Red Colobus Natural History

Korstjens, A., Hillyer, A., & Koné, I. (2022). Red Colobus Natural History. In I. Matsuda, C. Grueter, & J. Teichroeb (Eds.), *The Colobines: Natural History, Behaviour and Ecological Diversity* (Cambridge Studies in Biological and Evolutionary Anthropology, pp. 108-127). Cambridge: Cambridge University Press. doi:10.1017/9781108347150.010

Red Colobus Natural History (Chapter 9) - The Colobines (cambridge.org)

Final Draft version – July 2020

Amanda H. Korstjens[1], Alison P. Hillyer[2], Inza Koné[3]

1. Bournemouth University, Department of Life and Environmental Sciences, LEAP: Landscape Ecology and Primatology, Poole, UK. akorstjens@Bournemouth.ac.uk

2. Faculty of Animal Science, University Centre Reaseheath, Nantwich, Cheshire CW5 6DF. aphillyer@outlook.com

3. Centre Suisse de Recherches Scientifiques en Côte d’Ivoire, 01 BP 1303 Abidjan 01, Côte d’Ivoire, inza.kone@csrs.ci

Text Pages: 51; Figures: 2; Tables: 6

Abstract

This chapter reviews current knowledge of the red colobus, *Piliocolobus,* a polytypic widespread colobine living in sub-Saharan African forests, woodlands, mangroves, and riparian forests. The taxonomy of *Piliocolobus* has undergone many changes and is still unresolved, resulting in confusion and possibly hindering conservation efforts. Red colobus is known for being the favourite prey of chimpanzees in many locations, and in several populations red colobus associate with guenons to reduce predation risk. Less well-known are their sexual swellings, which vary greatly in size across the genus, and their graded vocal repertoire that lacks a long call, but in some cases includes female mating calls. Noisy, large multi-female multi-male groups, female dispersal, philopatric males that form coalitions, and lack of female allomothering are considered the norm for the genus but these are not universal. Red colobus is facing extirpation in many locations due to human hunting and forest destruction. Various serious diseases and parasites are also reported for many populations and are often associated with human encroachment into their habitat. Much about the social behaviour is yet to be studied, especially in the less-studied central African species assemblage.

Keywords: polytypic; polyspecific association; sexual swellings; threatened; female dispersal; male philopatry; multi-female multi-male groups; red colobus action plan; guenons; cercopithecines; coalitions; copulation calls; parasites; diseases; Treponema; hunting; fragmentation; mangroves.

Introduction

The red colobus, genus *Piliocolobus* (or genus *Procolobus* and subgenus *Piliocolobus*), is a polytypic genus with an unresolved taxonomy. The genus shows wide variation in morphological and behavioural features. The presence of pronounced sexual swellings (which they share with olive colobus), that vary greatly among species, sets this genus apart from sister genus *Colobus*. Red colobus species are wide-spread across sub-Saharan Africa but their distribution is closely linked to the presence of forests because of their largely arboreal lifestyle, and they do not often adapt well to human-dominated landscapes (except *P. kirkii*). The genus *Piliocolobus* is rare among colobines for typically living in large multi-female multi-male social groups with female-biased dispersal and male philopatry. However, several exceptions to this pattern suggest a flexible social system. Red colobus species are Vulnerable to Critically Endangered with the main threats being hunting and forest destruction by human activities.

Taxonomy

Red colobus is considered a monophyletic clade (Wang *et al.* 2012). The taxonomy is disputed but typically has 18 recognised taxonomic groups put into 17-18 species by Mittermeier *et al.* (2013) (Table 1). The difficulty in settling on a taxonomic categorization is likely related to the fact that the taxa occur allo-patrically, with a possible hybrid zone in the Eastern central range (Colyn 1993; Struhsaker 2010) (Figure 1). The Western clade is considered a relatively ancient radiation (Grubb *et al.* 2003; Ting 2008) and consists of a large central range for *P. badius* with closely related species *P. temminckii* to the North-West and the most likely extinct *P. waldroni* to the direct East. West-central Africa has the closely related but isolated species *P. pennantii*, *P. epieni*, and *P. preussi*. In East Africa three isolated species occur: *P. kirkii* on Unguja Island, Zanzibar; *P. gordonorum* in the Udzungwa Mountain range; and *P. rufomitratus* in the Tana River area. *P. tephrosceles* occurs in several isolated populations along the rift valley. A large central African forest area harbours the most taxonomic variation, probably due to contracting and expanding forests in the Pleistocene, it contains: *P. tholloni*, *P. oustaleti*, *P. parmienteri*, *P. foai*, *P. semlikiensis*, *P. ellioti*, *P. bouvieri*, *P. langi*, and undefined species/subspecies *P. lulindicus*. Oates and Ting (2015) argue that the taxonomic confusion may have had implications for the conservation status and protection of different red colobus taxa.

Table 1: Information on taxonomy and main study sites listed per red colobus species.

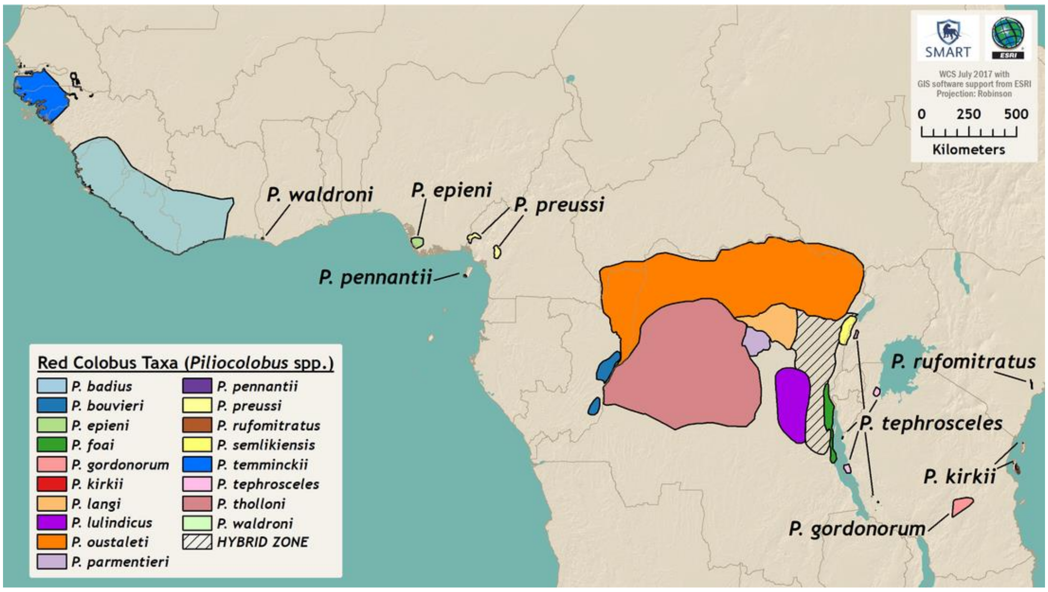

Figure 1: Distribution map of red colobus species from www.Piliocolobus.org permission to use granted by Drew Cronin (see also Cronin et al. 2018)

Morphological Features

Variation in the typically red and black pelage, vocalisations, female sexual swellings, body size (Table 2), and cranial morphology is extensive (Butynski *et al.* 2013; Groves 2007; Grubb *et al.* 2013; Struhsaker 2010). There is distinct sexual dimorphism in crania (males having a sagittal crest and robust orbital ridges) across red colobus taxa but male and female body size differences vary and are less than those among genus *Colobus* (Struhsaker 2010). Cardini and Elton (2009) show that red colobus cranial shape is more driven by phylogeny while size is more sensitive to recent adaptations. They suggest a link between body size and forest productivity as measured by rainfall, but also that smaller size evolved in the more isolated populations (e.g. *P. kirkii* and *P. rufomitratus*). Scapular and forelimb morphology indicates that red colobus have more flexibility in the shoulder to facilitate greater arm flexion, abduction and elevation than genus *Colobus* (Dunham *et al.* 2015, 2017). Taï red colobus (*P. badius*) most commonly use quadrupedal walking (53%), leaping (17.8%) and climbing (17%) when they move but also use arm swing in 3.7% of observations (unlike the other sympatric monkeys), and are mostly found in the upper canopy (McGraw 1998).

Variation in sexual swelling size does not appear to reflect variation in sex ratio in the group and shows an inconsistent relationship with sexual size dimorphism but may be mostly following a phylogenetic signal (Table 2; Korstjens unpublished; Struhsaker 2010). Two interesting but unstudied features restricted to a few species are the small perineal swelling in young males, which resembles the swelling of the females but is made up of adipose tissue (Kuhn 1972), and the presence of an exaggerated female clitoris (Struhsaker 2010; pers. obs.).

Table 2: Body weight and swelling size information for red colobus species.

Distribution

Piliocolobus species occur across sub-Saharan Africa (Figure 1) but have a less wide distribution than the closely related genus *Colobus* (Korstjens & Dunbar 2007). Current distribution and inter-specific variations are likely the result of the combined effects of allopatric speciation, human disturbance leading to severe fragmentation and isolation of populations, human persecution for meat, competition with cercopithecines (which are often better at travelling across fragmented habitats), and climate change (Burgess *et al.* 1998; Cardini & Elton 2009; Delson 1994; Struhsaker 2010; Ting 2008). Most populations are becoming ever more isolated, leading to further morphological and behavioural differences between taxonomic groups. For example, Cardini and Elton (2011) show that *P. eliotti* has a distinct cranial shape and suggest it has had limited genetic influxes in the recent past. Still, more research on these central African species is needed as this species is also considered to grade into *P. langi* and shows variable pelage coloration (Kaisala *et al*. 2020; Grubb *et al*. 2003) Cranial analyses showed that island species *P. kirkii*, has undergone morphologic evolutionary acceleration leading to adaptations to their island habitat (in Zanzibar) with less sexual dimorphism and smaller crania than the nearest continental red colobus species (Nowak *et al.* 2008). Small, fragmented populations could hold valuable representatives of this vulnerable example of primate radiation.

Habitat and Climate

Red colobus are arboreal, forest-dependent species occurring in highest densities in minimally disturbed forest habitats with high levels of tree coverage; while riparian forests or forest fragments are also important (e.g. Gautier-Hion & Brugière 2005).

Zanzibar red colobus (*P. kirkii*) around Jozani inhabits mostly forested land (85.5% of observations, primary, secondary, forest edge, thickets), but is also found in fields with agricultural tree crops (called shambas in the local area and publications; 4.5%), and mangroves (4.5%; Davenport *et al.* 2019). *P. badius* does not use secondary forest as much as other primates in Tiwai island (Fimbel 1994). Likewise, Udzungwa red colobus, *P. gordonorum*, abundance increases in large blocks of mature semi-deciduous and evergreen forest at relatively low elevation with large basal area of trees, abundance of climbers and limited human disturbance (Cavada *et al.* 2019). Higher densities at lower altitudes have been linked to the higher abundance of young leaves (Rovero *et al.* 2009; Rovero & Struhsaker 2007), but *P. gordonorum* has been recorded at up to 2200 m above sea level (asl; Dinesen *et al.* 2001).

In many areas, climate change (especially reduced rainfall and increased heat in Western Africa), human expansion and persecution force the red colobus into forest refuges that are used less by humans e.g.: swamps in the Niger Delta, *P. epieni*: (Grubb & Powell 1999; Luiselli *et al.* 2015); Senegal's mangroves (Galat-Luong & Galat 2005); Gambian coastal forests (pers. obs.; Mayhew *et al*. 2020); and Zanzibar mangroves and marsh lands (Nowak & Lee 2013). Most red colobus populations occur in regions experiencing 22-26°C mean annual temperature and limited temperature variation across months (standard deviations 1.21-3.26°C), with high levels of rainfall (576-1242 mm per year) and good tree cover (30-95%; Figure 2).

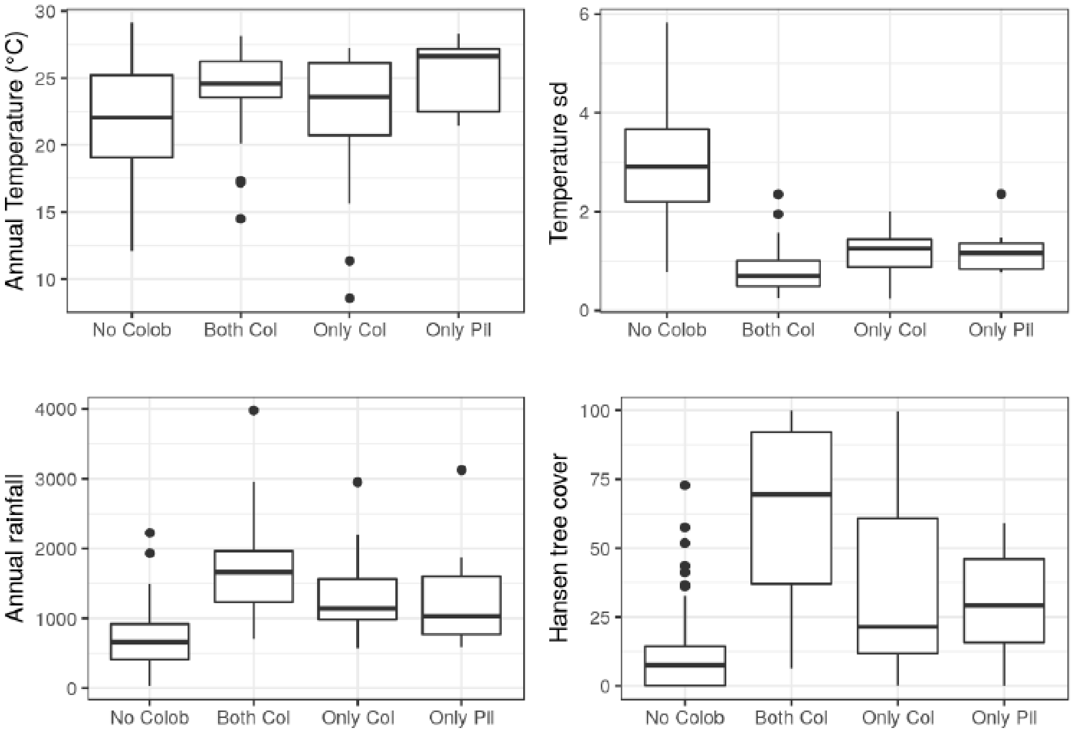

Figure 2: Comparison of mean annual temperature (in °C), mean temperature variation across months (in standard deviation across monthly averages), mean annual rainfall (mm), and Hansen's tree cover value (% of woody cover) for locations with Piliocolobus and Colobus present (Both Col: N=41), with only Colobus present (Only Col: N=51), with only Piliocolobus present (Only Pil: N=7) and without colobines (No Colob: Absent N=103). All sites contained at least one species of diurnal primate and most are based on protected area location data or study site locations with a minimum distance of 1 degree latitude or longitude separation between sites; dataset by Korstjens, Lehmann, and Dunbar, e.g. see Korstjens and Dunbar (2007). The Hansen tree cover measurement, which is based on remote sensing data and not actual tree height data gives a good indication of percentage vegetation cover of approximately >5m height but should not be considered as an absolute value of forest cover. Boxplots show median, quartiles, minimum and maximum (within 1.5 IQR) and outliers.*

Research Efforts

Most recent red colobus research focuses on conservation status, demography, parasites, diseases, and response to fragmentation. The focus on conservation is likely due to the raising of subspecies to species level, a renewed appreciation of the critical status of many red colobus species, and the difficulty of running long-term resource-intensive behavioural studies. A red colobus action plan has brought many red colobus researchers together (see www.*Piliocolobus*.org) to promote more research and conservation to save red colobus species across Africa. There is a distinct lack of red colobus publications dealing with their natural history (demography, group size, diet, behaviour) outside the most intensely studied sites of: Kibale National Park (NP) in Uganda (*P. tephrosceles*; sites Kanyawara, Ngogo, and several forest fragments near the park), Taï NP in Ivory Coast (*P. badius*), Tana river delta in Kenya (*P. rufomitratus*), Zanzibar archipelago Tanzania (*P. kirkii*), and Abuko NP in The Gambia (*P. temminckii*) and many of these studies are not recent (Table 2-6). Long term population trends are available for most of these but also additional sites, including the Udzungwa region in Tanzania (*P. gordonorum*), Korup NP Cameroon (*P. preusii*), Fathala Senegal (*P. temminckii*), and Bioko Island, Equatorial Guinea (*P. pennantii*). There are still many gaps in our knowledge of red colobus biology and the variation across the taxon in their behaviours, demography, and even morphology, especially for the variable central African species-complex.

Feeding Ecology

The most consumed dietary items by red colobus are leaves, fruits, and flowers, with leaf material (including petioles and leaf buds) typically dominating the diet but there is wide variation among sites and months within sites, which is likely the result of fluctuating availability (Table 3). Bark is a common food item in Kibale (0.3-4.5% of annual diet) but less reported elsewhere (Chapman *et al.* 2002). Some geophagy also occurs, mostly from termite mounds, the forest floor and soil from fallen rocks (Pebsworth *et al.* 2019). Diets vary greatly between months (e.g. Tiwai: Davies *et al.* 1999; Taï: Korstjens *et al.* 2007) and between groups occupying different forest areas within the same general region, showing the importance of long term and multi-group studies (Kibale NP: Chapman *et al.* 2002; Chapman & Chapman 1999).

Red colobus density has been linked to density of food trees and leaf quality, in particular a positive relationship to the protein to fibre ratio in leaves (Chapman & Chapman, 2000a; Chapman *et al.* 2002; Oates *et al.* 1990; but for a critique and reanalyses, see Gogarten *et al.* 2012). Red colobus actively select food on the basis of protein to fibre ratio and general digestability, whilst energy content is not selected for (Wasserman & Chapman 2003); but nutrient content and sugar content can also be relatively high (Danish *et al.* 2006). Consumption of low-quality food in one month leads to increased gluco-corticoid (stress) levels in the subsequent month (Chapman *et al.* 2015). Food selection also allows red colobus to buffer against seasonal fluctuations in mineral content within their environment, leading to a relatively stable nutrient intake but a potential shortage of sodium content (Rode *et al.* 2003). Similarly, despite differences in food items and species selection, protein to fibre ratios of food consumed were very similar across seven Kibale area groups (Ryan *et al.* 2013). Red colobus diets may include various food items with high levels of estrogenic compounds which correlated positively with levels of aggression and sexual behaviour but negatively with frequency of grooming in Kibale red colobus (Wasserman *et al.* 2012). In Zanzibar, charcoal eating (incl. from human kilns) helps red colobus with detoxification of secondary compounds from the Indian almond and mango leaves that they consume in the agricultural mosaics near villages (Cooney & Struhsaker 1997; Struhsaker *et al.* 1997).

New non-invasive methods help us gain greater understanding of food selection and health. Chapman *et al.* (2005) showed that faecal nitrogen levels can be used to determine the levels of protein in the diet, and thus habitat quality for colobines, with less need for measuring the nitrogen in the trees that the primates feed from. Measuring physical traits and condition of animals using parallel lasers along with photographs also has great potential for many unanswered questions on temporal and taxonomic variation in physical traits (Rothman *et al.* 2008).

The facio-cranial adaptations of *P. badius* show a relatively limited bite force compared to that of the genus *Colobus*, which supports the observations that *Colobus* more commonly feed on seeds encased within hard (wooded) husks (Koyabu & Endo 2009), but bite-force is still more than expected for a species consuming mostly soft food items (Daegling & McGraw 2001; McGraw *et al.* 2016).

Leaf quality can vary greatly, not only among species but also among individual trees and among sites, although temporal variation in quality was minimal in Kibale (Chapman *et al.* 2003). In Kibale, over a 25-year period (see some variation for that area in Table 3), leaf quality went down for those trees that had been monitored in this time. However, overall food availability and the average quality of leaves across trees in the forest went up because the availability of high quality trees in the forest had increased (Chapman *et al.* 2015). Red colobus' over-consumption of leaves and flowers can result in reduced recruitment and fruiting ability in preferred tree species (Kibale, *Markhamia lutea* (Bignoniaceae): Chapman *et al.* 2013; Zanzibar, Siex 2005). Likewise, they may also have a role as seed dispersers (Koné *et al.* 2008). Red colobus get most of their fluids from their diet and water from arboreal water-reservoirs (leaves, tree holes) but have been observed drinking water more extensively in dry regions or periods (e.g. The Gambia, Hillyer *et al.* 2015; mangrove forests in Zanzibar, Nowak 2008).

Table 3: Diet of red colobus species across their range based on studies of at least 8 months

Activity Patterns

Red colobus activity budgets vary across species, sites and time periods (Table 4). Although data on time budgets is scarce, Korstjens and Dunbar (2007) found that moving time correlated positively with group biomass and negatively with rainfall, while feeding time correlated positively with group size and rainfall variability. The resulting time-budget based models were able to predict distribution patterns of red colobus monkeys as reliable as did standard niche models. Overall, roughly 30-58% of the time is spent resting, 20-46% feeding, 5-22% moving, and 2-12% socializing. Red colobus in an unprotected forest rested more and ate more mature leaves (Chapman *et al.* 2007), consumed food from more plant species and spent more time feeding (Milich *et al.* 2014b) than those in undisturbed forest in and near Kibale NP. Steel (2012) found that *P. gordonorum* fed more and rested less in the dry compared to the wet season.

Table 4. Activity budgets of red colobus studies >8 months with size (Grpsz), number of adult females (AF) and males (AM) of the study groups included, feeding and foraging (feed), climbing and travelling (move), resting and inactive or auto-

grooming (rest) and grooming or social activities (social; for most studies this is equivalent to grooming time as they did not mention other social activities).

Range Use

Red colobus home-ranges vary widely from about 5.5 to 100 ha and daily travel distance from 310 to 1040 m (Table 5). Home range size and day journey length variation over different spatial and temporal scales are at best weakly positively correlated to group size (data in Table 5), but sometimes this expected relationship is only apparent when food availability is considered (Gogarten *et al.* 2014; Isbell 2012). Predation patterns can also affect ranging; for example, Ngogo red colobus decreased group size (Stanford 1995) but increased home range area from 93 ha in 1976-1983 to 257-360 ha in 2001-2002, possibly to reduce encounter rates and predictability in response to chimpanzee hunting (Lwanga *et al.* 2011). In marginal habitats, small red colobus groups may have correspondingly small home ranges as a result of fragmentation and poor food availability (e.g. Zanzibar red colobus in suboptimal habitats had ranges of only 5.5 to 8.8 ha, Nowak & Lee 2011). Red colobus appear to cross their home range in a way that suggests that their food is not patchily distributed. This is also confirmed by studies showing that they select relatively abundant food sources (Isbell 2012; Korstjens *et al.* 2007; Siex & Struhsaker 1999a). Kibale red colobus ranging follows Brownian motion patterns (associated with uniform food distribution) only in the dry season (Reyna-Hurtado *et al.* 2018). Bonnell *et al.* (2013) used an individual-based model to show that red colobus use a landmark-based memory and follow the leader foraging strategy.

Predation

Red colobus monkeys' main natural predators are African crowned eagles (*Stephanoaetus coronatus* [Accipitridae]), chimpanzees (*Pan troglodytes*), and leopards (*Panthera pardus* [Felidae]), but they are also hunted by golden cats (*Caracal aurata* (Felidae)*;* Bahaa-el-din *et al.* 2015), hyenas [Hyaenidae], crocodiles [Crocoddylidae] and large snakes. Royal pythons (*Python regius* [Pythonidae]) and crocodiles preyed on *P. temminckii* in Abuko Nature Reserve, The Gambia in the 1970s-1980s (Starin 1991). Pythons are no longer common in Abuko (APH personal observation; Hillyer, 2013). Hyenas and dogs (*Canis lupus familiaris* [Canidae]) hunt *P. temminckii* in Fathala, Senegal (Galat-Luong & Galat 2005). Overall predation rates on arboreal primates at Taï (by leopards, chimpanzees and crowned eagles) are positively correlated with group density and negatively with group size, putting predation rates on red colobus at an intermediate rate compared to sympatric primates (Shultz *et al.* 2004).

Where leopards occur, they are considered important red colobus predators (Hoppe-Dominik 1984; Struhsaker 2010; Zuberbühler & Jenny 2002). Leopard predation positively correlates with prey population density and body size (Zuberbühler & Jenny 2002). The African crowned eagle is another predator that takes red colobus monkeys of all age-sex classes where it occurs (Mcgraw *et al.* 2006; Mitani *et al.* 2001; Pobiner *et al.* 2007; Struhsaker & Leakey 1990). But, where all three main predators occur, chimpanzees tend to cause the highest mortality (Shultz *et al.* 2004).

Red colobus are often considered preferred prey of chimpanzees (80% of prey in Taï: Boesch 1994; 83% of kills in Ngogo: Watts & Amsler 2013; 83% of prey in Mahale: Hosaka *et al*. 2020). In Taï, chimpanzee hunts occur weekly throughout the year, and even daily in the hunting season (September through November), and individuals of all age-sex classes are killed (Boesch & Boesch-Achermann 2000). In Mahale, red colobus formed 16% of chimpanzee prey before 1976, but this suddenly increased in the 1980s to 83% in the 1990s and 2000s (i.e. >13 kg colobus meat consumed per chimpanzee per year), whilst population density of colobus, group hunting, and female chimpanzee participation in hunting increased (all factors reviewed in Hosaka *et al*. 2020). Chimpanzee hunting is less frequent in Gombe and Kanyawara in Kibale NP, but it still affects red colobus population structure and survival (Struhsaker, 2010). Attack rates in Gombe reach an average of one every 66-80 days (Stanford 1998a).

The highest chimpanzee predation rates occur in Ngogo, where chimpanzees killed around 167 red colobus per year from 1995-1998 and around 322 in 2002, representing 15-53% of the red colobus population (Teelen 2007b, 2008), resulting in a 89% red colobus population decline between 1975 and 2007 (Lwanga *et al.* 2011; Mitani *et al.* 2000; Teelen 2007a). Since 1999, this is the largest known chimpanzee community (total number = 145-205 members, including 24-35 adult males and *ca*. 42-63 adult females), with a 75% success rate per hunting attempt; killing as many as 13 individuals in a single attack (8 of which were infants; Watts & Mitani 2002, 2015). Chimpanzees are more likely to initiate a hunt when encountering red colobus where the forest is more open and trees are shorter (Watts & Mitani 2002), making the colobus more vulnerable. As chimpanzee encounter rates with red colobus are declining, the chimpanzees are hunting other prey more often, although hunting frequency upon encounter with red colobus has remained the same (Watts & Mitani 2015). High cortisol levels in Ngogo colobus may be the result of this intense hunting pressure (Aronsen *et al.* 2015). At nearby Kanyawara, where chimpanzees hunt less, red colobus had elevated cortisol concentrations for up to two days after a chimpanzee attack (Wasserman *et al.* 2013).

Anti-predation strategies

Red colobus anti-predation strategies vary among sites and depend on the predator-prey relationships. Strategies and adaptations include: large group size, arboreality, alarm calling, poly-specific associations, and cooperative defence by males. Red colobus high alarm-calling response is adapted to the hunting strategy of the predators with more calls given to ambush hunters like leopards, who depend on diurnal and crepuscular surprise attacks by hiding and waiting for opportunities in forest areas that primates use frequently (Jenny & Zuberbuhler 2005; Zuberbühler *et al.* 1999), than to pursuit hunters like chimpanzees. In Taï, red colobus will fall silent when chimpanzees are detected at distance and will approach Diana monkey groups if nearby; still, the loud red colobus female copulation calls can often be heard when the rest of the primates in the forest remain silent (pers. observation; McGraw & Zuberbuhler 2008). Similarly, while Diana monkeys adapt their anti-predator behaviour to human hunting strategies (Bshary 2001), red colobus monkey do not (Koné & Refisch 2007).

Red colobus at Gombe and Kibale do not flee like sympatric monkeys when chimpanzees approach, possibly because attack success increases when fleeing is attempted in the relatively open and low forests where attacks are most common (Stanford 1998a). In Kibale and Gombe, group cohesion and vigilance increase when chimpanzees are near (Stanford 1998a p127; Treves 1999). On chimpanzee approach, red colobus re-position whilst alarm calling. The calls change as individuals ascend higher into the canopy. The group will typically fall silent once the chimpanzees are close. If the chimpanzees decide to attack, the colobus initiate alarm calling again. In Gombe, juveniles were the most vulnerable members of the group and alarm call rate increased with the number of immatures present in the group (Stanford 1998a). The sometimes-prolonged attacks influence group repositioning and affect activity budgets. Gombe adult and subadult male colobus counterattack chimpanzees; clustering and alarm-calling, leaping and biting, commonly wounding chimpanzee hands, arms, back and scrotum. They will even jump onto the chimpanzees, sometimes managing to drive the chimpanzees away. More red colobus attacking chimpanzees in unison are better at thwarting an attack (Stanford 1998b). Females will attempt to escape with infants or even try to get them back after they are captured despite the risks to themselves (Stanford 1998a). Counter-attacks by male colobus also occur at Kanyawara, Kibale (A. Georgiev. pers. comm.). In contrast, at Ngogo and Taï, subadults and adults are most commonly killed (Boesch 1994; Teelen 2008). Consequently, all red colobus individuals in a group will seek higher positions in the canopy and will try to escape when under attack.

Red colobus are regularly found in poly-specific associations with cercopithecines, often more than expected by chance (Fathala: Galat-Luong & Galat 2005; Kibale: Chapman & Chapman 2000b; Korup: Astaras *et al.* 2008; Zanzibar: Struhsaker 1999, 2000; Taï: Holenweg *et al.* 1996; Wachter *et al.* 1997). Typically, a long-term partnership among specific guenon and red colobus groups forms (probably due to home-range overlap) (Höner *et al.* 1997). Poly-specific associations with cercopithecines are considered an anti-predation strategy of red colobus against ground predators, in particular chimpanzees, as cercopithecines typically detect ground predators quicker than do colobus (Bshary & Noë 1997a). Support for this suggestion comes from studies showing that red colobus will initiate associations after hearing a chimpanzee vocalisation (Taï: McGraw and Zuberbuhler 2008); and association rates are higher for populations with higher chimpanzee densities and during times when there are more infants in a group (Kibale: Chapman & Chapman 2000b). These associations may have some ecological costs but these are likely low, as dietary overlap is minimal between the species (Wachter *et al.* 1997); but red colobus travel farther when in association with red tail monkeys in Kibale (Chapman & Chapman 2000b). Red colobus in Taï are more likely to come to the ground or lower strata while they are mingling with a terrestrial sooty mangabey group (McGraw & Bshary 2002); and most observations of ground activity of Temminck's red colobus occur when green monkeys are present (Galat-Luong 1988; Galat-Luong & Galat 2005).

The arboreal guenons (*Cercopithecus* spp.; the most common preferred association partner of red colobus) are considered to benefit from poly-specific association because red colobus are typically found in the upper strata where they provide a sentinel function and protective layer for the smaller guenons that are more often prey of crowned eagles (Mitani *et al.* 2001; Schultz *et al.* 2004; Struhsaker & Leakey 1990). Kane and McGraw (2018) showed that Diana monkeys do not adjust their behaviour much as a result of these associations although synergistic effects of association and a chimpanzee hunting season resulted in expanded use of the main canopy (versus lower strata), decreased fruit and increased invertebrate consumption. In Kibale, Kanyawara and Ngogo, red-tailed monkeys (*Cercopithecus ascanius*) appear to be mostly responsible for initiating interactions with red colobus (Chapman & Chapman 2000b; Teelen 2007a). *P. badius* in Tiwai (Oates & Whitesides 1990) and *P. tephrosceles* in Gombe (Stanford 1998a) do not associate with cercopithecines more than expected by chance, probably because prey-predator dynamics are different from those elsewhere. In Tiwai, hunting pressure by chimpanzees and eagle attacks are low (Whitesides 1989). In Gombe, the open woodland allows red colobus to hear and see the relatively noisy approach of chimpanzee hunting parties without the sentinel role of guenons (Stanford 1998a, 2002). The difference in chimpanzee-red colobus predator-prey relationships are thought to be the result of three major differences between Taï and Gombe (Bshary & Noë 1997a): 1) Gombe forests are lower and more open, allowing easier detection of predators and prey and less escape opportunities for red colobus; 2) red colobus/chimpanzee body-size ratio is more equal in Gombe than in Taï, making a red colobus male counter-attack more likely to result in injury to the chimpanzee; and 3) chimpanzees in Taï use complex cooperative hunting strategies to pursue the prey whilst Gombe chimpanzees may attack simultaneously but do not have differentiated hunting roles. Stern and Goldstone (2005) suggested that red colobus would hesitate longer before leaping than other primates in Kibale, possibly making them an easier prey for chimpanzees. At most sites where red colobus intermingle with guenons, individuals of both species groom or play with each other.

Social Organization

Red colobus group sizes range from 3 to over 100 and vary among sites, groups at the same sites, and study periods. Most populations have relatively large groups with multiple males and multiple females with their offspring (Table 6) and female-biased dispersal from the natal group (see also Teichroeb, this volume). Smaller groups are commonly found in the more degraded, disturbed or marginal sites and are considered a response to ecological constraints (Gorgarten *et al.* 2015; Nowak & Lee 2011; Struhsaker 2010). One-male groups were reported in the early studies of Tana River red colobus (Marsh 1979) where now, female to male sex ratios appear to have decreased, but male numbers per group are still low (Table 6) (Karere *et al.* 2004). A recent survey showed that group sizes for *P. kirkii* were greater in protected areas (20.6) than in unprotected areas (12.8), with a lower female to male ratio outside protected areas (Table 6) (Davenport *et al.* 2019). In Kibale NP, the 'small camp group' at Kanyawara increased from 59 in 2006 to 104 in 2011 (and it is still growing, C. Chapman 2019 pers. comm.), at the very upper level of group sizes in the park but following the park-wide trend of an increase in mean group size (from 28 to 47 in that period) but not density (Table 6) (Gogarten *et al.* 2015). The group size increase may be related to overall increased food availability and quality (Chapman *et al.* 2015), although protein to fibre ratio of specific individual trees decreased between the 1970s to 2000s (Rothman *et al.* 2015). Very large groups are expected to split up as group size exceeds a habitat-specific threshold. In Taï, two study groups (Bad1 and Bad2) each contained around 90 individuals in 1997 but they were regularly splitting into sister fractions from 1994-1998, before they split up permanently. During and after the splitting process sister-groups shared the original home range and partner Diana monkey group before slowly separating (Bshary 1995; van Oirschot 2000). In 1999, based on individual recognition of the majority of individuals, Bad1A and B contained 41 and 64 and Bad2A and B 60 and 44 individuals respectively (Table 6) (Korstjens *et al.* 2007).

Red colobus individuals are observed solitary or as a pair external to established bisexual groups in many locations. Decker (1994) also saw small groups of >2 young male *P. rufomitratus*. Typically these pairs or solitary individuals are associated with either cercopithecine or black-and-white colobus groups, during the transitory period between emigration and immigration but often are only observed for a few days (e.g.

Taï: pers. obs.; Abuko: pers obs. and Starin 1991; Tiwai: Fimbel 1994; Zanzibar: Davenport & Machaga 2007; Tana River: Karere *et al.* 2004; Udzungwa: Marshall *et al.* 2005; fragments near Kibale: Onderdonk & Chapman 2000).

Female dispersal is reported for all study sites but the presence of solitary males and some observations of male immigrations into study groups suggests that males are not always philopatric in all populations. The Zanzibar red colobus groups living in human-dominated landscapes, the Jozani shambas subpopulation, showed dispersal of both sexes (including evidence of immigration by males). This fit the pattern of affiliative bonds among females who actively defended their group at the more intense inter-group interactions in this densely populated subpopulation (Siex 2003; Siex & Struhsaker 1999a). Dispersal by both sexes was also common in the *P. temminckii'*s population in Abuko, possibly due to the degraded condition of this small forest fragment in relatively dry habitat (Starin 1994). Whilst a genetic signal supports female dispersal and male philopatry in the same species in Guinea Bissau's Cantanhez NP (Minhós *et al.* 2015). Male take-overs sometimes accompanied by suspected infanticide were recorded in Tana River red colobus (Decker 1994a; Marsh 1978, 1979b).

In Taï *P. badius*, of 12 individually-followed (for at least a few days) solitary individuals, 3 were subadult females, 8 were subadult males, and 1 was an adult male (sexing young individuals in this population is difficult because of the lack of clitoris in females and still undescended testicles in most solitary males). Another juvenile male (with deformity) spent 9 months in exile of the study group before re-integrating into his natal group as a subadult. At least 5 study males matured and stayed in their natal group, and one adult male from a neighbouring group successfully joined a study group. Extra-group females were never observed for more than a week in the area whilst such males were observed for months. Dispersal was still considered to be female-biased based on the short time that females would be solitary, the appearance of shy females in study groups, and disappearance of all recognised subadult females after their first swelling period (reviewed in Korstjens *et al.* 2007).

In Kibale, female relatedness within the group was higher for the small group than for the large group (Miyamoto *et al.* 2013), suggesting an effect of competition on female dispersal that had not been detected based on behavioural observations. Detailed monitoring of group membership is greatly hindered in large red colobus groups because females are difficult to recognize individually and many immigrants can be relatively young (probably no red colobus researchers have managed 100% recognition of immatures in focal groups of considerable size).

Red colobus at several study sites show fission-fusion tendencies in which groups split up into smaller units from time to time, either in response to food availability or because the group as a whole is getting relatively large and fluid fission-fusion patterns precede a more permanent group split (Korstjens 2001; Nowak & Lee 2011; Oates 1994; Siex & Struhsaker 1999a; Starin 1994; Struhsaker *et al.* 2004; van Oirschot 1999).

Table 6: Red colobus group size and composition across Africa. Please note that group size estimation for the large red colobus groups in dense forest is notoriously difficult and estimation of subadult sex in species without elaborate clitoris is very difficult; In the table, individuals of unknown sex or unknown age-sex are not listed, please see the original publications for further information and possible constraints on the reliability of individual estimates.

Inter-group relationships

Inter-group relationships vary across red colobus populations and taxa, but typically range from neutral to agonistic, involving some threat displays or even chasing; and home-ranges tend to overlap at least a little. *P. tephrosceles* in Kibale have few agonistic encounters (6.5-36% of encounters, Isbell 1983; Struhsaker 2010). In Taï, *P. badius*, overlap between home-ranges is small, 30-50% of encounters include agonistic acts of males only (mostly threats and some chases), and encounters occurred only once per 21-30 full observation days (Korstjens *et al.* 2002, 2007). In Zanzibar, males were the main aggressors in encounters in the forest subpopulation whilst all individuals engaged in inter-group aggression in the shamba populations (Siex 2003). Similarly, in Abuko, females and males both engaged in inter-group aggression (Starin 1991, 1994).

Intra-group aggression and affiliation

Food competition is not directly evident in red colobus monkeys as most of their food does not seem to be contestable and is considered abundant. However, scramble competition is detectable in Kibale NP (Snaith & Chapman 2005, 2008) and larger groups have higher stress levels (Chapman *et al.* 2015). Larger group size resulted in higher dietary diversity, more time travelling, and less time feeding and socializing (Gorgarten *et al.* 2014). Typically, most aggressive interactions in red colobus occur among adult males or from males to females with minimal aggression among females. But young subadult males may suffer intense aggression by males as they mature (pers. obs. in Taï). As a result of the males' greater involvement in within- and between-group fights and squabbles and predator defence, red colobus males tend to have more ‘healed’ fractures than females (*P. preusii* in Cameroon: Chapman & Legge 2009; and *P. tephrosceles* in Kibale: Arlet *et al.* 2009).

Notable here is that aggression rates observed in the Zanzibar shamba population outside Jozani NP, are greater than those observed in the Jozani forest groups (2.48 versus 0.25 observations/hour), stylized male-male presents were 7 times higher and wounds were also more frequent (Siex 2003). In *P. tephrosceles*, the frequency of agonistic interactions was 0.12 events/hour (Struhsaker & Leland 1979). Aggressive interactions commonly involved physical contact in Siex’s study (13% and 24% of observed events in Jozani forest and shambas respectively), whilst Struhsaker reports only 15 events with physical contact over 1112 hours. Most aggressive interactions in Siex’s study occurred among adult males but in the shamba group, juveniles were also often involved in aggression. Werre (2000) reports only two cases of aggressive physical contact in a 12 months study on *P. epieni*, with other agonistic encounters involving mostly males chasing males or sometimes females. Korstjens *et al.* (2007) report 0.19 agonistic interactions among females, 0.42 among males, and 0.41 from males towards females per focal follow hour. Only 1 intra-group agonistic support among females and 13 among males were recorded over 76 observation days (Korstjens 2001; Korstjens *et al.* 2002; Korstjens *et al.* 2007).

Cohesiveness and bonding

Typically, red colobus groups are widely dispersed throughout the canopy but grooming and close proximity are common during resting. Habitat structure and exposure to anthropogenic disturbance (e.g., proximity to people and habitations) also may affect cohesiveness. For examples, in Zanzibar, shamba groups were more cohesive than Jozani forest groups (Siex 2003). The importance and strength of male-

male bonds varies among populations and is sometimes expressed through grooming and ritualised male-male presents and hugs. Male-male grooming was common in Struhsaker & Leland's (1979) study at Kibale Kanyawara, while other studies recorded very few grooming bouts among males: in Taï (Korstjens 2001), Zanzibar (Siex 2003), and Guinea Bissau (Minhós *et al.* 2015). Males in Taï spent more time with neighbours nearby than did females but did not spent more time with males than females and did not groom either sex very often (Korstjens 2001, p76). Females in Taï spent as much time sitting next to or grooming males as females, but if corrected for sex ratio, females showed a preference in grooming and proximity for males (Korstjens *et al.* 2002). In *P. epieni,* most grooming bouts were among males or from female to male with very little male to female grooming (Werre 2000). Female-female bonds, expressed by grooming, were stronger than those among other age-sex classes in Guinea Bissau (Minhós *et al.* 2015), Abuko (Starin 1994), and the Zanzibar shambas population (Siex 2003). Interestingly, the pattern observed by Siex (2003) in Zanzibar's shambas groups may be an adaptation to the increased population density and disturbance levels to those areas, as an earlier study in 1980-1981 reported strong male-male bonds and stable male group membership in the same shamba group (Mturi 1991). Abuko is also heavily disturbed and isolated, with frequent male and female migration among only 5 residential groups, and female involvement in inter-group aggression. In Abuko, the population size and isolation may have resulted in relatively closely related females who had typically more stable group membership than males (who had higher death rates and migrated) (Starin 1994). Coalitions in intra-group encounters in Abuko were rare but occurred in interactions with extra-group males or inter-group encounters and involved most often female-male coalitions (Starin 1994).

Mating systems, Reproduction and Sexual Behaviour

Detailed information on birth rates, receptive periods, mating strategies, and sexual behaviour require long term studies on recognized individuals, something that is difficult with red colobus. Instead, birth rates can be estimated from female to infant or juvenile ratios in groups (Table 6). This ratio shows variation across populations and tends to show the expected trend of less infants per female (i.e. lower reproductive rate) in more degraded habitats. In the Udzungwa mountain range, natality and infant survival appears positively related to forest quality (Struhsaker *et al.* 2004).

Sexual interactions are probably far more common in red colobus than other colobines due to the long receptive period and sexual swellings of females and the large multi-male groups with strong male sperm competition (Struhsaker 2010). Both females and males initiate sexual interactions but males do so more than females. Females often solicit or accept matings even while they are pregnant. Females tended to solicit interactions and mate more promiscuously when pregnant than during the earlier swelling periods; while males were less interested in females with post-conception swellings than pre-conception swellings (Beziers *et al.* 2009; Hobeika *et al.* 2009; Korstjens *et al.* 2008; Piachaud *et al.* 2009) Females may refuse or flee to avoid copulating with particular males, who then typically threaten and chase them. Male mate-guarding was observed at Taï (AHK pers. obs.) and consortships were observed in the Tana River area (Mbora & McGrew 2002).

Males are considered multiple-mounters and sperm coagulates to form a sperm plug that subsequent males regularly try to remove before mating (AHK pers. obs.). Multiple males will mate with a female in quick succession, often pushing the preceding male off the female during a copulation (AHK pers. obs.). Although variable among species, males sometimes have their feet on the female's ankles during copulation and the female sometimes turns around and grasps or touches the male (Struhsaker 2010; AHK pers. obs.). Infants are regularly observed to pull or jump on the males during copulation. Starin (2001) observed *P. temminckii* mothers preventing their daughters from mating in some cases, whilst an orphaned subadult female faced no restraints. Most copulations occur while females have a sexual swelling (Struhsaker 2010). In *P. badius*, 90-95% of 287 copulations recorded occurred while the female had a swelling (AHK unpubl.).

In *P. badius, P. temminckii* and *P. preussi,* females produce copulation calls during or sometimes before or after the male mounts her (up to 79% of sexual interactions included a female copulation call in Taï; AHK unpubl.). In *P. temminckii*, females advertise their receptivity through jumping and receptivity quavers but seem to stay silent during copulation (Galat-Luong & Galat 2005; Starin 1991; Struhsaker 1975). Starin (1991, 1994, 2001) reported that turnover of the single breeding male was so regular in Abuko, that this male was often not present for much of the lactation period of infants conceived during his tenure. The elaborate displays of the females there may promote extra-group copulations, which were observed in this population (Starin 1991, 1994, 2001), but not in the nearby Taï population of *P. badius* (Korstjens pers. obs.). Infanticide by males has been recorded but appears rare and requires further study (Nowak 2007; Decker 1994a; Marsh 1978, 1979b).

Mating and births are seasonal in some but not all locations and seasons are often not very tightly defined. Taï females had most births at the end of the wet season (75% of observed births occurred from November to January; AHK unpubl.), which coincides with the end of the intense chimpanzee hunting season. Most sexual interactions occurred between January and June (copulation call rates fell from 4-7 calls per hour to 0.5-2 calls per hour in July-December). Up to half the females (12 of 24) in the study group were seen to mate on a single day during the mating season, while outside of this season only two females were receptive on any given day at Taï (AHK unpubl.). Zanzibar colobus in marginal habitats had slightly more births in one group in the 1st wet and in another group in the 1st dry season (Nowak & Lee 2011); slightly more births occurred in Abuko in the dry season but births were most constrained by strong intra-group synchrony which may be a side effect of the regular changes in dominant males (Starin 1988, 1991); very weak seasonality is suggested for Kibale, and most other locations (Struhsaker 2010).

Inter-birth interval is unknown for most species. *P. badius* at Taï had mean inter-birth intervals of 15.6 months for 12 identified females (18.8 for 8 surviving infants and 8.0 for 4 infants that disappeared before the age of 10 months). This is short compared to those at other sites: Gombe, 19.2-24.2 months (Stanford 1998a); Abuko 29.4 (Starin 1988, 1991); and Kibale 24.4 (Struhsaker 2010). *P. kirkii* appears to have the slowest reproductive rate recorded based on infants per adult female ratios (Table 6). Sexual swelling periods can last from one to 2 weeks (AHK unpubl.; Milich *et al.* 2014a; Struhsaker 2010). Females in disturbed forests had shorter periods of swelling tumescence, restricted mating more to maximum tumescence, and copulated less than those in old-growth forest in Kibale (Milich *et al.* 2014a).

Allomothering

Red colobus have very low frequencies of allomothering, but infants sometimes play on other females’ laps in Taï (usually, with females that are close associates of the mother) and some allomothering was observed in Zanzibar in the shamba population (Siex 2003). Old juvenile or subadult males have been observed to suckle from females in several species (Struhsaker 2010).

Diseases and parasites

Understanding the potential for zoonotic and anthropozoonotic disease transfer is increasingly important due to increased risks of human-wildlife pathogen transmission as forests are degraded and hunting of red colobus is common. Gastrointestinal parasites are common and diverse (e.g. Taï: Kouassi *et al.* 2015). The red colobus-specific version of SIV_{wrc} (Liégeois *et al.* 2009) and herpes are common in *P. badius* in Taï (Leendertz *et al.* 2011; Locatelli, *et al.* 2008b) but they are not being transmitted to the chimpanzees, despite regular consumption of red colobus by chimpanzees (Leendertz *et al.* 2011; Murthy *et al.* 2013). Two other retroviruses, STLV-1wrc and SFVwrc, on the other hand have been transmitted to the chimpanzees (reviewed in Leendertz *et al.* 2011). Whilst an anthrax-like virus regularly kills red colobus in Taï, with very few individuals showing an immune response, suggesting high virulence (Zimmermann *et al.* 2017). A SIV_{wrc} strain found in Temminck's red colobus in Abuko was closely related but distinct from that in Taï (Locatelli, *et al.* 2008a). Logging and an increase in the proportion of forest edge led to higher parasite/disease prevalence in Kibale red colobus. Parasite and food abundance synergistically limited population density around Kibale NP where the reduction of food sources in already fragmented forests directly led to reduced population density, whilst parasite prevalence increased with population density (review in Chapman *et al.* 2013). Parasite richness and prevalence are greater in Tana River red colobus living outside compared to inside the National Park and correlate positively with colobus density. Colobus parasite prevalence and richness were lower than those for the more terrestrial mangabeys that live in larger groups and range further (Mbora & McPeek 2009)

Increased contact between primates and humans is leading to increased risks of disease and parasite transmission (Paige *et al.* 2014) and the risk of emergent strains of some very dangerous viruses (e.g. simian haemorrhagic fever virus Bailey *et al.* 2014). *Treponema pallidum* infections, the cause of human yaws have been observed in red colobus in West Africa (Mayhew et al. 2020; Gogarten et al. 2016; Fribourg-Blanc & Mollaret 1969). Few studies look at the effect of diseases or parasites on red colobus behavioural ecology. Parasite and disease pressures can drive selection for variable MHC in Kibale red colobus (Simons *et al.* 2017). Red colobus, at this site also alter their behaviour when infected with whip worms. Infected colobus rest more but move, groom and copulate less, and feed more on bark from species with known medicinal properties (Ghai *et al.* 2015).

Conservation

Red colobus throughout their range show a declining population trend due to habitat reduction (leading to fragmentation, increased parasite/disease transmission and vulnerability, stress, reduced food availability, and increased exposure to climatic extremes and change) and over-hunting (IUCN 2020). In the longer-term, isolated populations can go extinct through stochastic processes. The most threatened members of the radiation include: *P. waldroni*, *P. pennantii*, *P. rufomitratus*, *P. epieni* and *P. preussii* (Cronin *et al.* 2018). There have recently been some hopeful sightings of species thought to have been locally extirpated, including *P. waldroni* in the Ivory Coast (Bitty *et al.* 2015; McGraw 2005; Oates *et al.* 2000) and *P. bouvieri* in The Republic of Congo (Devreese, 2015). In Zanzibar archipelago, there appears to be a good-sized *P. kirkii* population but recruitment is low with only 0.3 infants and 0.25 juveniles/subadults per adult female, supporting the IUCN status of Endangered (Davenport *et al.* 2019; Table 6). This species is under serious threat from forest destruction. At least one translocation of a large group of colobus has proven successful as a way of relocating threatened groups (Struhsaker & Siex 1998). Road kill and feral dogs also threaten this population (Olgun *et al*. 2020; Georgiev *et al*. 2019).

Temminck's colobus is under serious threat from forest destruction, hunting, human encroachment, increasing temperatures and drought in western Africa (Galat *et al.* 2009; Hillyer *et al.* 2015; Mayhew *et al*. 2020). In Fathala, human encroachment, increased hunting by dogs, and increased drought have led to a reduction in suitable habitat. *P. temminckii* has adapted by: 1) consuming more fruit and using new foods (e.g. grasses, herbs, seeds); 2) more terrestrial locomotion (facilitated by associating with terrestrial cercopithecines); 3) increased time in poly-specific associations; 4) using open habitats more than before; and 5) using mangrove swamps for resting and feeding (Galat-Luong & Galat 2005). Throughout Guinea Bissau there are significant conservation concerns as red colobus are absent in forests with heavy human disturbance and in decline overall, there is a clear genetic signal for a recent bottleneck and restricted female dispersal (Minhós *et al.* 2016).

P. rufomitratus saw a 5% decline between 1994 and 2001 at Tana River due to habitat loss (Karere *et al.* 2004). Anthropogenic and some natural causes resulted in a 34.5% reduction in forest cover in lower Tana River with areas inside the National Park being affected a little less than those outside the park (38% versus 29% reduction) (Moinde-Fockler *et al.* 2007; Wahungu *et al.* 2005). High genetic diversity was found within and between small populations in those fragmented forests, suggesting that the meta-population was large and fragmentation still recent relative to red colobus generation times; a Pliocene-Pleistocene interval bottleneck signature was also detected (Mbora & McPeek 2010). Group size has decreased significantly in Tana River red colobus since 1978 from around 20 to only 9 outside and 12 individuals per group inside the park in 1988, whilst in 2000, group size outside the park increased to 11 and that inside reduced to 10 individuals per group. The number of immatures per adult female did not change but the number of females per male decreased significantly in this time period, suggesting that females suffered greater survival stresses than males (Mbora & Meikle 2004).

Kibale NP has seen a 3.9% annual increase in red colobus populations since the 1970s due to their colonizing of regenerating plantations (Chapman *et al.* 2018). While only two viable populations of *P. epieni* were left in the Niger Delta in 2013, where habitat destruction and lack of protection are driving the species to extinction (Ikemeh 2015).

Fragmentation often leads to crop-foraging which can result in retaliatory killing (e.g. *P. tephrosceles* in Tanzania: Kibaja 2014; *P. temminckii* in The Gambia: Mayhew 2020). The multi-level effects of fragmentation on red colobus populations near Kibale National park included increased transmission of parasites between humans and primates, severe forest degradation leading to reduction in food trees, increased physiological stress levels in red colobus, increased parasite load and eventually a strong reduction in population size (83% between 2000 and 2010) (reviewed in: Chapman *et al.* 2013; Chapman *et al.* 2006). Individual-based models can be used to help predict the effects of habitat fragmentation, climate change and parasite pressures under varying scenarios (Bonnell *et al.* 2016, 2018). Over 28 years, in Kibale forest areas, low-intensity logging had limited impact on red colobus populations but high-intensity logging led to reduced population densities and a slow recovery rate (Chapman *et al.* 2000).

The Udzungwa red colobus is facing severe threats throughout their range, including the impacts of human-induced fires, fragmentation and hunting (Cavada *et al.* 2019; Dinesen *et al.* 2001). Using a novel landscape genetics approach, Ruiz-Lopez *et al.* (2016) showed that Udzungwa red colobus genetic diversity was still similar across isolated forest blocks, but there was very limited gene flow among the blocks, showing recent disturbance of gene flow being affected by the frequency of human-induced fires and the fragmentation of the area by human activities. They recommend establishment of corridors between the forest fragments to conserve the genetic diversity in the population. Human activities lead to smaller group sizes, while abundance is lower and parasite diversity is higher at higher elevation in the Udzungwa region (Marshall *et al.* 2005; Barelli *et al.* 2019). Abundance is linked to the mean basal area of large trees (>20 cm Diameter at Breast Height) and species richness of their food trees (Rovero & Struhsaker 2007). In the same area, red colobus in only recently isolated forest fragments, surrounded by human landscapes, showed lower diversity in gut microbiome than those in less disturbed forest, indicative of a less varied diet. Importantly, they had lost some micro-organisms used for detoxification of plant compounds, which has important implications for translocation, as these individuals would struggle more with the plants in mature forest that contain more toxic compounds (Barelli *et al.* 2015, 2020). In contrast, microbiome did not differ between red colobus from Kibale National Park and those from surrounding forest fragments (Mccord *et al.* 2014).

Hunting by humans is a particularly great threat to West and Central African red colobus, where they are among the first to disappear from forests (Kaisala *et al*. 2020;

Covey & McGraw 2014; Gonedelé Bi *et al.* 2014; Koné & Refisch 2007; Oates 1996; Refisch & Koné 2005), but hunting also occurs in more Eastern populations (e.g. Udzungwa: Rovero *et al.* 2015). In Sierra Leone, red colobus is the preferred primate meat for market because it dries well and they are often hunted to extinction locally, but primate meat is not considered a delicacy and hunting is driven by economic conditions (Davies *et al.* 2007). Likewise, in Ivory Coast, they are the primates most likely to be extirpated, affected more than other monkeys by hunting and the ones benefitting most from reduced hunting near research or tourism camps (Campbell *et al.* 2011; Gonedelé Bi *et al.* 2014; N'Goran *et al.* 2012; Refisch & Koné 2005). Hunting and illegal cocoa farming inside protected areas in Ivory Coast led to the absence of red colobus in all 23 protected areas surveyed in 2010-2013 (excluding Taï NP) (Bitty *et al.* 2015). One of the most extensive long-term studies on bushmeat has been done on Bioko Island where the Critically Endangered *P. pennantii* is considered the primate species least tolerant to hunting and without stronger intervention it is likely to go extinct (Cronin *et al.* 2016, 2017). The little-studied central African species, *P. ellioti* and *P. langi*, are threatened heavily by forest destruction, hunting, and mining, but have also suffered periodic fatal epidemics (Kaisala *et al.* 2020).

Poaching can also be the result of vengeful pursuit due to perceived or real threat of crop-raiding in agricultural plots. *P. kirkii* are considered a pest due to their coconut consumption, but their feeding leads to increased crop yield due to a pruning effect (Siex & Struhsaker 1999b). Poaching of colobus has been suspected in Pirang Community Forest, The Gambia (APH & Roy Armstrong, pers. obs.). Children throw items at colobus on the boundaries of protected land (APH pers. obs.). Free-ranging domestic dogs are an added threat as a result of human encroachment on reserves (e.g. P. temminck's colobus in Fathala Forest, Senegal: Galat-Luong & Galat 2005; Abuko

Nature Reserve: APH, pers. obs..; Bijilo Forest Park, The Gambia: Roy Armstrong, pers. comm.; *P. kirkii*: Georgiev *et al*. 2019).

Serious declines of *P. preussi* due to overhunting in Korup NP have been reported repeatedly, leading to a lower contribution of red colobus to bushmeat due to their rarity (Hofner *et al.* 2018; Linder & Oates 2011; Bobo *et al.* 2017; Waltert *et al.* 2002). Bobo *et al.* (2017) report hunting, habitat destruction, and disease as the main causes of the decline of up to 80% of red colobus in Korup between 2000 and 2011; they are also hunted as a pet and for local rituals or medicine (Bobo *et al.* 2012; Fonkwo *et al.* 2018). Village abandonment can, however, help populations recover (Korup 2007-2008; Baya and Storch 2010).

Increased protection of Jozani forest in Zanzibar appears to have benefitted red colobus but the evident resentment of local people regarding their exclusion from the forest shows the complexities of trying to conserve primates (Salum 2009). This and previously mentioned studies identify the importance of understanding the complex relationship between humans and red colobus monkeys if we are to be successful in saving these primates.

Conservation concerns are also raised in relation to the presence of researchers who may bring diseases and parasites, or may increase the risk of the animals being shot by hunters as habituated groups do not flee from humans. Passive Acoustic Monitoring (PAM) and landscape genetic analysis may reduce these risks as they do not require habituation of animals and researchers are not close to the animals. PAM, may be less effective, however, for the short, low sound intensity calls of red colobus which lacks discrete loud calls, e.g. in Taï N. P., recall rates were lower for *P. badius* than for cercopithecines and *Colobus polykomos* (Heinicke *et al.* 2015). A novel landscape genetic approach found fire and proximity to villages to be the most important drivers with regard to genetic differentiation in *P. gordonorum* in Udzungwa (Ruiz-Lopez *et al.* 2016). Microbiome of the gut and vagina may also reveal new understanding of the phylogenetic relatedness among species and the influence of diet and recent environmental changes on populations (Yildirim *et al.* 2010, 2014).

Conclusion

This review shows the wide variation in red colobus natural history patterns but also highlights a lack of work on central African populations and a lack of recent studies on behaviour and ecology. Red colobus are also notable among the colobines for showing relatively great variation in group size, inter-group and intra-group relationships, and dispersal patterns that suggest extreme flexibility in social systems in response to ecological pressures. Unfortunately, red colobus are threatened throughout their range and some of the observed flexibility is the direct result of populations trying to survive in greatly degraded and fragmented populations that are unlikely to be resilient against further degradation and the synergistic effects between habitat degradation, greater human-wildlife interactions and climate change.

Reference List

Arlet, M. E., Carey, J. R., & Molleman, F. 2009. Species, age and sex differences in type and frequencies of injuries and impairments among four arboreal primate species in Kibale National Park, Uganda. *Primates*, **50**(1), 65–73.

Aronsen, G. P., Beuerlein, M. M., Watts, D. P., & Bribiescas, R. G. 2015. Redtail and red colobus monkeys show intersite urinary cortisol concentration variation in Kibale National Park, Uganda. *Conservation Physiology*, **3**(1). doi:10.1093/conphys/cov006

Astaras, C., Mühlenberg, M., & Waltert, M. 2008. Note on drill (*Mandrillus leucophaeus*) ecology and conservation status in korup National Park, southwest cameroon. *American Journal of Primatology*, **70**(3), 306–310.

Bahaa-el-din, L., Henschel, P., Butynski, T. M., … Hunter, L. 2015. The African golden cat *Caracal aurata*: Africa's least-known felid. *Mammal Review*, **45**(1), 63–77.

Bailey, A. L., Lauck, M., Weiler, A., … O'Connor, D. H. 2014. High genetic diversity and adaptive potential of two simian hemorrhagic fever viruses in a wild primate population. *PLoS ONE*, **9**(3). doi:10.1371/journal.pone.0090714

Barelli, C., Albanese, D., Donati, C., … De Filippo, C. 2015. Habitat fragmentation is associated to gut microbiota diversity of an endangered primate: implications for conservation. *Scientific Reports*, **5**.

Barelli, C., Gonzalez-Astudillo, V., Mundry, R., … Gillespie, T. R. 2019. Altitude and Human Disturbance Are Associated with Helminth Diversity in an Endangered Primate, *Procolobus gordonorum*. *PLOS ONE* 14(12): e0225142. https://doi.org/10.1371/journal.pone.0225142

Barelli, C., Pafčo, B., Manica, M., … Hauffe, D. C. 2020. Loss of protozoan and metazoan intestinal symbiont biodiversity in wild primates living in unprotected forests. *Sci Rep* **10,** 10917.

Baya, L., & Storch, I. 2010. Status of diurnal primate populations at the former settlement of a displaced village in cameroon. *American Journal of Primatology*, **72**(7), 645–652.

Beziers, P., Hobeika, S., & Korstjens, A. H. 2009. Are dominant males more successful reproductively? *Folia Primatologica*, **80**(2), 151–152.

Bitty, E.A., Gonedelé Bi, S., Bené, J. C. K., Kouassi, P. K., & McGraw, W. S. 2015. Cocoa farming and primate extirpation inside cote d'Ivoire's protected areas. *Tropical Conservation Science*, **8**(1), 95–113.

Bobo, K. S., Ntumwel, C. B., Aghomo, F. F., & DSCHANG, C. 2012. Hunter's perception on uses of preuss's red colobus *Procolobus preussi* and red-capped mangabey *Cercocebus torquatus*, and related conservation issues, in the Nkwende hills area, southwest Cameroon. *Life Sciences Leaflets*, **8**, 28–34.

Boesch, C. 1994. Chimpanzee-red colobus monkeys: a predator-prey system. *Animal Behaviour*, **47**(5), 1135–1148.

Boesch, C., & Boesch-Achermann, H. 2000. *The chimpanzees of the Taï Forest: behavioural ecology and evolution*, Oxford: Oxford University Press.

Bonnell, T. R., Campennì, M., Chapman, C. A., … Sengupta, R. 2013. Emergent group level navigation: an agent-based evaluation of movement patterns in a folivorous primate. *PLoS ONE*, **8**(10).

Bonnell, T. R., Ghai, R. R., Goldberg, T. L., Sengupta, R., & Chapman, C. A. 2016. Spatial patterns of persistence for environmentally transmitted parasites: effects of regional climate and local landscape. *Ecological Modelling*, **338**, 78–89.

Bonnell, T. R., Ghai, R. R., Goldberg, T. L., Sengupta, R., & Chapman, C. A. 2018. Spatial configuration becomes more important with increasing habitat loss: a simulation study of environmentally-transmitted parasites. *Landscape Ecology*, **33**(8), 1259–1272.

Bshary, R. 1995. *Rote stummelaffen, Colobus badius, und Dianameerkatzen, Cercopithecus diana, im Taï-Nationalpark, Elfenbeinküste: Wozu assoziieren sie?*, Ludwig-Maximilian-Unviersität München, München.

Bshary, R. 2001. Diana monkeys, cercopithecus diana, adjust their anti-predator response behaviour to human hunting strategies. *Behavioral Ecology And Sociobiology*, **50**(3), 251–256.

Bshary, R., & Noë, R. 1997a. Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioral Ecology And Sociobiology*, **41**(5), 321–

333.

Bshary, R., & Noë, R. 1997b. Red colobus and diana monkeys provide mutual protection against predators. *Animal Behaviour*, **54**(6), 1461–1474.

Burgess, N. D., Clarke, G. P., Hermitage, T., … Rodgers, W. A. 1998. Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**(3), 337–367.

Butynski, T. M., Grubb, P., & Kingdon, J. 2013a. *Procolobus badius*: western red colobus. In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *The Mammals of Africa*, London: Bloomsbury Publishing, pp. 128–134.

Butynski, T. M., Grubb, P., & Kingdon, J. 2013b. *Procolobus pennantii* pennant's red colobus (Bioko red colobus). In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa: Volume II Primates*, London: Bloomsbury, pp. 137–141.

Butynski, T. M., Kingdon, J., & Kalina, J. (Eds.). (2013d). *Procolobus gordonorum* Udzungwa red colobus (Iringa / Uhehe / Gordon's red colobus). In *Mammals of Africa : Primates*, London: Bloomsbury, pp. 148–151.

Butynski, T. M., & Kingdon, J. 2013. *Procolobus preussi* preuss's red colobus. In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa: Volume II Primates*, London: Bloomsbury, pp. 134–136.

Butynski, T. M., Kingdon, J., & Kalina, J. 2013c. *Mammals of Africa: Volume II Primates*, 1st edn, London: Bloomsbury.

Campbell, G., Kuehl, H., Diarrassouba, A., Goran, P. K. N., & Boesch, C. 2011. Long-term research sites as refugia for threatened and over-harvested species. *Biology Letters*, **7**(5), 723–726.

Cardini, A., & Elton, S. 2009. Geographical and taxonomic influences on cranial variation in red colobus monkeys (Primates, Colobinae): introducing a new approach to 'morph' monkeys. *Global Ecology and Biogeography*, **18**(2), 248–263.

Cardini, A., & Elton, S. 2011. GeMBiD, a geometric morphometric approach to the study of biological diversity: an example study of the red colobus (*Procolobus* [*Piliocolobus*]) species complex. *International Journal of Primatology*, **32**(2), 377–389.

Cavada, N., Tenan, S., Barelli, C., & Rovero, F. 2019. Effects of anthropogenic disturbance on primate density at the landscape scale. *Conservation Biology*, **33**(4), 873–882.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., & Struhsaker, T. T. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology*, **14**(1), 207–217.

Chapman, C. A., Bonnell, T. R., Sengupta, R., Goldberg, T. L., & Rothman, J. M. 2013a. Is *Markhamia lutea*'s abundance determined by animal foraging? *Forest Ecology and Management*, **308**, 62–66.

Chapman, C. A., Bortolamiol, S., Matsuda, I., … Valenta, K. 2018. Primate population dynamics: variation in abundance over space and time. *Biodiversity and Conservation*, **27**(5), 1221–1238.

Chapman, C. A., & Chapman, L. J. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, **40**(1), 215–231.

Chapman, C. A., & Chapman, L. J. 2000a. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology*, **21**(4), 565–585.

Chapman, C. A., & Chapman, L. J. 2000b. Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behavioral Ecology And Sociobiology*, **47**, 129–139.

Chapman, C. A., Chapman, L. J., Bjorndal, K. A., & Onderdonk, D. A. 2002a. Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology*, **23**(2), 283–310.

Chapman, C. A., Chapman, L. J., & Gillespie, T. R. 2002b. Scale issues in the study of primate foraging: red colobus of Kibale National Park. *American Journal Of Physical Anthropology*, **117**(4), 349–363.

Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. 2003. Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology*, **24**(2), 317–333.

Chapman, C. A., Cohn, A., Wasserman, M. D., … Ziegler, T. E. 2006. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology*, **131**(4), 525–534.

Chapman, C. A., Ghai, R. R., Jacob, A. L., … Goldberg, T. L. 2013b). Going, going, gone: a 15-year history of the decline in abundance of primates in forest fragments. In L. K. Marsh & C. A. Chapman, eds., *Primates in Fragments: Complexity and Resilience*, Springer Press, pp. 89–100.

Chapman, C. A., Naughton-Treves, L., Lawes, M. J., Wasserman, M. D., & Gillespie, T. R. 2007. Population declines of colobus in western Uganda and conservation value of forest fragments. *International Journal of Primatology*, **28**(3), 513–528.

Chapman, C. A., Schoof, V. A. M., Bonnell, T. R., Gogarten, J. F., & Calme, S. 2015. Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370**(1669). doi:10.1098/rstb.2014.0112

Chapman, C. A., Webb, T., Fronstin, R., Wasserman, M. D., & Santamaria, A. M. 2005. Assessing dietary protein of colobus monkeys through faecal sample analysis: a tool to evaluate habitat quality. *African Journal of Ecology*, **43**(3), 276–278.

Chapman, T. J., & Legge, S. S. 2009. The dangers of multi-male groupings: trauma and healing in cercopithecoid monkeys from cameroon. *American Journal of Primatology*, **71**(7), 567–73.

Clutton-Brock, T. H. 1974. Activity patterns of red colobus (colobus *badius tephrosceles*). *Folia Primatologica*, **21**, 161–187.

Clutton-Brock, T. H. 1975a. Feeding behaviour of red colobus and black and white colobus in east Africa. *Folia Primatologica*, **23**, 165–207.

Clutton-Brock, T. H. 1975b. Ranging behaviour of red colobus (colobus *badius tephrosceles*) in the gombe National Park. *Animal Behaviour*, **23**, 706–722.

Colyn, M. 1993). Coat colour polymorphism of red colobus monkeys (colobus *badius*, primates, colobinae) in eastern zaire: taxonomic and biogeographic implications. *Journal of African Zoology*, **107**(4), 301–320.

Cooney, D. O., & Struhsaker, T. T. 1997. Adsorptive capacity of charcoals eaten by Zanzibar red colobus monkeys: implications for reducing dietary toxins. *International Journal of Primatology*, **18**(2), 235–246.

Covey, R., & McGraw, W. S. 2014. Monkeys in a west African bushmeat market:

implications for cercopithecid conservation in eastern liberia. *Tropical Conservation Science*, **7**(1), 115–125.

Cronin, D. T., Riaco, C., Linder, J. M., … Hearn, G. W. 2016. Impact of gun-hunting on monkey species and implications for primate conservation on bioko island, equatorial guinea. *Biological Conservation*, **197**, 180–189.

Cronin, D. T., Sesink Clee, P. R., Mitchell, M. W., … Gonder, M. K. 2017. Conservation strategies for understanding and combating the primate bushmeat trade on bioko island, equatorial guinea. *American Journal of Primatology*, **79**(11). doi:10.1002/ajp.22663

Cronin, D. T., Linder, J., Ting, N. and Ekwoge Abwe 2018: Coordinators of the Red Colobus Conservation Action Plan. Blog post for National Geographic. https://blog.nationalgeographic.org/2018/05/29/saving-Africas-most-threatened-primate-group-from-extinction/ accessed on 16 September 2019.

Daegling, D. J., & McGraw, W. S. 2001. Feeding, diet, and jaw form in west African colobus and procolocus. *International Journal of Primatology*, **22**(6), 1033–1055.

Danish, L., Chapman, C. A., Hall, M. B., Rode, K. D., & Worman, C. O. 2006. 18 the role of sugar in diet selection in redtail and red colobus monkeys. In G. Hohmann, M. M. Robbins, & C. Boesch, eds., *Feeding ecology in apes and other primates*, Vol. 48, Cambridge University Press, p. 473.

Davenport N. E. and Machaga, S.J., T. R. B. M. 2007. Census and conservation assessment of the red colobus (*Procolobus*rufomitratus *tephrosceles*) on the ufipa plateau, southwest Tanzania:newly-discovered, threatened and extinct populations. *Primate Conservation*, **22**, 97–105.

Davenport, T. R. B., Fakih, S. A., Kimiti, S. P., Kleine, L. U., Foley, L. S., & De Luca, D. W. 2019. Zanzibar's endemic red colobus *Piliocolobus kirkii*: first systematic and total assessment of population, demography and distribution. *ORYX*, **53**(1), 36–44.

Davies, A. G., Oates, J. F., & Dasilva, G. L. 1999. Patterns of frugivory in three west African colobine monkeys. *International Journal of Primatology*, **20**(3), 327–357.

Davies, A. G., Schulte-Herbrüggen, B., Kümpel, N. F., & Mendelson, S. 2007. Hunting and trapping in gola forests, south-eastern sierra leone: bushmeat from farm, fallow and forest. *Bushmeat and Livelihoods: Wildlife Management and Poverty Reduction*, 15–31.

Decker, B. S. 1994a. Effects of habitat disturbance on the behavioral ecology and demographics of the tana river red colobus (colobus *badius* ruformitratus). *International Journal of Primatology*, **15**(5), 703–737.

Decker, B. S. 1994b. Endangered primates in the selous game reserve and an imminent threat to their habitat. *Oryx*, **28**(3), 183–190.

Delson, E. 1994. Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In A. G. Davies & J. F. Oates, eds., *Colobine monkeys*, Cambridge University Press, pp. 11–43.

Delson, E., Terranova, C. J., Jungers, W. L., Sargis, E. J., & Jablonski, N. G. 2000. *Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa*. *Anthropological papers of the AMNH*, Vol. 83, New York, NY: American Museum of Natural History.

Devreese, L. 2015. 'World's first photo of monkey thought extinct in Congo'. https://www.cercocebus.be/press/ Accessed June 2017.

Dinesen, L., Lehmberg, T., Rahner, Ma. C., & Fjeldsa, J. 2001. Conservation priorities for the forests of the Udzungwa mountains, Tanzania, based on primates, duikers and birds. *Biological Conservation*, **99**, 223–236.

Diouck, D. 1999. Adaptations aux modifications du milieu des colobes bais (colobus *badius* temmincki) de la forêt de fathala, parc national du delta du saloum, sénégal.

Dunham, N. T., Kane, E. E., & McGraw, W. S. 2015. Scapular morphology and forelimb use during foraging in four sympatric cercopithecids. *Folia Primatologica*, **86**(5), 474–489.

Dunham, N. T., Kane, E. E., & McGraw, W. S. 2017. Humeral correlates of forelimb elevation in four west African cercopithecid monkeys. *American Journal of Physical Anthropology*, **162**(2), 337–349.

Fimbel, C. 1994. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at tiwai, sierra leone, west Africa. *Biological Conservation*, **70**(3), 277–286.

Fonkwo, S. N., Mbida, M., Angwafo, T. E., & Ebua, V. B. 2018. Hunting of preusss red colobus (*Procolobus preussi*) in korup National Park, cameroon. *International Journal of Biodiversity and Conservation*, **10**(2), 100–105.

Fonkwo, S. N., Mbida, M., Angwafor, T. E., & Ebua, V. B. 2015. Activity budget of preuss's red colobus (*Procolobus preussi*) in korup National Park, south-west region, cameroon. *International Journal of Biological and Chemical Sciences*, **9**(4), 1799–1808.

Fribourg-Blanc, A., & Mollaret, H. H. 1969. Natural treponematosis of the African primate. *Primates in Medicine*, **3**, 113.

Galat-Luong, A. 1988. Monkeys in the Pirang forest. Pirang. Ecological Investigations in a Forest Island in the Gambia. *Stiftung Walderhaltung in Afrika, Hamburg, and Bundesforschungsanstalt für Forst-und Holzwirtschaft, Hamburg, Warnke Verlag, Reinbek.*

Galat-Luong, A., & Galat, G. 2005. Conservation and survival adaptations of temminck's red colobus (*Procolobus badius* temmincki), in senegal. *International Journal of Primatology*, **26**(3), 585–603.

Galat, G., & Galat-Luong, A. 1985. La communauté de primates diurnes de la Forêt de Taï, Côte d'Ivoire. *Revue d'Ecologie-La Terre et La Vie*, **40**, 3–32.

Galat, G., Galat-Luong, A., & Nizinski, G. 2009. Increasing dryness and regression of the geographical range of temminck's red colobus *Procolobus badius temminckii*: implications for its conservation. *Mammalia: International Journal of the Systematics, Biology & Ecology of Mammals*, **73**(4), 365–368.

Gatinot, B. L. 1975. *Ecologie d'un Colobe bai (Colobus badius temmincki, Kuhl 1820) dans un milieu marginal au Senégal*, Université de Paris.

Gatinot, B. L. 1977. Le régime alimentaire du colobe bai au sénégal. *Mammalia*, **41**, 373–402.

Gatinot, B. L. 1978. Characteristics of the diet of west African red colobus. In D. J. Chivers & J. Herbert, eds., *Recent advances in primatology, Vol. 1: Behaviour*, Vol. 1, New York: Academic Press, pp. 253–255.

Gautier-Hion, A., & Brugière, D. 2005. Significance of riparian forests for the conservation of central African primates. *International Journal of Primatology*, **26**(3), 515–523.

Georgiev, A. V., Melvin, Z. E., Warketin, A. S., Winder, I. C., & Kassim, A. 2019. Two cases of dead-infant carrying by female Zanzibar red colobus (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park, Zanzibar. *African Primates*, ***13***, 57-60.

Gevaerts, H. 1992. Birth seasons of cercopithecus, cercocebus and colobus in zaire. *Folia Primatologica*, **59**(2), 105–113.

Ghai, R. R., Fugère, V., Chapman, C. A., Goldberg, T. L., & Davies, T. J. 2015. Sickness behaviour associated with non-lethal infections in wild primates. *Proceedings of the Royal Society B: Biological Sciences*, **282**(1814). doi:10.1098/rspb.2015.1436

Gogarten, J. F., Bonnell, T. R., Brown, L. M., Campenni, M., Wasserman, M. D., & Chapman, C. A. 2014. Increasing group size alters behavior of a folivorous primate. *International Journal of Primatology*, **35**(2), 590–608.

Gogarten, J. F., Guzman, M., Chapman, C. A., Jacob, A. L., Omeja, P. A., & Rothman, J. M. 2012. What is the predictive power of the colobine protein-to-fiber model and its conservation value? *Tropical Conservation Science*, **5**(3), 381–393.

Gogarten, J. F., Jacob, A. L., Ghai, R. R., … Chapman, C. A. 2015. Group size dynamics over 15+ years in an African forest primate community. *Biotropica*, **47**(1), 101–112.

Gogarten, J. F., Düx, A., Schuenemann, V. J., ... & Leendertz, F. H. 2016. Tools for opening new chapters in the book of Treponema pallidum evolutionary history. *Clinical Microbiology and Infection*, *22*(11), 916-921.

Gonedelé Bi, S., Bitty, A., Ouatara, K., & Scott Mcgraw, W. 2014. Primate surveys in côte d'ivoire's sassandra-bandama interfluvial region with notes on a remnant population of black-and-white colobus. *African Journal of Ecology*, **52**(4), 491–498.

Groves, C. P. 2007. The taxonomic diversity of the colobinae of Africa. *Journal of Anthropological Sciences*, **85**, 7–34.

Grubb, P., Butynski, T. M., Oates, J. F., … Struhsaker, T. T. 2003. Assessment of the diversity of African primates. *International Journal of Primatology*, **24**(6), 1301–1357.

Grubb, P., & Powell, C. B. 1999. Discovery of red colobus monkeys (*Procolobus badius*) in the niger delta with the description of a new and geographically isolated subspecies. *Journal Of Zoology*, **248**(1), 67–73.

Grubb, P., Struhsaker, T. T., & Siex, K. S. 2013. Subgenus *Piliocolobus* red colobus monkeys. In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa: Volume II Primates*, Bloomsbury Publishing, pp. 125–128.

Gunderson, V. 1977. Some observations on the ecology of colobus *badius* temmincki, abuko nature reserve, the gambia, west Africa. *Primates*, **18**(2), 305–314.

Hall, J. S., White, L., Williamson, E. A., Inogwabini, B.-I., & Ilambu, O. 2003. Distribution, abundance, and biomass estimates for primates within kahuzi-biega lowlands and adjacent forest in eastern drc. *African Primates*, **6**(1&2), 35–42.

Heinicke, S., Kalan, A. K., Wagner, O. J. J., Mundry, R., Lukashevich, H., & Kühl, H. S. 2015. Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods in Ecology and Evolution*, **6**(7), 753–763.

Hillyer, A. P., Armstrong, R., & Korstjens, A. H. 2015. Dry season drinking from terrestrial man-made watering holes in arboreal wild temminck's red colobus, the gambia. *Primate Biology*, **2**(1), 21–24.

Hobeika, S., Beziers, P., & Korstjens, A. H. 2009. The accuracy of sexual swellings as indicators for the reproductive status of female red colobus (*Piliocolobus tephrosceles*). *Folia Primatologica*, **80**(2), 161–162.

Hofner, A. N., Jost Robinson, C. A., & Nekaris, K. A. I. 2018. Preserving preuss's red colobus (*Piliocolobus preussi*): an ethnographic analysis of hunting, conservation, and changing perceptions of primates in ikenge-bakoko, cameroon. *International Journal of Primatology*, **39**(5), 895–917.

Holenweg, A.-K., Noë, R., & Schabel, M. 1996. Waser's gas model applied to associations between red colobus and diana monkeys in the Taï National Park, ivory coast. *Folia Primatologica*, **67**, 125–136.

Höner, O., Leumann, L., & Noë, R. 1997. Dyadic associations of red colobus and diana monkey groups in the Taï National Park, ivory coast. *Primates*, **38**(3), 281–291.

Hoppe-Dominik, B. 1984. Etude du spectre des proies de la panthère, panthera pardus, dans le parc national de Taï en côte d'Ivoire. *Mammalia*, **48**(4), 477–487.

Hosaka, K., Nakamura, M., & Takahata, Y. 2020. Longitudinal Changes in the Targets of Chimpanzee (*Pan troglodytes*) Hunts at Mahale Mountains National Park: How and Why Did They Begin to Intensively Hunt Red Colobus (*Piliocolobus rufomitratus*) in the 1980s? *Primates* **61**(3), 391-401.

Ikemeh, R. A. 2015. Assessing the population status of the critically endangered niger delta red colobus (*Piliocolobus* epieni). *Primate Conservation*, **29**, 87–96.

Isbell, L. A. 1983. Daily ranging behaviour of red colobus (colobus *badius tephrosceles*) in kibale forest, Uganda. *Folia Primatology*, **41**, 34–48.

Isbell, L. A. 2012. Re-evaluating the ecological constraints model with red colobus monkeys (*Procolobus rufomitratus tephrosceles*). *Behaviour*, **149**(5), 493–529.

IUCN 2020. *The IUCN Red List of Threatened Species. Version 2020-2*. https://www.iucnredlist.org. Downloaded on 09 July 2020.

Jenny, D., & Zuberbuhler, K. 2005. Hunting behaviour in west African forest leopards. *African Journal of Ecology*, **43**(3), 197–200.

Kane, E. E., & McGraw, W. S. 2018. Effects of chimpanzee (pan troglodytes) hunting seasonality and red colobus (*Piliocolobus badius*) association on diana monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire. *International Journal of Primatology*, **39**(4), 532–546.

Kaisala, D., Falay, P., Mande, C., Hart, J. A., Inventory, S. D., & Kinshasa, D. R. C. 2020. Rediscovery of the Kisangani Red Colobus. Report to Global Wildlife Conservation and the Frankfurt Zoological TL2 Project. Available at: https://www.bonoboincongo.com/wp-content/uploads/2020/03/2020-February-Kisangani-Red-Colobus-REPORT.pdf

Karere, G. M., Oguge, N. O., Kirathe, J., Muoria, P. K., Moinde, N. N., & Suleman, M. A. 2004. Population sizes and distribution of primates in the lower tana river forests, Kenya. *International Journal of Primatology*, **25**(2), 351–365.

Kibaja, M. 2014. Diet of the ashy red colobus (*Piliocolobus tephrosceles*) and crop-raiding in a forest-farm mosaic, Mbuzi, Rukwa region, Tanzania. *Primate Conservation*, **28**(1), 109–116.

Knauf, S., Gogarten, J. F., Schuenemann, V. J., … Batamuzi, E. K. 2018. Nonhuman primates across sub-saharan Africa are infected with the yaws bacterium treponema pallidum subsp. pertenue. *Emerging Microbes & Infections*, **7**(1), 1–4.

Koné, I., Lambert, J. E., Refisch, J., & Bakayoko, A. 2008. Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: implications for the conservation of forest fragments. *Tropical Conservation Science*, **1**(3), 293–306.

Koné, I., & Refisch, J. 2007. Can monkey behavior be used as an indicator for poaching pressure? a case study of the diana guenon (*Cercopithecus diana*) and the western red colobus (*Procolobus badius*) in the Taï National Park, Côte d'Ivoire. In W. S. McGraw, K. Zuberbühler, & R. Noë, eds., *Monkeys of the Taï Forest,* Cambridge, UK: Cambridge University Press, pp. 257–298.

Korstjens, A. H. 2001. *The mob , the secret sorority , and the phantoms: an analysis of the socio-ecological strategies of the three colobines of Taï. Ph.D. thesis,* Utrecht University, Utrecht.

Korstjens, A. H., Bergmann, K., Deffernez, C., … Schippers, E. P. 2007. How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines. In S. McGraw, K. Zuberbuhler, & R. Noë, eds., *The Monkeys of the Taï Forest, Ivory Coast: An African Primate Community*, Cambridge: Cambridge University Press, pp. 72–108.

Korstjens, A. H., & Dunbar, R. I. M. 2007. Time constraints limit group sizes and distribution in red and black-and-white colobus monkeys. *International Journal of Primatology*, **28**(3), 551–575.

Korstjens, A. H., Hobeika, S., Beziers, P., & Heistermann, M. 2008. What *Procolobus* can tell us about the evolution of female sexual signals. *Primate Eye*, **96**(Special Issue), 19.

Korstjens, A. H., Sterck, E. H. M., & Noe, R. 2002. How adaptive or phylogenetically inert is primate social behaviour? a test with two sympatric colobines. *Behaviour*, **139**(2), 203–225.

Kouassi, R. Y. W., McGraw, W. S., Yao, P. K., … Candolfi, E. 2015. Diversity and prevalence of gastrointestinal parasites in seven non-human primates of the Taï National Park, côte d'ivoire. *Parasite*, **22**. doi:10.1051/parasite/2015001

Koyabu, D. B., & Endo, H. 2009. Craniofacial variation and dietary adaptations of African colobines. *Journal of Human Evolution*, **56**(6), 525–536.

Kuhn, H.-J. 1972. On the perineal organ of male *Procolobus badius*. *Journal of Human Evolution*, **1**(4), 371-376,IN5-IN8,377-378.

Leendertz, S. A. J., Locatelli, S., Boesch, C., … Leendertz, F. H. 2011. No evidence for transmission of sivwrc from western red colobus monkeys (*Piliocolobus badius badius*) to wild west African chimpanzees (pan troglodytes verus) despite high exposure through hunting. *BMC Microbiology*, **11**. doi:10.1186/1471-2180-11-24

Liégeois, F., Lafay, B., Formenty, P., … Peeters, M. 2009. Full-length genome characterization of a novel simian immunodeficiency virus lineage (sivolc) from olive colobus (Procolobus verus) and new sivwrcpbb strains from western red colobus (*Piliocolobus badius badius*) from the Taï forest in ivory coast. *Journal of Virology*, **83**(1), 428–439.

Linder, J. M., & Oates, J. F. 2011. Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation*, **144**(2), 738–745.

Locatelli, S., Lafay, B., Liegeois, F., Ting, N., Delaporte, E., & Peeters, M. 2008a). Full molecular characterization of a simian immunodeficiency virus, sivwrcpbt from Temminck's red colobus (*Piliocolobus badius temminckii*) from abuko nature reserve, the gambia. *Virology*, **376**(1), 90–100.

Locatelli, S., Liegeois, F., Lafay, B., … Peeters, M. 2008b. Prevalence and genetic diversity of simian immunodeficiency virus infection in wild-living red colobus monkeys (*Piliocolobus badius badius*) from the Taï forest, Côte d'Ivoire. sivwrc in wild-living western red colobus monkeys. *Infection, Genetics and Evolution*, **8**(1), 1–14.

Luiselli, L., Amori, G., Akani, G. C., & Eniang, E. A. 2015. Ecological diversity, community structure and conservation of Niger delta mammals. *Biodiversity and Conservation*, **24**(11), 2809–2830.

Lwanga, J. S., Struhsaker, T. T., Struhsaker, P. J., Butynski, T. M., & Mitani, J. C. 2011. Primate population dynamics over 32.9 years at ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, **73**(10), 997–1011.

Maisels, F., Gauthierhion, A., & Gautier, J. P. 1994. Diets of 2 sympatric colobines in zaire: more evidence on seed-eating in forests on poor soils. *International Journal of Primatology*, **15**(5), 681–701.

Marsh, C. W. 1978. *Ecology and Social Organization of the Tana River Red Colobus, Colobus Badius Ruformitratus*, Bristol University Library.

Marsh, C. W. 1979a. Comparative aspects of social organization in the tana river red colobus, colobus *badius* ruformitratus. *Z. Tierpsychol.*, **51**(4), 337–362.

Marsh, C. W. 1979b. Female transference and mate choice among tana river red colobus. *Nature*, **281**(5732), 568–569.

Marsh, C. W. 1981a. Ranging behaviour and its relation to diet selection in tana river red colobus (*Colobus badius* rufomitratus). *Journal of Zoology*, **195**, 473–492.

Marsh, C. W. 1981b. Time budget of Tana River red colobus. *Folia Primatologica*, **35**(2–3), 147–178.

Marshall, A. R., Topp-Jørgensen, J. E., Brink, H., & Fanning, E. 2005. Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa mountains of Tanzania. *International Journal of Primatology,* **26**(1), 127–145.

Mayhew, M., Danzy Cramer, J., Fenton, L., Dittrich, A., & Armstrong, R., 2020. A new hotspot for Temminck's Red Colobus (*Piliocolobus badius temminckii*) in The Gambia: the feasibility of a community approach to conservation. *Primate Conservation* **34**. Online First.

Mbora, D. N. M., & McGrew, W. C. 2002. Extra-group sexual consortship in the Tana river red colobus (*Procolobus rufomitratus*)? *Folia Primatologica*, **73**(4), 210–213.

Mbora, D. N. M., & McPeek, M. A. 2009. Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. *Journal of Animal Ecology*, **78**(1), 210–218.

Mbora, D. N. M., & McPeek, M. A. 2010. Endangered species in small habitat patches can possess high genetic diversity: the case of the Tana river red colobus and mangabey. *Conservation Genetics,* **11**(5), 1725–1735.

Mbora, D. N. M., & Meikle, D. B. 2004. The value of unprotected habitat in conserving the critically endangered tana river red colobus (*Procolobus* rufomitratus). *Biological Conservation*, **120**(1), 91–99.

Mccord, A. I., Chapman, C. A., Weny, G., … Goldberg, T. L. 2014. Fecal microbiomes of non-human primates in western Uganda reveal species-specific communities largely resistant to habitat perturbation. *American Journal of Primatology,* **76**(4), 347–354.

McGraw, W. S. 1998. Comparative locomotion and habitat use of six monkeys in the Taï forest, ivory coast. *American Journal of Primatology*, **46**, 229–250.

McGraw, W. S. 2005. Update on the search for miss Waldron's red colobus monkey. *International Journal of Primatology*, **26**(3), 605–619.

McGraw, W. S., & Bshary, R. 2002. Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. *International Journal of*

Primatology, **23**(2), 311–325.

Mcgraw, W. S., Cooke, C., & Shultz, S. 2006. Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Taï Forest: implications for primate predation and early hominid taphonomy in south Africa. *American Journal of Physical Anthropology*, **131**(2), 151–165.

McGraw, W. S., van Casteren, A., Kane, E., Geissler, E., Burrows, B., & Daegling, D. J. 2016. Feeding and oral processing behaviors of two colobine monkeys in Taï Forest, Ivory Coast. *Journal of Human Evolution*, **98**, 90–102.

McGraw, W. S., & Zuberbuhler, K. 2008. Socioecology, predation, and cognition in a community of West African monkeys. *Evolutionary Anthropology*, **17**(6), 254–266.

Milich, K. M., Bahr, J. M., Stumpf, R. M., & Chapman, C. A. 2014a. Timing is everything: expanding the cost of sexual attraction hypothesis. *Animal Behaviour*, **88**, 219–224.

Milich, K. M., Stumpf, R. M., Chambers, J. M., & Chapman, C. A. 2014b. Female red colobus monkeys maintain their densities through flexible feeding strategies in logged forests in Kibale National Park, Uganda. *American Journal of Physical Anthropology*, **154**(1), 52–60.

Minhós, T., Chikhi, L., Sousa, C., … Bruford, M. W. 2016. Genetic consequences of human forest exploitation in two colobus monkeys in guinea bissau. *Biological Conservation*, **194**, 194–208.

Minhós, T., Sousa, C., Vicente, L. M., & Bruford, M. W. 2015. Kinship and intragroup social dynamics in two sympatric African colobus species. *International Journal of Primatology*, **36**(4), 871–886.

Mitani, J. C., Sanders, W. J., Lwanga, J. S., & Windfelder, T. L. 2001. Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behavioral Ecology And Sociobiology*, **49**(2–3), 187–195.

Mitani, J. C., Struhsaker, T. T., & Lwanga, J. S. 2000). Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *International Journal of Primatology*, **21**(2), 269–286.

Mittermeier, R. A., Rylands, A. B., & Wilson, D. E. 2013. *The mammals of the world, part 3: Primates*, Barcelona: Lynx Edicions.

Miyamoto, M. M., Allen, J. M., Gogarten, J. F., & Chapman, C. A. 2013. Microsatellite dna suggests that group size affects sex-biased dispersal patterns in red colobus monkeys. *American Journal of Primatology*, **75**(5), 478–490.

Moinde-Fockler, N. N., Oguge, N. O., Karere, G. M., Otina, D., & Suleman, M. A. 2007. Human and natural impacts on forests along lower tana river, Kenya: implications towards conservation and management of endemic primate species and their habitat. *Biodiversity and Conservation*, **16**(4), 1161–1173.

Mturi, F. A. 1991). *The feeding ecology and behavior of the red colobus monkey (Colobus badius kirkii)*, University of Dar es Salaam, Dar es Salaam.

Murthy, S., Couacy-Hymann, E., Metzger, S., … Ehlers, B. 2013. Absence of frequent herpesvirus transmission in a nonhuman primate predator-prey system in the wild. *Journal of Virology*, **87**(19), 10651–10659.

N'Goran, P. K., Boesch, C., Mundry, R., … Kühl, H. S. 2012. Hunting, law enforcement, and African primate conservation. *Conservation Biology*, **26**(3), 565–571.

Nowak, K. 2007. *Behavioural flexibility and demography of Procolobus kirkii across floristic and disturbance gradients*, University of Cambridge, Cambridge.

Nowak, K. 2008. Frequent water drinking by Zanzibar red colobus (*Procolobus kirkii*) in a mangrove forest refuge. *American Journal of Primatology,* **70**(11), 1081–1092.

Nowak, K., Cardini, A., & Elton, S. 2008. Evolutionary acceleration and divergence in *Procolobus kirkii*. *International Journal of Primatology,* **29**(5), 1313–1339.

Nowak, K., & Lee, P. C. 2011. Demographic structure of Zanzibar red colobus populations in unprotected coral rag and mangrove forests. *International Journal of Primatology,* **32**(1), 24–45.

Nowak, K., & Lee, P. C. 2013. Status of Zanzibar red colobus and Sykes's monkeys in two coastal forests in 2005. *Primate Conservation*, **27**(1), 65–73.

Oates, J. F. 1994. The natural history of African colobines. In A. G. Davies & J. F. Oates, eds., *Colobine monkeys*, Cambridge: Cambridge University Press, pp. 75–128.

Oates, J. F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*, **21**(1), 1–9.

Oates, J. F., Abedi-Lartey, M., McGraw, W. S., Struhsaker, T. T., & Whitesides, G. H. 2000). Extinction of a West African red colobus monkey. *Conservation Biology*, **14**(5), 1526–1532.

Oates, J. F., & Whitesides, G. H. 1990). Association between olive colobus (*Procolobus* verus), diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *American Journal Of Primatology*, **21**, 129–146.

Oates, J. F., Whitesides, G. H., Davies, A. G., … Mole, S. 1990). Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology*, **71**(1), 328–343.

Oates, J., & Ting, N. 2015. Ch. 15. conservation consequences of unstable taxonomies: the case of the red colobus monkeys. *Taxonomic Tapestries*, p321.

Olgun, H., Mohammed, M. K., Mzee, A. J., Green, M. E. L., Davenport, T. R. B., & Georgiev, A. V. 2020. The impact and implications of vehicle collisions on the endangered and endemic Zanzibar red colobus (*Piliocolobus kirkii*). *BioRxiv* 2020.01.17.906909; https://doi.org/10.1101/2020.01.17.906909

Onderdonk, D. A., & Chapman, C. A. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, **21**(4), 587–611.

Paige, S. B., Frost, S. D. W., Gibson, M. A., … Goldberg, T. L. 2014. Beyond bushmeat: animal contact, injury, and zoonotic disease risk in western Uganda. *EcoHealth*, **11**(4), 534–543.

Pebsworth, P. A., Huffman, M. A., Lambert, J. E., & Young, S. L. 2019. Geophagy among nonhuman primates: a systematic review of current knowledge and suggestions for future directions. *American Journal of Physical Anthropology*, **168**, 164–194.

Piachaud, M., Beziers, P., Hobeika, S., & Korstjens, A. H. 2009. What is the best strategy to access females in oestrus? *Folia Primatologica*, **80**(2).

Pobiner, B. L., DeSilva, J., Sanders, W. J., & Mitani, J. C. 2007. Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda. *Journal of Human Evolution*, **52**(6), 614–636.

Refisch, J., & Koné, I. 2005. Impact of commercial hunting on monkey populations in the Taï region, cote d'ivoire. *Biotropica*, **37**(1), 136–144.

Reyna-Hurtado, R., Teichroeb, J. A., Bonnell, T. R., … Chapman, C. A. 2018. Primates adjust movement strategies due to changing food availability. *Behavioral Ecology*, **29**(2), 368–376.

Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. 2003. Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology*, **24**(3), 541–573.

Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. 2015. Long-term declines in nutritional quality of tropical leaves. *Ecology*, **96**(3), 873–878.

Rothman, J. M., Chapman, C. A., Twinomugisha, D., Wasserman, M. D., Lambert, J. E., & Goldberg, T. L. 2008. Measuring physical traits of primates remotely: the use of parallel lasers. *American Journal of Primatology*, **70**(12), 1191–1195.

Rovero, F., Marshall, A. R., Jones, T., & Perkin, A. 2009. The primates of the Udzungwa mountains: diversity, ecology and conservation. *Journal of Anthropological Sciences*, **87**, 93–126.

Rovero, F., Mtui, A., Kitegile, A., Jacob, P., Araldi, A., & Tenan, S. 2015. Primates decline rapidly in unprotected forests: evidence from a monitoring program with data constraints. *PLoS ONE*, **10**(2). doi:10.1371/journal.pone.0118330

Rovero, F., & Struhsaker, T. T. 2007. Vegetative predictors of primate abundance: utility and limitations of a fine-scale analysis. *American Journal of Primatology*, **69**(11), 1242–1256.

Ruiz-Lopez, M. J., Barelli, C., Rovero, F., … Ting, N. 2016. A novel landscape genetic approach demonstrates the effects of human disturbance on the Udzungwa red colobus monkey (*Procolobus gordonorum*). *Heredity*, **116**(2), 167–176.

Ryan, A. M., Chapman, C. A., & Rothman, J. M. 2013. How do differences in species and part consumption affect diet nutrient concentrations? a test with red colobus monkeys in Kibale National Park, Uganda. *African Journal of Ecology*, **51**(1), 1–10.

Salum, L. A. 2009. Ecotourism and biodiversity conservation in jozani-chwaka bay National Park, zanzibar. *African Journal of Ecology*, **47**(SUPPL. 1), 166–170.

Schultz, S., Noë, R., McGraw, W. S., & Dunbar, R. I. M. 2004. A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, **271**(1540), 725–732.

Serge Bobo, K., Bonito Ntumwel, C., Florence Aghomo, F., & Aurele Ayemele, K. G. 2017. The conservation status of two threatened primates in the korup region, southwest cameroon. *Primate Conservation*, **31**(1), 37–48.

Shultz, S., Noe, R., McGraw, W. S., & Dunbar, R. I. M. 2004. A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society B-Biological Sciences*, **271**(1540), 725–732.

Siex, K. S. 2003. *Effects of population compression on the demography, ecology, and behavior of the Zanzibar red colobus monkey (Procolobus kirkii)*, Duke University, Durham.

Siex 2005. Habitat destruction, population compression and overbrowsing by the Zanzibar red colobus monkey (*Procolobus kirkii*); in J. D. Paterson & J. Wallis, eds, Commensalism and Conflict: The Human-Primate Interface. *Special topics in Primatology* **4**:294-337

Siex, K. S., & Struhsaker, T. T. 1999a. Colobus monkeys and coconuts: a study of perceived human- wildlife conflicts. *Journal of Applied Ecology*, **36**(6), 1009–

1020.

Siex, K. S., & Struhsaker, T. T. 1999b. Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *International Journal of Primatology*, **20**(2), 163–192.

Siex, K. S., & Struhsaker, T. T. 2013. *Procolobus kirkii* Zanzibar red colobus (Kirk's red colobus). In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa: Volume II Primates*, London: Bloomsbury, pp. 151–154.

Simons, N. D., Eick, G. N., Ruiz-Lopez, M. J., … Sterner, K. N. 2017. Cis-regulatory evolution in a wild primate: infection-associated genetic variation drives differential expression of mhc-dqa1 in vitro. *Molecular Ecology*, **26**(17), 4523–4535.

Snaith, T. V, & Chapman, C. A. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, **59**, 185–190.

Snaith, T. V, & Chapman, C. A. 2008. Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behavioral Ecology*.

Stanford, C. B. 1995. The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour*, **49**, 577–587.

Stanford, C. B. 1998a. *Chimpanzee and red colobus: The ecology of predator and prey*, 1st edn, Cambridge: Harvard University Press.

Stanford, C. B. 1998b. Predation and male bonds in primate societies. *Behaviour*, **135**(4), 513–533.

Stanford, C. B. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, **23**(4), 741–757.

Starin, E. D. 1988. Gestation and birth-related behaviors in Temminck's red colobus. *Folia Primatologica*, **51**(2–3), 161–164.

Starin, E. D. 1991. *Socioecology of the red colobus monkey in The Gambia with particular reference to female-male differences and transfer patterns*, Ph.D. Thesis, City University of New York, New York.

Starin, E. D. 1994). Philopatry and affiliation among red colobus. *Behaviour*, **130**(3–4), 253–270.

Starin, E. D. 2001. Patterns of inbreeding avoidance in Temminck's red colobus. *Behaviour*, **138**(4), 453–465.

Steel, I. R. 2012. *The Effects of Habitat Parameters on the Behavior, Ecology, and Conservation of the Udzungwa Red Colobus Monkey (Procolobus gordonorum)*, Ph.D. Thesis, Duke University.

Steel, R. I. 2014. Using multiple travel paths to estimate daily travel distance in arboreal, group-living primates. *Primates*, **56**(1), 71–75.

Stern, M., & Goldstone, R. 2005. Red colobus as prey: the leaping habits of five sympatric old world monkeys. *Folia Primatologica*, **76**(2), 100–112.

Struhsaker, T. T. 1975. *The red colobus monkey*, Chicago: University of Chicago Press.

Struhsaker, T. T. 2000. The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In C. J. Jolly & P. F. Whitehead, eds., *Old World Monkeys*, Cambridge, UK: Cambridge University Press, pp. 393–430.

Struhsaker, T. T. 2010. *The red colobus monkeys: variation in demography, behavior, and ecology of endangered species*, Oxford University Press.

Struhsaker, T. T., Cooney, D. O., & Siex, K. S. 1997. Charcoal consumption by

Zanzibar red colobus monkeys: its function and its ecological and demographic consequences. *International Journal of Primatology*, **18**(1), 61–72.

Struhsaker, T. T., & Grubb, P. 2013. *Procolobus rufomitratus* eastern red colobus. In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa: Volume II Primates*, London, pp. 142–147.

Struhsaker, T. T., Grubb, P., & Siex, K. S. 2013. *Procolobus gordonorum* Udzungwa red colobus (Iringa / Uhehe / Gordon's red colobus). In T. M. Butynski, J. Kingdon, & J. Kalina, eds., *Mammals of Africa : Primates*, London: Bloomsbury, pp. 148–151.

Struhsaker, T. T., & Leakey, M. 1990. Prey selectivity by crowned hawk-eagles on monkeys in the Kibale forest, Uganda. *Behavioral Ecology And Sociobiology*, **26**, 435–443.

Struhsaker, T. T., & Leland, L. 1979. Socioecology of five sympatric monkey species in the Kibale forest, Uganda. *Advances in the Study of Behavior*, **9**, 159–228.

Struhsaker, T. T., Marshall, A. R., Detwiler, K., … Butynski, T. M. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology*, **25**(3), 615–658.

Struhsaker, T. T., & Siex, K. S. 1998. Translocation and introduction of the Zanzibar red colobus monkey: success and failure with an endangered island endemic. *ORYX*, **32**(4), 277–284.

Teelen, S. 2007a. Influence of chimpanzee predation on associations between red colobus and red-tailed monkeys at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, **28**(3), 593–606.

Teelen, S. 2007b. Primate abundance along five transect lines at ngogo, Kibale National Park, Uganda. *American Journal of Primatology*, **69**(9), 1030–1044.

Teelen, S. 2008. Influence of chimpanzee predation on the red colobus population at Ngogo, Kibale National Park, Uganda. *Primates*, **49**(1), 41–49.

Thomas, S. C. 1991. Population-densities and patterns of habitat use among anthropoid primates of the ituri forest, zaire. *Biotropica*, **23**(1), 68–83.

Ting, N. 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of miocene origins for the living colobus monkeys. *Journal of Human Evolution*, **55**(2), 312–325.

Treves, A. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology*, **20**(1), 35–67.

Usongo, L. I., & Amubode, F. O. 2001. Nutritional ecology of preuss's red colobus monkey (colobus *badius preussi* rahm 1970) in Korup National Park, cameroon. *African Journal of Ecology*, **39**(2), 121–125.

van Oirschot, B. 1999). *Group fission in western red colobus (Procolobus badius) Taï National Park, Côte d'Ivoire*. *Institute of Evolutionary and Ecological Sciences*, Universiteit Leiden, Leiden.

van Oirschot, B. 2000. Group fission in Taï red colobus (*Procolobus badius*). *Folia Primatologica*, **71**(4), 205.

Wachter, B., Schabel, M., & Noë, R. 1997. Diet overlap and polyspecific associations of red colobus and diana monkeys in the Taï National Park, ivory coast. *Ethology*, **103**, 514–526.

Wahungu, G. M., Muoria, P. K., Moinde, N. N., Oguge, N. O., & Kirathe, J. N. 2005. Changes in forest fragment sizes and primate population trends along the river tana floodplain, Kenya. *African Journal of Ecology*, **43**(2), 81–90.

Waltert, M., Lien, Faber, K., & Muhlenberg, M. 2002. Further declines of threatened primates in the korup project area, south-west cameroon. *Oryx*, **36**(3), 257–265.

Wang, X. P., Yu, L., Roos, C., … Zhang, Y. P. 2012. Phylogenetic relationships among the colobine monkeys revisited: new insights from analyses of complete mt genomes and 44 nuclear non-coding markers. *PLoS ONE*, **7**(4). doi:10.1371/journal.pone.0036274

Wasserman, M. D., & Chapman, C. A. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal Of Animal Ecology*, **72**(4), 650–659.

Wasserman, M. D., Chapman, C. A., Milton, K., Gogarten, J. F., Wittwer, D. J., & Ziegler, T. E. 2012. Estrogenic plant consumption predicts red colobus monkey (*Procolobus rufomitratus*) hormonal state and behavior. *Hormones and Behavior*, **62**(5), 553–562.

Wasserman, M. D., Chapman, C. A., Milton, K., Goldberg, T. L., & Ziegler, T. E. 2013. Physiological and behavioral effects of capture darting on red colobus monkeys (*Procolobus rufomitratus*) with a comparison to chimpanzee (*Pan troglodytes*) predation. *International Journal of Primatology*, **34**(5), 1020–1031.

Watts, D. P., & Amsler, S. J. 2013. Chimpanzee-red colobus encounter rates show a red colobus population decline associated with predation by chimpanzees at Ngogo. *American Journal of Primatology*, **75**(9), 927–937.

Watts, D. P., & Mitani, J. C. 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, **23**(1), 1–28.

Watts, D. P., & Mitani, J. C. 2015. Hunting and prey switching by chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. *International Journal of Primatology*, **36**(4), 728–748.

Werre, J. L. R. 2000). *Ecology and behavior of the Niger Delta red colobus (Procolobus badius epieni)*, The City University of New York, New York.

Whitesides, G. H. 1989). Interspecific associations of diana monkeys, cercopithecus diana , in Sierra Leone, West Africa: biological significance or chance? *Animal Behaviour*, **37**(5), 760–776.

Yildirim, S., Yeoman, C. J., Janga, S. C., … Stumpf, R. M. 2014. Primate vaginal microbiomes exhibit species specificity without universal lactobacillus dominance. *ISME Journal*, **8**(12), 2431–2444.

Yildirim, S., Yeoman, C. J., Sipos, M., … Nelson, K. E. 2010. Characterization of the fecal microbiome from non-human wild primates reveals species specific microbial communities. *PLoS ONE*, **5**(11). doi:10.1371/journal.pone.0013963

Zimmermann, F., Köhler, S. M., Nowak, K., … Leendertz, F. H. 2017. Low antibody prevalence against bacillus cereus biovar anthracis in Taï National Park, côte d'ivoire, indicates high rate of lethal infections in wildlife. *PLoS Neglected Tropical Diseases*, **11**(9). doi:10.1371/journal.pntd.0005960

Zuberbühler, K., & Jenny, D. 2002. Leopard predation and primate evolution. *Journal of Human Evolution*, **43**(6), 873–886.

Zuberbühler, K., Jenny, D., & Bshary, R. 1999. The predator deterrence function of primate alarm calls. *Ethology*, **105**(5), 477–490.

Table 1: Taxonomic information for red colobus.

Region	**Mittermeier *et al.* (2013)**	**Struhsaker (2010)**[1]	**Grubb *et al*. (2003)**	**English name**	**Main study sites**	**IUCN**[2]
	17 spp in genus *Piliocolobus*	**18 taxa in 7 groups**	**18 taxa, subgenus *Piliocolobus***			
Sierra Leone, Ivory Coast, Liberia, Guinea	*P. badius*	*badius* (1)	*P. badius badius*	Western red or bay colobus	Taï, Tiwai	EN
Gambia, Senegal, Guinea, Guinea Bissau, and possibly Sierra Leone	*P. temminckii*	*temminckii* (1)	*P. b. temminckii*	Temminck's red colobus	Abuko, Fathalla	EN
Ivory coast & Ghana	*P. waldronae*	*waldroni* (1)	*P. b. waldroni*	Miss Waldron's red colobus		CR[3]
Bioko Island	*P. pennantii*	*pennantii* (3)	*P. pennantii pennantii*	Pennant's or Bioko red colobus	Bioko Island	CR
Niger Delta	*P. epieni*	*epieni* (5)	*P. p. epieni*	Niger Delta red colobus		CR
Congo	*P. bouvieri*	*bouvieri* (4)	*P. p. bouvieri*	Bouvier's red colobus		EN
SE Nigeria to SW Cameroon	*P. preussii*	*preussi* (2)	*P. preussi*	Preuss's red colobus	Korup NP	CR
Tana River, Kenya	*P. rufomitratus*	*rufomitratus* (6)	*P. rufomitratus rufomitratus*	Tana river red colobus	Tana River area	CR
DR Congo	*P. tholloni*	*tholloni* (5)	*P. r. tholloni*	Tshuapa red colobus		VU
CAR, DR Congo, South Sudan	*P. oustaleti*	*oustaleti* (5)	*P. r. oustaleti*	Oustalet’s red colobus		VU
DR Congo	*P. parmentieri*	*parmentieri* (5)	*P. r. parmentieri*	Lomami red colobus		EN
Congo basin	*P. tephrosceles*	*tephrosceles* (5)	*P. r. tephrosceles*	Eastern or Ash red colobus	Kibale (Kanyawara, Ngogo), Gombe	EN
Congo basin	*P. foai*	*foai* (5)	*P. r. foai*	Foa’s red colobus		EN
Congo basin	*P. semlikiensis*	*ellioti*	*P. r. ellioti*	Semliki red colobus		VU
DR Congo	*lulindicus'*	*lulindicus* (5)	*P. r. lulindicus*	Ulindi River red colobus		VU
DR Congo	*P. langi*	*langi* (5)	*P. r. langi*	Lang’s red colobus		EN
Zanzibar Archipelago	*P. kirkii*	*kirkii* (7)	*P. kirkii*	Zanzibar or Kirk's red colobus	Jozani-Chwaka Bay NP & nearby agricultural mosaics; Kiwengwa FR, Uzi Island mangroves	EN
Udzungwa, Tanzania	*P. gordonorum*	gordonorum (7)	*P. gordonorum*	Udzungwa red colobus	Udzungwa	VU

[1] The numbers are arbitrary indicators of taxonomic group membership as suggested by Struhsaker (2010) (species with the same number group together). NP = National Park, FR = Forest Reserve; [2] IUCN 2020 *The IUCN Red List of Threatened Species. Version 2020-2*. https://www.iucnredlist.org. Downloaded on 09 July 2020; [3] Possibly extinct.

Table 2: Weight and swelling size information for species that have such information

	Body mass adult females			**Body mass adult males**				
	Mean	**Min-Max**	**Sample size**	**Mean**	**Min-Max**	**Sample size**	**Sex Dimorphism (F/M)**	**Swelling Size**
P. badius	7.8	5.0 to 10.0	37	8.4	6.4 to 9.6	17	1.08	Large
P. temminckii								Large
P. waldroni	5.8	5.5 to 6.0	2	6.4	6.3 to 6.5	2	1.10	
P. pennantii	10		1	11		1	1.10	Large
P. epieni								Medium (donut size)[1]
P. preussii	7.3		1			0		Very Large
P. rufomitratus	7.2	6.0 to 8.0	7	9.7	9.0 to 10.0	3	1.35	Small
P. tholloni	estimated small range 7-10 kg							Medium?
P. oustaleti	estimated mid range 8-11 kg							Large
P. parmentieri								Large
P. tephrosceles	5.8		1	10.5		1	1.81	Small
P. kirkii	6.8	5.5 to 8.4	25	7	5.5 to 9.4	26	1.03	Small
P. gordonorum								Medium/ Large

Weight is mostly taken from Delson et al. (2000) but all sources are summarised in the relevant profiles in Butynski *et al.* (2013) Mammals of Africa: Volume II Primates; whilst information on swelling size is based on AHK personal observations and Struhsaker (2010). Species profiles: *P. badius*, *P. temminckii*, *P. waldroni* in Butynski *et al.* (2013a); *P. pennantii* in Butynski et al. (2013b); *P. preussi* in Butynski & Kingdon (2013); *P. rufomitratus, P. epieni, P. tholloni, P. oustaleti, P. parmentieri, P. tephrosceles* in Struhsaker & Grubb (2013); *P. kirkii* in Siex & Struhsaker (2013); *P. gordonorum* in Struhsaker et al. (2013). Notes: [1] Werre (2000).

Table 3: Diet of red colobus species across their range based on studies of at least 8 months

Location	**Species**	**TL**	**YL**	**ML**	**FR**	**(SD)**	**FRTTot**	**FL**	**OT**	**Ref**	**study period**
Taï NP	*badius*	49.6	46	3.5	28.8		28.8	19.5	2.1	A	1990s
Tiwai	*badius*	51.9	31.7	20.2	5.9	25.3	31.2	16.1	0.8	B	1980s
Salongo	*tholloni*	60.7	54.3	6.4	37.9		37.9	1.4	0	C	1990s
Tana River Mchelelo 70s	*ruformitratus*	66.2	52.4	11.5	24.1	0.9	25	6.2	2.6	D	1970s
Tana River Mchelelo 80s	*ruformitratus*	63.4	61.2	2.2	21.7		21.7	13.3	1.6	E	1980s
Tana River Baomo South 80s	*ruformitratus*	47.2	45.9	1.3	25.6		25.6	26.7	0.5	E	1980s
Zanzibar, Jozani Forest	*kirkii*	64.5	50.6	13.9	31.5	0	31.5	8	-4	F	1980s
Zanzibar, Jozani shambas	*kirkii*	70	64.2	5.8	23.5	0	23.5	8.1	-1.6	F	1980s
Zanzibar, Jozani Forest	*kirkii*	68.1	50.7	1	23.7	1.8	25.5	4.8	1.6	G	1999
Zanzibar, Jozani shambas	*kirkii*	81.7	54.9	0.8	5.1	0.1	5.2	5.5	7.6	G	1999
Zanzibar Kiwengwa	*kirkii*	60.3	48.2	7.4	22.9	4.7	27.7	11.8	0.2	G	2003-2006
Zanzibar Uzi	*kirkii*	66.9	61.4	0	23.2	1.3	24.5	7.4	1.2	G	2003-2006
Gombe	*tephrosceles*	78.5	37.3	44.1	11.4	0	11.4	9.7	0.4	I	Jan69-Jun70
Gombe	*tephrosceles*	72.2			24.6		24.6		3.2	J	1990s
Kibale Kanyawara K30	*tephrosceles*	68.2	45.6	22.6	6.3	6	12.3	9.9	9.6	L	1970s
K30, Kanyawara, camp	*tephrosceles*	86.9	55.8	13.3	5.7		5.7	2.4		L	Aug94-Jul95
K30, Kanyawara, camp	*tephrosceles*	86.0	58.8	10.2	7.6		7.6	1.5		L	Aug95-Jul96
K30, Kanyawara, camp	*tephrosceles*	81.5	71.9	2.4	7.9		7.9	1.4		L	Aug96-Jul97
K30, Kanyawara, camp	*tephrosceles*	89.2	75.8	5.6	6.6		6.6	3.5	2.2	L	Aug98-Jul99
Sebatoli, Kibale, Uganda	*tephrosceles*	86.9	79.5	7.4	6.4		6.4	3.3	3.4	M	Jul96-Jun97
K30,Kanyawara, Kibale	*tephrosceles*	81.7	71.8	9.9	6.7		6.7	2	9.6	M	Jul96-Jun97
Dura, Kibale	*tephrosceles*	78.4	73.8	4.6	13.9		13.9	6.2	1.5	M	Jul96-Jun97
Mainaro, Kibale	*tephrosceles*	75.5	59.3	16.2	10.8		10.8	7.2	6.5	M	Jul96-Jun97
K30, Kanyawara, Big	*tephrosceles*	89.1	83.5	5.6	6.6		6.6	3.5	0.8	N1	Jul98-Jun99
K30, Kanyawara, small	*tephrosceles*	83.8	70.5	13.3	8.9		8.9	0.8	6.5	N2	Jul98-Jun99
Mikana is part of K14	*tephrosceles*	93.6	91.6	2	3		3	2.2	1.2	N	Jul99-May00
Nkuruba, fragments	*tephrosceles*	88.8	70.4	18.4	1.9		1.9	2.3	7	N	Aug99-Apr00

Location	**Species**	**TL**	**YL**	**ML**	**FR**	**(SD)**	**FRTTot**	**FL**	**OT**	**Ref**	**study period**
K15 Kanyawara, Kibale	*tephrosceles*	72.4	69.8	2.6	17.2		17.2	2.3	8.1	O	Jul94-Jul97
Kahunga Kibale NP	*tephrosceles*	69.8	48.8	21	3.1		3.1	22.7	4.4	O	Jul95-Jun96
Abuko NR	*temminckii*	46.9	34.9	11.4	38.8	2.9	41.7	8.6	2.8	P	1978-83
Fathala	*temminckii*	48	42.6	5.4	17.4	18.5	35.9	8.7	7.4	Q	1970s
Fathala	*temminckii*	76.4	70.1	6.3			18.8		4.8	R	1994-1996
Magombera, Mwanihana (Udz)	*gordonorum*	70.8	48.2	15.5	5.3	13.5	18.8	4.4	6	S	2009-2010
Gbanraum, Niger Delta	*epieni*	73.7	56.8	4.7	4.0	10.2	14.1	9.6	2.6	T	Sep96-Aug97
Korup NP	*preussi*	88.91	88.91	0	0.87		0.87	10.2		U	1991-1993

TL= total leaf matter including various non-vegetative plant parts (incl. petioles, stems, herbs, pith if those were provided) and YL and ML; YL= young leaf, including leaf buds, young petioles and undetermined buds; ML= mature leaf is restricted to recorded mature leaf; FR = fruit pulp (if different from Fruit total) or situations in which fruit is consumed whole; (SD) = seeds if these were identified separately from consumed fruit, typically, this was the case when only the seed is consumed and there is no fruit pulp or it is discarded; FL= flowers including flowerbuds; OT = other; Ref = References: A. Korstjens & Dunbar (2007); B. Davies *et al.* (1999), Oates (1994); C. Maisels et al (1994); Marsh (1981); E. Decker (1994); F. Mturi (1991) cited in Struhsaker (2010) average of 2 groups; F. Siex (2003); H. Nowak (2007) p335; I. Clutton-Brock (1975); J. Stanford (1998) p111 (read off graph); K. Struhsaker (2010) average of two study groups; L. Chapman *et al.* (2002b); M. Chapman & Chapman, (2000a); N. Rode *et al.* (2003), N1=large group (n=48), N2=small group (n=24); O. Chapman & Chapman (1999); P. Starin (1991) and Oates (1994); Q. Gatinot (1977, 1978); R. Diouck (1999); S. Steel (2012), Udz=Udzungwa; T. Werre (2000); U. Usongo & Amubode (2001).

Table 4. Activity budgets of red colobus studies >8 months with size (Grpsz), number of adult females (AF) and males (AM) of the study groups included, feeding and foraging (feed), climbing and travelling (move), resting and inactive or autogrooming (rest) and grooming or social activities (social, for most studies this is equivalent to grooming time as they did not mention other social activities).

Site	**Species**	**Grpsz**	**AF**	**AM**	**Feed**	**Move**	**Rest**	**Social Groom**	**Reference**
Taï NP	*badius*	52.0	18.5	10.5	44.9	18.9	29.9	6.3	Korstjens & Dunbar (2007)
Tiwai	*badius*	33.0	13.0	7.0	37.0	5.0	55.0	3.0	Davies *et al.* (1999)
Tana River Mchelelo 70s	*ruformitratus*	21.5	16.0	1.0	31.5	6.4	57.3	2.9	Marsh (1981)
Tana River Mchelelo 80s	*ruformitratus*	9.7	4.0	1.0	28.6	21.5	48.0	0.2	Decker (1994)
Tana River Baomo S 80s	*ruformitratus*	23.5	11.3	1.0	23.3	24.4	50.0	0.2	Decker (1994)
Abuko	*temminckii*	26.2	10.8	2.0	21.3	12.5	52.1	12.6	Starin (1991)
Magombera, Mwanihana (Udz)	*gordonorum*	38.3	19.0	3.5	25.3	12.3	58.0	3.3	Steel (2012)
Gombe	*tephrosceles*	23.0	11.2	6.0	29.1	13.1	48.2	10.1	Stanford (1998)
Kibale Kanyawara K30 70s	*tephrosceles*	23.9	9.2	2.7	44.8	9.1	34.6	4.5	Struhsaker (2010) p220
Kibale Ngogo	*tephrosceles*	31.8	11.3	6.25	32.0	8.7	35.6	7.3	Struhsaker (2010) p220
Gombe	*tephrosceles*	82	24	11	25.0	8.0	54.0	5.5	Clutton-Brock (1974)
Kibale Kanyawara K14,K30	*tephrosceles*	67.2			30.875	9.4	52.575	5.6	Isbell (2012)[1]
Kibale NP logged 1	*tephrosceles*	57 to 98			45.8	7.9	37.7	6.4	Gogarten *et al.* (2014)
Zanzibar, Jozani Forest	*kirkii*	30	10.1	2.47	28.7	12.1	47.3	5.3	Siex (2003)
Zanzibar, Jozani shambas	*kirkii*	37.5	14.9	4.7	28.6	6.0	43.8	8.3	Siex (2003)
Kibale NP logged	*tephrosceles*	44	18	6	46.0	14.0	36.0	4.0	Milich *et al.* (2014b)[2]
Kibale NP oldgrowth	*tephrosceles*	53.5	18.5	10	35.0	18.0	41.0	6.0	Milich *et al.* (2014b)[2]
Gbanraum, Niger Delta	*epieni*	59.5	26	6.5	30.1	31.7	32.5	5.7	Werre (2000) p168
Korup NP	*preussi*	variable			16.3	13.1	25.7	1.6	Fonkwo *et al.* (2015)[3]

Notes: social time is mostly made up of grooming or entirely made up of social grooming if the study provided this information; [1]Isbell (2012): average of AM and AF activities in two forest areas; [2]Milich *et al.* 2014: adult females only; [3]Fonkwo *et al.* (2015) recorded behaviour using scan sampling of groups encountered along the trails so group size varies, the table shows the values obtained for adult individuals only.

Table 5. Ranging data from studies of >8 months

Site	**Species**	**Decade**	**Group size**	**HR**	**DJL (m)**	**Reference**
Taï NP	*badius 1b*	1990s	64.0	65.7	822.0	Korstjens (2001)
Taï NP	*badius 2a*	1990s	60.0	50.3	922.0	Korstjens (2001)
Tiwai	*badius*	1990s	33.0	52.5		Davies *et al.* (1999)
Abuko	*temminckii*	1980s	26.2	33.5		Starin (1991)
Abuko	*temminckii*	1970s	24	4.5		Gunderson (1977) group A average of wet and dry season
Abuko	*temminckii*	1970s	40	11.7		Gunderson (1977) group B average of wet and dry season
Abuko	*temminckii*	1970s	38	6.1		Gunderson (1977) group C average of wet and dry season
Fathala	*temminckii*	1970s	31.4	13.2		Gatinot (1975)
Tana River Mchelelo 70s	*ruformitratus M*	1970s	21.5	10.3	603.0	Marsh (1981a)
Tana River Mchelelo 70s	*ruformitratus O*	1970s	15.2	9.5	603.0	Marsh (1981a)
Tana River Mchelelo 80s	*ruformitratus*	1980s	9.7	11.5	531.5	Decker (1994)
Tana River Baomo South 80s	*ruformitratus*	1980s	23.5	13.0	460.5	Decker (1994)
Kibale Kanyawara K30 70s	*tephrosceles*	1970s	24.0	98.0		Struhsaker (2010) p222
Kibale Kanyawara K14,K30	*tephrosceles*	1980s	67.2		568.6	Isbell (2012) - average of two forest areas used
Kibale Ngogo	*tephrosceles*		31.8	92.8		Struhsaker (2010) p222
Gombe	*tephrosceles*	1970s	82.0	114.0		Clutton-Brock (1975)
Gombe	*tephrosceles*	1990s	23.0	75.0		Stanford (1998)
Zanzibar, Jozani Forest	*kirkii*	1990s	36.4	19.0	565.3	Siex & Struhsaker (1999b); Siex 2003
Zanzibar, Jozani shambas	*kirkii*	1990s	28.5	8.1	310.3	Siex & Struhsaker (1999b); Siex 2003 p 156 (DJL)
Zanzibar Kiwengwa Coral rag forest	*kirkii*	2000s	12.6	19.6	591.0	Nowak & Lee (2011); Nowak (2007)
Zanzibar Uzi Mangrove	*kirkii*	2000s	22.0	5.5	475.2	Nowak & Lee (2011); Nowak (2007)
Magombera, Mwanihana (Udz)	*gordonorum*	2000s	38.3	10.6	1038.4	Steel (2014)
Gbanraum, Niger Delta	*epieni*	1990s	59.5	72.8	1040.0	Werre (2000) p168

Notes: HR = Home range size (ha), DJL = mean Day Journey Length. Please note that methods for estimating home range size differs widely among studies and the original sources should be consulted in any comparative studies.

Table 6: Social organisation: group size and composition, please note that group size estimation for the large red colobus groups in dense forest is notoriously difficult and estimation of subadult sex in species without elaborate clitori is very difficult; In the table, individuals of unknown sex or unknown age-sex are not listed, please see the original publications for further information and possible constraints on the reliability of individual estimates; N=number of groups counted; Mn, Min & Max are mean, minimum and maximum group size respectively; AF & AM are number of adult females and males respectively; F range and M range gives the minimum and maximum number of adult females and males in the group; SA=subadults; Juv=juveniles; I=infants; AF/M is sex ratio; I/AF and I&J/AF give the ratio of infants or young immatures respectively per adult female.

Ref	**Species: *P.***	**Site**	**Study period**	**N**	**Mn**	**Min**	**Max**	**AF**	**F range**	**AM**	**M range**	**SA**	**Juv**	**Inf**	**AF/M**	**I/AF**	**I&J/AF**
1	***temminckii***	Senegal, Fathala	1973-1975	12	32.1	9	62	13.3	5 -27	6.7	3-13	2.3	4.5	5.4	1.99	0.41	0.74
2	***temminckii***	Senegal, Fathala	1990-1994	14	25.0	9	38										
2	***temminckii***	Senegal, Fathala	1996-2002	14	16.0												
3	***temminckii***	Abuko, study groups	1970s	3	34.0	24	40										
4	***temminckii***	Abuko all groups	1980s	5	23.0	14	32										
4	***temminckii***	Abuko study groups	1980s	2	25.9	25	27	10.8	25-27	2.1	2- 3	3.8	5.0	3.8	5.12	0.35	0.82
5	***temminckii***	Canthanaz NP, Guinea Bissou. Study group	2008-2009	1	27.0			10.0		3.0			6.0	8.0	3.33	0.80	1.40
6	***temminckii***	Abuko groups	2013	3	34.8												
7	***temminckii***	Pirang, Gambia	1980s	3	18.0	17	20										
3	***temminckii***	Kilimi, Sierra Leone	1981-1982	5	7.5		20										
8	***temminckii***	Sambel Kunda Area	2019	21	31.04[4]	3	60										
8	***temminckii***	Kuntaur-Sapo	2019	13	11.0[4]	6	40										
8	***temminckii***	Georgetown-Bansang	2019	18	13.5[4]	2	47										
8	***temminckii***	Bansang-Karantaba	2019	37	10.0[4]	3	49										
9	***badius***	Taï Ivory Coast	1996-1999	4	52.3	41	64	18.3	14-22	10.5	6-14	5.0	9.5	9.0	1.74	0.49	1.01
10	***badius***	Tiwai, Study group	1990s	1	33.0			13.0		7.0					1.86		
11	***badius***	Taï Ivory Coast	1970s	17	36.8	8	70	13.0		3.0			8.0	4.0	4.33	0.31	0.92
12	***badius***	Taï, study groups	1990s	2	73.0	70	75	28.0		17.0					1.65		
3	***badius***	Gola F.R. Sierra Leone	*ca.* 1980s			20	>60										
3	***badius***	Sierra Leone	1950s				>100										
13	***tephrosceles***	Kanyawara, group CW	1970-1988	1	23.9			9.2		2.7		0.5	8.9	2.6	3.37	0.28	1.24

Ref	**Species: *P.***	**Site**	**Study period**	**N**	**Mn**	**Min**	**Max**	**AF**	**F range**	**AM**	**M range**	**SA**	**Juv**	**Inf**	**AF/ M**	**I/A F**	**I&J /AF**
13	***tephrosceles***	Kanyawara study group	1977	1	18.0			8.0		3.0		1.0	6.0	0.0	2.67	0.00	0.75
13	***tephrosceles***	Kanyawara, Karambi Road	1995	1	55.0			17.0		2.0		8.0	11.0	8.0	8.50	0.47	1.12
13	***tephrosceles***	Kanyawara, Karambi Road	2000	1	27.0			8.0		6.0		1.5	5.5	6.0	1.33	0.75	1.44
14	***tephrosceles***	Kanyawara K30 study group	2006	1	59.0												
14	***tephrosceles***	Kanyawara K30 study group	2011	1	104.0												
14	***tephrosceles***	Kibale NP: Sebatoli, Dura, Mainaro, Kanyawara	1996-1998	55	28.4												
14	***tephrosceles***		2010-2011	27	46.6												
14	***tephrosceles***	Kibale Kanyawara K30, K15, K14 census	1996-1998	33	35.3												
14	***tephrosceles***		2010-2011	16	47.5												
15	***tephrosceles***	Kanyawara, old growth forest	2005-2006	?	52.1												
14	***tephrosceles***	Kibale Kanyawara K30	1996-1998	14	37.2												
14	***tephrosceles***		2010-2011	11	52.1												
16	***tephrosceles***	Sebatoli Kibale NP	1996-1997	5	14.2												
16	***tephrosceles***	K30 Kanyawara Kibale	1996-1997	15	40.0												
16	***tephrosceles***	Dura river Kibale NP	1996-1997	14	34.0												
16	***tephrosceles***	Mainaro Kibale NP	1996-1997	5	30.5												
13a	***tephrosceles***	Ngogo RUL grp	1978-1983	1	31.8	21	54	11.3		6.3		1.3	7.3	4.7	1.81	0.42	1.06
13b	***tephrosceles***	Ngogo BRE group	1978	1	71-75			17.0		10.0		3.0	24.0	10.0	1.70	0.59	2.00
13c	***tephrosceles***	Ngogo	2003	1	42-45			16.0		10.0		4.0	8.0	3.0	1.60	0.19	0.69
13d	***tephrosceles***	Ngogo HTL group	1976-1980	1	9.1			2.1		3.4		1.7	1.2	0.7	0.62	0.31	0.89
17	***tephrosceles***	Ngogo 4 study groups, 3 years	2001-2003	4	39.5			11.2		6.8		2.9	3.8	3.7	1.65	0.33	0.66
18	***tephrosceles***	Dura river bridge area	1970	1	28.0			12.0		4.0			3.0	7.0	3.00	0.58	0.83
19	***tephrosceles***	Gombe, Kahama study group	1969/1970	1	82.0			24.0		11.0		23.0	13.0	8.0	2.18	0.33	0.88
19	***tephrosceles***	Upper Mkenke troop	1969/1970	1	38												
19	***tephrosceles***	Nyasanga troop	1969/1970	1	55												
19	***tephrosceles***	Sleeping Valley troop	1969/1970	1	~30												

Ref	**Species: *P.***	**Site**	**Study period**	**N**	**Mn**	**Min**	**Max**	**AF**	**F range**	**AM**	**M range**	**SA**	**Juv**	**Inf**	**AF/ M**	**I/A F**	**I&J /AF**
19	***tephrosceles***	Upper Kahama troop	1969/1970	1	>70												
19	***tephrosceles***	Bigodi (Kibale)	1969/1970	1	64			28	28-32	10		10		12	3.20	0.38	0.38
19	***tephrosceles***	Kanyawara (Kibale)	1969/1970	1	58			17	17-21	11	11-13			3	1.62	0.14	0.14
20	***tephrosceles***	Gombe, Kasakela, Kakombe, Mikenka	1991	5	23.0			11.2	5-16	6.0	4-8	0.6	1.6	1.8	1.87	0.16	0.30
13e	***tephrosceles***	Kabuga Valley Gombe	1995	1	61.0			19.0		16.0		13.0	5.0	8.0	1.19	0.42	0.68
13f	***tephrosceles***	Businde Valley Gombe	1994	1	48.0			22.0		8.0		6.0	4.0	8.0	2.75	0.36	0.55
21	***rufomitratus***	Tana River, single counts	1973-1975	13	18.1	12	30	9.7	5-18	1.5	1-2	0.5	3.9	2.3	6.64	0.24	0.64
22	***rufomitratus***	Tana River Single counts	1986-1988	17	11.6	4	37	5.9	2-18	1.1	1-2	0.1	1.6	3.0	5.27	0.50	0.76
23	***rufomitratus***	1. East of Tana River	1999-2001	24	9.6	4	19	4.5	1-8	1.3	1-2	0.8	1.1	1.7	3.49	0.38	0.62
23	***rufomitratus***	2. West of Tana River	1999-2001	31	11.2	4	31	5.2	1-15	1.9	1-7	1.2	1.2	1.3	2.72	0.25	0.49
23	***rufomitratus***	1. Inside Tana River PNR	1999-2001	29	9.6	5	20	4.3	1-8	1.6	1-3	1.0	1.1	1.3	2.70	0.31	0.57
23	***rufomitratus***	2. Outside Tana River PNR	1999-2001	26	11.5	5	31	5.5	1-15	1.7	1-7	1.2	1.2	1.7	3.27	0.30	0.51
24	***kirkii***	Jozani Shamba groups	1992-1993	7	29.0	8	47	10.9	2-19	1.7	1-3	1.7	6.9	6.2	6.59	0.57	1.20
24	***kirkii***	Jozani Shamba groups	1999	4	37.5	20	65	14.9	8-24	4.7	2-10	0.7	10.6	6.4	3.17	0.43	1.14
24	***kirkii***	Jozani Forest groups	1992-1993	4	30.0	24	43	10.1	6-16	2.5	2-3	1.3	7.6	3.0	4.08	0.30	1.05
24	***kirkii***	Jozani Forest groups	1999	3	31.1	23	36	12.0	10-13	3.9	2-6	2.9	7.7	2.9	3.10	0.24	0.88
25	***gordonorum***	Magombera Forest	1970s	2	28.0	23	33	10.0	9-11	4.0	3-5	0.5	7.0	5.0	2.50	0.50	1.20
13g	***gordonorum***	Kalunga Forest, 7 visits	1998-2004	>5	15.4	8	28	6.8	3-13	2.7	1-8	1.1	2.5	2.0	2.51	0.29	0.66
13h	***gordonorum***	Magombera Forest	1992	4	33.3	26	42	16.0	11-26	2.0	1-3	2.3	5.3	7.3	8.00	0.45	0.78
13i	***gordonorum***	Magombera Forest	2004, 05, 06	10	31.2	24	47	15.2	8-24	2.6	1-5	1.8	4.8	5.6	5.85	0.37	0.68
26	***gordonorum***	Mwanihana, Udzungwa	1998-2000	12	36.1	7	62	15.8	4-29	4.0	1-6	1.8	5.8	6.8	3.90	0.43	0.80
27	***gordonorum***	Luhombero forest, 1350-2100m asl	1991-2000	46	18.0	1	50										
27	***gordonorum***	Ukami	1991-2000	?	17.0	9	25										
27	***gordonorum***	Udzungwa Scarp, 300-2050m	1991-2000	?		12	15										
27	***gordonorum***	Matundu	1991-2000	8	12.0	5	20										

Ref	**Species: *P.***	**Site**	**Study period**	**N**	**Mn**	**Min**	**Max**	**AF**	**F range**	**AM**	**M range**	**SA**	**Juv**	**Inf**	**AF/M**	**I/AF**	**I&J/AF**
27	***gordonorum***	Mwanihana Forest <1000m asl	1970/1980s	?	23.3	1	75										
27	***gordonorum***	Mwanihana Forest >1000m asl	1970/1980s	?	25.0												
27	***gordonorum***	Magombera Forest	1970/1980s	?	34.0	26	50										
27	***gordonorum***	Nyumbanitus 1400-1900m	1991-2000	13	18.0	10	35										
27	***gordonorum***	Matundu forest – swamp	1991-2000	8	12.0	5	20										
28	***kirkii***	Chwaka, Unguja Island	2013-2015	3	10.7			4.7		2.0			2.0	2.0	2.33	0.43	0.86
28	***kirkii***	Dunga FR plantation, Unguja I.	2013-2015	1	5.0			2.0		2.0			1.0	0.0	1.00	0.00	0.50
28	***kirkii***	Jambiani, Unguja I.	2013-2015	11	12.0			6.1		2.1			1.6	2.2	2.91	0.36	0.63
28	***kirkii***	Jozani-Chwaka Bay NP, Unguja I.	2013-2015	141	20.6			11.2		3.1			2.9	3.4	3.60	0.31	0.57
28	***kirkii***	Cheju, Unguja I.	2013-2015	7	12.7			5.6		2.6			1.1	3.4	2.17	0.62	0.82
28	***kirkii***	Kiwengwa FR, Unguja I.	2013-2015	37	17.0			8.9		3.1			1.9	3.0	2.87	0.34	0.55
28	***kirkii***	Kizimkazi, Unguja I.	2013-2015	15	8.6			4.9		1.6			0.9	1.2	3.08	0.24	0.42
28	***kirkii***	Maji Mekundu, Unguja I.	2013-2015	1	13.0			7.0		1.0			3.0	2.0	7.00	0.29	0.71
28	***kirkii***	Marumbi, Unguja I.	2013-2015	4	7.5			2.8		2.0			1.3	1.5	1.38	0.55	1.00
28	***kirkii***	Bungi Usalaama, Unguja I.	2013-2015	2	32.5			20.5		3.0			4.5	4.5	6.83	0.22	0.44
28	***kirkii***	Mchangamle, Unguja I.	2013-2015	23	15.9			9.6		2.4			2.1	1.8	3.93	0.19	0.41
28	***kirkii***	Kitogani, Unguja I.	2013-2015	17	11.8			6.2		2.1			1.5	1.9	2.92	0.31	0.56
28	***kirkii***	Uzi/Vundwe, Unguja I.	2013-2015	16	14.6			7.8		2.4			2.0	2.4	3.21	0.30	0.56
28	***kirkii***	Ukondoroni, Unguja I.	2013-2015	24	14.3			8.0		2.2			2.2	2.0	3.62	0.24	0.52
28	***kirkii***	Umbuji, Unguja I.	2013-2015	2	18.5			8.5		4.0			3.0	3.0	2.13	0.35	0.71
28	***kirkii***	Uroa, Unguja I.	2013-2015	4	8.3			3.0		3.3			1.0	1.0	0.92	0.33	0.67
28	***kirkii***	Masinginig FR, Unguja I.	2013-2015	10	30.9			19.2		3.6			2.5	5.6	5.33	0.29	0.42
28	***kirkii***	Michamvi, Unguja I.	2013-2015	1	3.0			1.0		1.0			1.0	0.0	1.00	0.00	1.00
28	***kirkii***	Jambiani-Muyuni, Unguja I.	2013-2015	9	11.4			5.8		1.8			1.4	2.4	3.25	0.42	0.67
28	***kirkii***	Shambas south of Jozani-Chwaka Bay NP, Unguja I.	2013-2015	10	13.9			7.9		2.2			1.5	2.3	3.59	0.29	0.48

Ref	**Species: *P.***	**Site**	**Study period**	**N**	**Mn**	**Min**	**Max**	**AF**	**F range**	**AM**	**M range**	**SA**	**Juv**	**Inf**	**AF/ M**	**I/A F**	**I&J /AF**
28	***kirkii***	Unguja Ukuu, Unguja I.	2013-2015	4	14.3			5.8		2.0			5.0	1.5	2.88	0.26	1.13
29	***kirkii***	Kwiwenga Good habitat	2004-2005	3	15.3			6.2		2.8		0.7	2.6	1.9	2.20	0.30	0.73
29	***kirkii***	Kwiwenga, edge habitat	2004-2005	3	8.3			3.6		1.5		0.3	1.8	1.0	2.46	0.28	0.77
29	***kirkii***	Uzi good	2004-2005	3	23.1	1		8.5		2.7		1.7	5.3	2.9	3.14	0.34	0.96
29	***kirkii***	Uzi edge habitat	2004-2005	3	21.8	3		8.5		2.3		1.2	4.1	2.0	3.65	0.23	0.71
30	***foai***	Ituri Forest blocks	1986	32	19.2	13	43										
31	***foai***	Kahuzi-Biega NP, lowland sector, DRC	1994-1995	8	46.3												
32a	***preussi***	Korup NP, Cameroon	1970s	7	>47	>24	>80										
32b	***preussi***	Korup NP, Cameroon	2001-2003	23	35.0	10	130										
33	***preussi***	Korup NP, study group	1991-1993	1	40.0												
34	***pennantii***	Bioko Island, Rio Epola	1992	14	~14	5	30				1-3						
34a	***tholloni***	Salonga, Zaire	1990s	1	>60												

Information on a few additional study groups is provided in Table 2. References: **1.** Gatinot (1975); **2**. Galat-Luong & Galat (2005); **3**. Butynski *et al.* (2013a); **4**. Starin (1991); **5**. Minhós *et al.* (2015); **6**. Hillyer unpubl. several counts per group; **7**. Galat-Luong (1988); **8**. Mayhew et al. (2020); **9**. Korstjens (2001); **10**. Oates (1994); **11**. Galat & Galat-Luong (1985); **12**. Höner *et al.* (1997); **13**. Struhsaker (2010) Appendix 3.1 & Chapter 3 (some are single counts and some are averages over multiple study years); **14**. Gogarten *et al.* (2015); **15**. Chapman *et al.* (2015); **16**. Chapman *et al.* (2002a); **13a**. Struhsaker, average of 16 counts page 54 & 290 in 13; **13b**. Struhsaker single count; **13c**. Struhsaker single count between trails E-G; p. 290; **13d**. 23 counts by Lysa Leland; 17. Teelen (2008), see also 13 p. 47 for sex ratio and the assumptions made to calculate those; 18. Struhsaker (1975) in 13; **19**. Clutton-Brock (1972) p15 (the range for AF and AM value consists of "AF - (AF+AF?)" and "AM-(AM+AM; **20**. Stanford (1998a); **13e**. S. M. Kamenya cited in 13; **13f**. Watts 1994 cited in 13; **21**. Marsh (1979a), Struhsaker (2000); **22**. Decker (1994b); **23**. Mbora (2003) 55 groups counted and divided in two different ways; **24**. Siex (2003); **25**. Struhsaker & Leland (1977) see also 13; **13g**. Struhsaker, Marshall, and Rovero unpublished, 7 visits over 6 years in 13; **13h**. Decker in 1992 cited in Struhsaker *et al.* (2004) in 13; **13i**. Mtalawanda and Ngulumiro trails by T.T. Struhsaker, A. M. Marshall and F. Rovero (unpubl.) in 13; **26**. Struhsaker *et al.* (2004) also in 13; **27.** Dinesen *et al.* (2001) for 1990-2000 survey, citing other sources for older surveys; **28**. Davenport *et al.* (2019); **29**. Nowak & Lee (2011); **30**. Thomas (1991); **31**. Hall *et al.* (2003); **32**. Butynski & Kingdon (2013) citing **32a**. Struhsaker 1975, 2000a; **32b**. citing Dunn & Okon 2003 unpubl. report; **33**. Usongo & Amubode (2001); **34**. Struhsaker (2000); **34a**. Maisels *et al.* (1994) cited in 34. [4]Median group size provided in the reference.