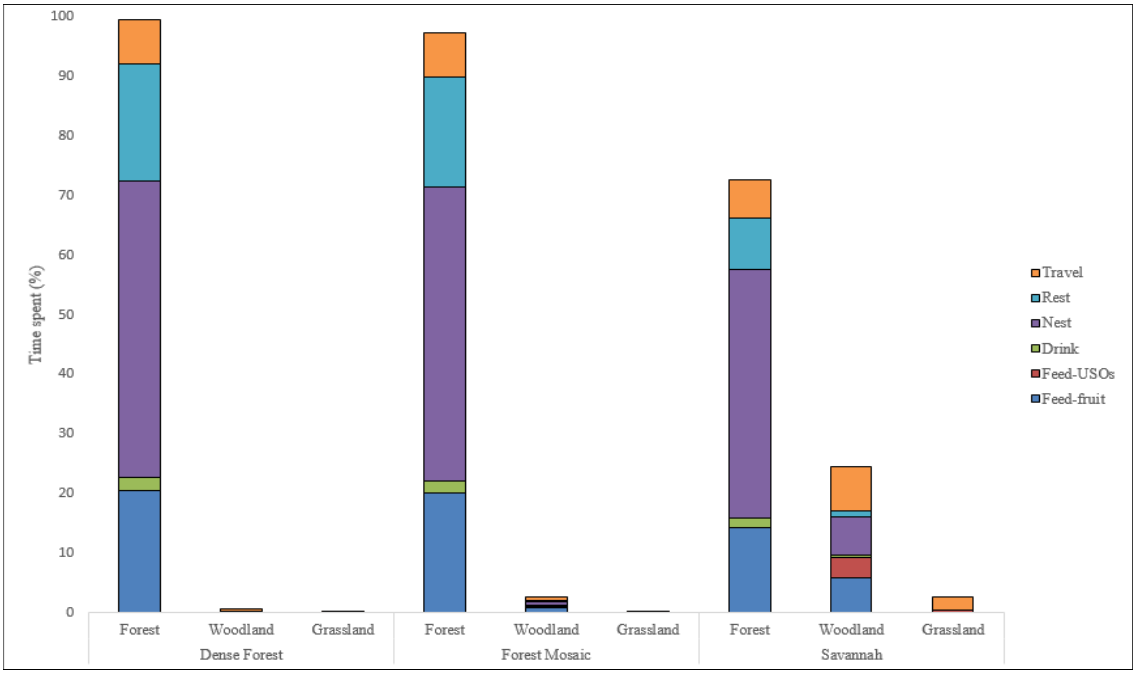


Figure A6.11.2. Model output (24 hours) for time spent on different activities (i.e. feeding, drinking, nesting, resting and travelling) in different vegetation types (i.e. forest, woodland, and grassland) for *Ardipithecus* in dense forest, forest mosaic and savannah environments (Chapter 6). For *Ardipithecus*, feeding time is spent on fruit and USOs.

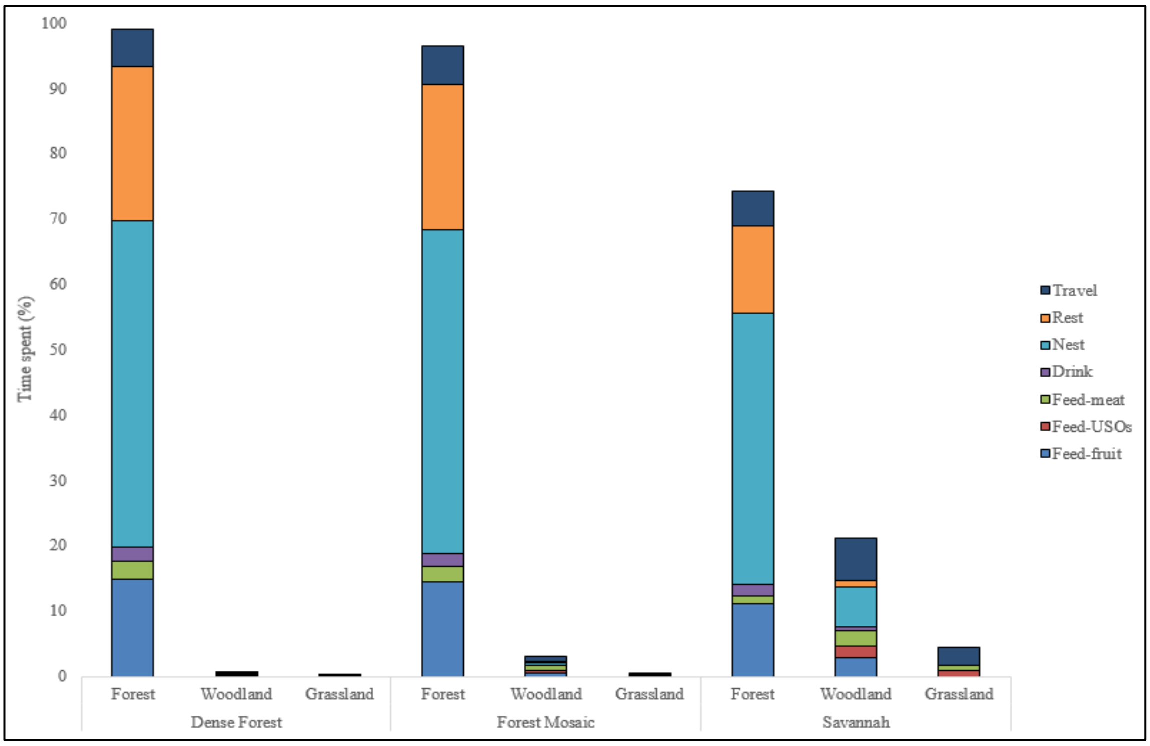


Figure A6.11.3. Model output (24 hours) for time spent on different activities (i.e. feeding, drinking, nesting, resting and travelling) in different vegetation types (i.e. forest, woodland, and grassland) for *Australopithecus* in dense forest, forest mosaic and savannah environments (Chapter 6). For *Australopithecus*, feeding time is spent on fruit, USOs and meat.

Comparing behavioural vegetation type usage across landscapes

Although feeding on fruit, nesting, drinking and resting were never observed in grassland for chimpanzees, *Ardipithecus* and *Australopithecus*, and feeding on USOs was never observed in forest vegetation, time spent on other activities within different vegetation types differed significantly for the three hominid species between environments (in all cases, Kruskal-Wallis tests: $N_{1,2,3} = 30$, $H \geq 28.4$, $df = 2$, $p < 0.001$). When comparing time spent in forest vegetation types for example (Table A6.11.1), it could be shown that across the three species, individuals in dense forests spent significantly more time nesting, resting and drinking in forest vegetation as compared to individuals in mosaic and savannah landscapes, and individuals in mosaics spent significantly more time nesting, resting, and drinking in forest vegetation than individuals in savannahs (Table A6.11.2). For all three species, individuals in forests and mosaics travelled and fed on fruit for significantly more time in forest vegetation than individuals in savannah environments. Chimpanzees in dense forests travelled for significantly more time and fed on fruit for significantly less time in forest vegetation as compared to mosaic landscapes. *Ardipithecus* and *Australopithecus* in forest and forest mosaic environments did not differ significantly in their time spent travelling in forest vegetation, but feeding on fruit in forest was significantly more in forests as compared to mosaics. *Australopithecus* in forests spent significantly more time feeding on meat in forest vegetation types as compared to mosaic and savannah landscapes, and *Australopithecus* in mosaics spent significantly more time feeding on meat in forest vegetation than *Australopithecus* in savannah landscapes (Table A6.11.2).

For time spent in woodland vegetation types (Table A6.11.1), it could be shown that, for all three hominid species, individuals in savannah environments spent significantly more time drinking, nesting, resting, travelling and feeding on fruit in woodland vegetation types than individuals in forests and mosaics, and individuals in mosaics spent significantly more time on nesting, resting, drinking, travelling and feeding on fruit in woodland as compared to individuals in forests (Table A6.11.2). For *Ardipithecus* and *Australopithecus*, individuals spent significantly more time feeding on USOs in woodland vegetation in savannah environments as compared to forests and mosaics, and in mosaic landscapes as compared to forests. For *Australopithecus*, feeding time on meat in woodland was significantly less for individuals in forests as compared to mosaics and savannahs, and for mosaics as compared to savannahs (Table A6.11.2).

When comparing time spent in grassland vegetation types (Table A6.11.1), model results showed that across the three species, individuals in savannah environments spent significantly more time travelling in grassland than individuals in forests and mosaics, and individuals in mosaic landscapes spent significantly more times travelling in grassland than in forests (Table A6.11.2). *Ardipithecus* and *Australopithecus* fed for significantly more time on USOs in grassland in savannah environments as compared to forests and mosaics, but time spent feeding on USOs in grassland did not significantly differ between forests and forest mosaics. *Australopithecines* fed on meat for significantly more time in grassland in savannah landscapes as compared to forests and mosaics, and significantly more in mosaics as compared to forests (Table A6.11.2).

Comparing behavioural vegetation type usage across species

Time spent on different activities in different vegetation types differed significantly between chimpanzees, *Ardipithecus* and *Australopithecus* across landscapes (in all cases, Kruskal-Wallis tests: $N_{1,2,3} = 30$, $H \geq 7.3$, $df = 2$, $p \leq 0.025$). Exceptions were 1) time spent nesting in woodland vegetation in dense forest, forest mosaic and savannah environments, 2) time spent resting in woodland vegetation in dense forests and forest mosaics, 3) time spent nesting in savannah environments, and 4) time spent drinking in forest and woodland vegetation in dense forests. Across environments, feeding on fruit, nesting, resting and drinking were never observed in grassland vegetation types across species. Similarly, feeding on USOs for *Ardipithecus* and *Australopithecus* was never observed in forest vegetation types.

Across forest, mosaic and savannah environments, chimpanzees spent significantly more time feeding on fruit and travelling in forest vegetation types as compared to *Ardipithecus* and *Australopithecus*, and *Australopithecus* travelled and fed on fruit for less time in forest vegetation than *Ardipithecus* (Table A6.11.3). Similarly, *Australopithecus* spent significantly more time feeding on USOs in grassland than *Ardipithecus* across environments, and time spent resting in forest vegetation was significantly more for *Australopithecus* as compared to chimpanzees and *Ardipithecus*, and significantly less for chimpanzees than *Ardipithecus* across landscapes (Table A6.11.3).

Across forest and mosaic environments, *Australopithecus* spent significantly more time nesting in forest vegetation types than chimpanzees, time spent nesting in forest vegetation was not significantly different for chimpanzees and *Ardipithecus*, and for *Ardipithecus* and *Australopithecus*, and additionally no significant differences were observed in time spent feeding on USOs in woodland for *Ardipithecus* and *Australopithecus* (Table A6.11.3). In savannah environments, however, *Ardipithecus* spent more time feeding on USOs in woodland than *Australopithecus* (Table A6.11.3).

Table A6.11.1. Model output (i.e. mean ± standard deviation) on time spent on different activities (i.e. feeding, drinking, nesting, resting and travelling) in different vegetation types (i.e. forest, woodland and grassland) for chimpanzees, *Ardipithecus ramidus* and *Australopithecus anamensis/ afarensis* simulated in dense forest (F), forest mosaic (M) and savannah (S) landscapes. Chimpanzees are parameterised to only feed on fruits, *Ardipithecus* feeds on fruits and underground storage organs (USOs), and *Australopithecus* feeds on meat, fruit and USOs.

	Chimpanzees			***Ardipithecus***			***Australopithecus***		
	F	**M**	**S**	**F**	**M**	**S**	**F**	**M**	**S**
Feed-fruit-forest	21.1±0.8	21.3±1.9	16.0±6.1	20.6±0.9	20.1±2.0	14.2±5.4	14.8±3.3	14.5±3.5	11.2±4.4
Feed-fruit-woodland	0.1±0.4	0.8±1.5	3.3±2.8	0.2±0.6	0.9±1.8	5.8±4.1	0.1±0.4	0.5±1.2	2.8±2.7
Feed-fruit-grassland	-	-	-	-	-	-	-	-	-
Feed-USOs-forest	-	-	-	-	-	-	-	-	-
Feed-USOs-woodland	-	-	-	0.1±0.3	0.3±0.9	3.4±3.0	0.1±0.3	0.3±0.8	1.8±2.0
Feed-USOs-grassland	-	-	-	0.0±0.0	0.0±0.1	0.5±1.2	0.1±0.3	0.1±0.5	0.9±1.5
Feed-meat-forest	-	-	-	-	-	-	2.8±1.8	2.3±1.9	1.1±1.5
Feed-meat-woodland	-	-	-	-	-	-	0.2±0.8	0.8±1.4	2.4±2.1
Feed-meat-grassland	-	-	-	-	-	-	0.1±0.5	0.2±0.7	0.9±1.3
Drink-forest	2.1±0.1	2.0±0.3	1.5±0.8	2.1±0.1	2.0±0.2	1.7±0.6	2.1±0.1	2.0±0.3	1.8±0.6
Drink-woodland	0.0±0.1	0.1±.03	0.4±0.4	0.0±0.1	0.1±0.2	0.5±0.6	0.0±0.1	0.1±0.3	0.5±0.5
Drink-grassland	-	-	-	-	-	-	-	-	-
Nest-forest	49.8±0.9	49.3±4.2	40.3±18.1	49.9±0.8	49.2±4.3	41.6±16.8	49.9±0.4	49.5±2.8	41.5±16.8
Nest-woodland	0.1±0.7	0.5±4.0	7.6±17.4	0.1±0.6	0.7±4.2	6.4±16.0	0.0±0.2	0.4±2.6	6.3±15.7
Nest-grassland	-	-	-	-	-	-	-	-	-
Rest-forest	18.4±2.5	16.0±0.4	9.8±5.8	19.6±2.2	18.4±3.3	8.8±5.7	23.6±2.8	22.4±3.8	13.4±7.1
Rest-woodland	0.0±0.1	0.1±0.6	9.8±5.8	0.0±0.1	0.1±0.7	0.9±2.1	0.0±0.2	0.2±0.8	0.9±2.5
Rest-grassland	-	-	-	-	-	-	-	-	-
Travel-forest	8.1±1.7	8.3±2.1	7.6±3.0	7.4±1.5	7.4±1.7	6.4±2.7	5.9±1.6	5.8±1.7	5.3±2.3
Travel-woodland	0.1±0.4	1.2±1.8	8.1±6.2	0.1±0.3	0.7±1.4	7.6±5.5	0.2±0.5	0.8±1.4	6.4±5.5
Travel-grassland	0.1±0.2	0.2±0.5	4.0±4.2	0.0±0.0	0.1±0.3	2.1±3.0	0.1±0.2	0.2±0.4	2.8±3.5

Table A6.11.2. *Post-hoc* Mann-Whitney U tests statistics for the comparisons of time spent on different activities in different vegetation types for chimpanzees, *Ardipithecus* and *Australopithecus* across dense forest (F), forest mosaic (M) and savannah (S) environments. '*' denotes a significant difference. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)								
	Chimpanzees			***Ardipithecus***			***Australopithecus***		
	F vs M	**F vs S**	**M vs S**	**F vs M**	**F vs S**	**M vs S**	**F vs M**	**F vs S**	**M vs S**
Feed-fruit-forest	M > F Z = -3.2*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -5.3*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -3.0*	F > S Z = -6.7*	M > S Z = -6.6*
Feed-fruit-woodland	M > F Z = -6.7*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.6*	S > F Z = -6.7*	S > M Z = -6.7*	M > F Z = -6.6*	S > F Z = -6.7*	S > M Z = -6.7*
Feed-fruit-grassland	-	-	-	-	-	-	-	-	-
Feed-USOs-forest	-	-	-	-	-	-	-	-	-
Feed-USOs-woodland	-	-	-	M > F Z = -6.1*	S > F Z = -6.8*	S > M Z = -6.7*	M > F Z = -6.8*	S > F Z = -6.8*	S > M Z = -6.7*
Feed-USOs-grassland	-	-	-	M = F Z = -2.1**	S > F Z = -7.1*	S > M Z = -7.0*	M = F Z = -2.0**	S > F Z = -7.7*	S > M Z = -6.7*
Feed-meat-forest	-	-	-	-	-	-	F > M Z = -5.5*	F > S Z = -6.7*	M > S Z = -6.7*
Feed-meat-woodland	-	-	-	-	-	-	M > F Z = -6.7*	S > F Z = -6.7*	S > M Z = -6.7*
Feed-meat-grassland	-	-	-	-	-	-	M > F Z = -2.8*	S > F Z = -6.7*	S > M Z = -6.7*
Drink-forest	F > M Z = -5.6*	F > S Z = -7.0*	M > S Z = -6.8*	F > M Z = -4.7*	F > S Z = -7.1*	M > S Z = -6.8*	F > M Z = -5.4*	F > S Z = -6.9*	M > S Z = -6.4*
Drink-woodland	M > F Z = -7.1*	S > F Z = -7.2*	S > M Z = -6.9*	M > F Z = -4.8*	S > F Z = -7.2*	S > M Z = -6.8*	M > F Z = -6.8*	S > F Z = -7.2*	S > M Z = -6.9*
Drink-grassland	-	-	-	-	-	-	-	-	-
Nest-forest	F > M Z = -4.7*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -5.3*	F > S Z = -6.8*	M > S Z = -6.7*	F > M Z = -5.1*	F > S Z = -6.8*	M > S Z = -6.7*
Nest-woodland	M > F Z = -3.7*	S > F Z = -7.0*	S > M Z = -6.7*	M > F Z = -3.9*	S > F Z = -7.0*	S > M Z = -6.6*	M > F Z = -3.2*	S > F Z = -7.1*	S > M Z = -6.8*
Nest-grassland	-	-	-	-	-	-	-	-	-
Rest-forest	F > M Z = -6.7*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -5.9*	F > S Z = -6.7*	M > S Z = -6.7*	F > M Z = -6.2*	F > S Z = -6.7*	M > S Z = -6.7*
Rest-woodland	M > F Z = -3.5*	S > F Z = -6.9*	S > M Z = -6.7*	M > F Z = -4.6*	S > F Z = -6.9*	S > M Z = -6.6*	M > F Z = -4.1*	S > F Z = -6.9*	S > M Z = -6.5*
Rest-grassland	-	-	-	-	-	-	-	-	-
Travel-forest	M > F Z = -3.6*	F > S Z = -3.3*	M > S Z = -4.6*	M = F Z = -0.2**	F > S Z = -5.5*	M > S Z = -5.5*	M = F Z = -1.0**	F > S Z = -4.7*	M > S Z = -4.4*
Travel-woodland	M > F Z = -6.8*	S > F Z = -6.8*	S > M Z = -6.7*	M > F Z = -6.6*	S > F Z = -6.8*	S > M Z = -6.7*	M > F Z = -6.8*	S > F Z = -6.7*	S > M Z = -6.7*
Travel-grassland	M > F Z = -6.4*	S > F Z = -6.9*	S > M Z = -6.7*	M > F Z = -4.6*	S > F Z = -7.1*	S > M Z = -6.7*	M > F Z = -4.4*	S > F Z = -6.8*	S > M Z = -6.7*

*significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$); **no significant difference, i.e. $p > 0.0167$.

Across mosaic and savannah environments, *Australopithecus* travelled for more time in grassland than *Ardipithecus* and chimpanzees, and chimpanzees travelled more time in grassland than *Ardipithecus* (Table A6.11.3). Whereas chimpanzees and *Australopithecus* also travelled for significantly more time in grassland than *Ardipithecus* in forest environments, no significant differences were observed in grassland travel times between chimpanzees and *Australopithecus* (Table A6.11.3).

In dense forests, *Ardipithecus* spent more time feeding on fruit in woodland than *Australopithecus* and chimpanzees, and no significant differences were observed for chimpanzees and *Australopithecus* (Table A6.11.3). Additionally, *Australopithecus* spent more time on travel in woodland than *Ardipithecus*, but differences in time spent travelling in woodland were not significantly different between *Ardipithecus* and chimpanzees, and between chimpanzees and *Australopithecus* (Table A6.11.3).

Within mosaic landscapes, time spent drinking in forest was not significantly different between species (Table A6.11.3). *Australopithecus* spent significantly less time feeding on fruit in woodland than *Ardipithecus* and chimpanzees, but no significant differences were observed between the latter two species. *Ardipithecus* spent significantly less time drinking and travelling in woodland vegetation as compared to chimpanzees and *Australopithecus*, chimpanzees travelled for more time in woodland than *Australopithecus*, and *Australopithecus* and chimpanzees did not differ significantly in their time spent drinking in woodland (Table A6.11.3).

For savannah environments, it was shown that *Australopithecus* fed significantly less time on fruit in woodland as compared to chimpanzees and *Ardipithecus*, and chimpanzees spent significantly less times feeding on fruit in woodland than *Ardipithecus* (Table A6.11.3). *Australopithecus* spent significantly more time drinking in forest vegetation than *Ardipithecus* and chimpanzees, and chimpanzees drank for less time in forest than *Ardipithecus*. No significant differences were found for time spent drinking in woodland vegetation between *Australopithecus* and *Ardipithecus*, but chimpanzees spent significantly less time drinking in woodland than the two early hominin species. Similarly, no significant differences were observed between early hominins in time spent resting in woodland, but chimpanzees rested for significantly more times in woodland than *Ardipithecus* and *Australopithecus*. Chimpanzees and *Ardipithecus* spent significantly more time travelling in woodland than *Australopithecus*, but time spent travelling in woodland times for chimpanzees and *Ardipithecus* did not differ significantly (Table A6.11.3).

Table A6.11.3. *Post-hoc* Mann-Whitney U tests statistics for the comparisons of time spent on different activities in different vegetation types in dense forest, forest mosaic and savannah environments between chimpanzees (Ch), *Ardipithecus* (Ar) and *Australopithecus* (Au). An '*' denotes a significant difference. In all cases, N = 30.

	***Post-hoc* Mann-Whitney U tests** ($N_{1,2}$ = 30 in all cases)								
	Dense Forest			***Forest Mosaic***			***Savannah***		
	Ch vs Ar	**Ch vs Au**	**Ar vs Au**	**Ch vs Ar**	**Ch vs Au**	**Ar vs Au**	**Ch vs Ar**	**Ch vs Au**	**Ar vs Au**
Feed-fruit-forest	Ch > Ar Z = -6.7*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.4*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -4.4*	Ch > Au Z = -6.6*	Ar > Au Z = -6.3*
Feed-fruit-woodland	Ar > Ch Z = -3.3*	Ch = Au Z = -0.6**	Ar > Au Z = -3.6*	Ch = Ar Z = -1.5**	Ch > Au Z = -3.8*	Ar > Au Z = -4.2*	Ar > Ch Z = -6.5*	Ch > Au Z = -3.7*	Ar > Au Z = -6.6*
Feed-fruit-grassland	-	-	-	-	-	-	-	-	-
Feed-USOs-forest	-	-	-	-	-	-	-	-	-
Feed-USOs-woodland	-	-	Ar = Au Z = -0.5**	-	-	Ar = Au Z = -0.5**	-	-	Ar > Au Z = -6.2*
Feed-USOs-grassland	-	-	Au > Ar Z = -4.2*	-	-	Au > Ar Z = -4.7*	-	-	Au > Ar Z = -5.1*
Drink-forest	-	-	-	Ch = Ar Z = -2.5**	Ch = Au Z = -0.7**	Ar = Au Z = -2.1**	Ar > Ch Z = -5.6*	Au > Ch Z = -6.3*	Au > Ar Z = -3.2*
Drink-woodland	-	-	-	Ch > Ar Z = -4.6*	Ch = Au Z = -2.5**	Au > Ar Z = -3.0*	Ar > Ch Z = -4.7*	Au > Ch Z = -4.8*	Au = Ar Z = -0.5**
Drink-grassland	-	-	-	-	-	-	-	-	-
Nest-forest	Ch = Ar Z = -2.0**	Au > Ch Z = -3.0*	Ar = Au Z = -0.9**	Ch = Ar Z = -0.3**	Au > Ch Z = -2.5*	Ar = Au Z = -2.2**	-	-	-
Nest-woodland	-	-	-	-	-	-	-	-	-
Nest-grassland	-	-	-	-	-	-	-	-	-
Rest-forest	Ar > Ch Z = -6.6*	Au > Ch Z = -6.7*	Au > Ar Z = -6.7*	Ar > Ch Z = -6.6*	Au > Ch Z = -6.7*	Au > Ar Z = -6.7*	Ch > Ar Z = -3.3*	Au > Ch Z = -6.7*	Au > Ar Z = -6.7*
Rest-woodland	-	-	-	-	-	-	Ch > Ar Z = -4.6*	Ch > Au Z = -4.1*	Ar = Au Z = -0.6**
Rest-grassland	-	-	-	-	-	-	-	-	-
Travel-forest	Ch > Ar Z = -6.4*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -6.4*	Ch > Au Z = -6.7*	Ar > Au Z = -6.7*	Ch > Ar Z = -4.8*	Ch > Au Z = -6.5*	Ar > Au Z = -5.3*
Travel-woodland	Ch = Ar Z = -2.1**	Au = Ch Z = -1.9**	Au > Ar Z = -3.6*	Ch > Ar Z = -5.9*	Ch > Au Z = -4.7*	Au > Ar Z = -3.0*	Ch = Ar Z = -2.1**	Ch > Au Z = -5.3*	Ar > Au Z = -4.0*
Travel-grassland	Ch > Ar Z = -6.5*	Ch = Au Z = -2.1**	Au > Ar Z = -4.8*	Ch > Ar Z = -6.4*	Ch > Au Z = -3.0*	Au > Ar Z = -4.5*	Ch > Ar Z = -6.6*	Ch > Au Z = -5.4*	Au > Ar Z = -4.3*

*significant difference, i.e. $p < 0.0167$ (Bonferroni correction applied for *post-hoc* Mann-Whitney U tests: $\alpha = 0.05 / 3 = 0.0167$); **no significant difference, i.e. $p > 0.0167$.