Patterns & Processes in Chimpanzee Hunting Behaviour

The Chimps and the Carnivores: are they really so different?

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Abstract:

Chimpanzees and large, social, mammalian carnivores hunt similarly, yet few studies use comparative methodologies to help understand these animals hunting behaviour. This thesis investigates the extent of current knowledge of chimpanzee hunting in the context of what, how and why chimpanzees hunt. Furthermore it investigates whether the high hunting success of chimpanzees is related to their choice of relatively small prey. This is done by comparing chimpanzee hunting to that of other social carnivores that hunt relatively large prey, wolves, *Canis lupus,* African hunting dogs, *Lycaon pictus,* spotted hyena, *Crocuta crocuta,* and the lion, *Panthera leo*.. Chimpanzees are highly successful hunters compared to large social carnivores. Chimpanzees preferentially hunt relatively small prey compared to the carnivores studied. The mediation analysis shows that the high hunting success of chimpanzees is partially mediated by them hunting prey of a smaller relative size.

A comprehensive review of chimpanzees, *Pan troglodytes*, as predators as well as a mediation analysis on the relationship between prey size and hunting success across the five social predators is presented. It is shown that chimpanzees prefer hunting arboreal primates, particularly the red colobus monkey, *Piliocolobus* sp.. Seasonality in hunting prevalence occurs at some study sites but is not ubiquitous. Adult and adolescent males conduct the majority of hunts and often hunt in groups. Chimpanzees at the Taï Forest, Cote d'Ivoire, hunt more cooperatively (fulfilling different roles) than documented elsewhere. This has been likened to hunting by large social carnivores, specifically African lions and African hunting dogs*.* The traditional explanations of the reasoning behind chimpanzee hunting that have currently been proposed are not well supported. A more recently proposed explanation, the meat-scrap hypothesis provides an important avenue for future research and the explanation for chimpanzee hunting is likely to be related to nutritional, rather than social factors.

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Chapter 1 – Background

Rationale:

Mammalian predators that hunt in groups vary in their ability to succeed in capturing mammalian prey. These same predators also vary to some extent in the size of prey that they hunt. Chimpanzees of all well-studied populations are known to hunt and consume mammalian prey although the nature of the nutritional and social benefits of this behaviour is not well understood. They have a high hunting success rate when compared to large social carnivores but hunt smaller prey. This study investigates the extent of knowledge regarding the patterns and process of chimpanzee hunting as well as the contrast in hunting success between chimpanzees and other large mammalian social predators. It is known that size is a determinant of prey selection for social carnivores; therefore, this study aims to determine whether the variation in the size of prey selected by group hunting predators can explain the variation in hunting success among these species. Specifically, it will test the hypothesis that the high hunting success rates achieved by chimpanzees is related to the fact that they hunt relatively small prey.

Introduction

Meat, the flesh of vertebrate prey animals, is an important resource for many mammals. For carnivores and omnivores alike, mammalian prey are energy rich food items that are ephemeral and unpredictable in their occurrence (Smith et al. 2012). Raw meat, organs and bones contain high concentrations of iron, calcium, iodine and zinc, vitamin A, many B vitamins, vitamin C and other essential micronutrients, as well as easily metabolisable protein and fat (Milton, 1999).

The hunting success rate (defined as the likelihood of capturing prey once an attempt has been made) of a predator is influenced by three types of factors (Funston et al. 2001). First are predator related factors, including sex, individual body size, age, and group size (Funston et al., 2001; Holekamp et al., 1997; MacNulty et al., 2011; MacNulty et al., 2009). Second are prey related factors, including prey species, prey size, defensive ability, escape behaviour, body condition, group structure, habitat etc.; these factors also influence the selection of prey by predators (Funston et al., 2001; Griffiths, 1980; Radloff & Du Toit, 2004). Third, environmental factors include external influences such as vegetation cover, snow depth and visibility (Funston et al., 2001; Sand, et al., 2006).

It has been hypothesised that there is a negative (interspecific) relationship between the body size of prey and the hunting success achieved by a predator. This is suggested as being caused by the increased difficulty of subduing large prey and the increased risk of injury whilst doing so (Griffiths, 1980; Wilson, 1975). Hunting success is thought to decline with increasing prey size but this has not previously been tested at an interspecific level. Predators that hunt prey animals many times smaller than themselves (e.g. planktivorous fish hunting zooplankton) often achieve success rates close to 100% (Griffiths, 1980). In contrast predators that hunt large prey (e.g. lions hunting buffalo) are less successful (Griffiths, 1980; Schaller, 1972). It is critical to note that a prey is only small or large relative to the predator's size. From hereon size will be referred to in relative terms unless stated otherwise.

As our closest extant genetic relative, the chimpanzee is a useful tool for understanding the evolution of our early ancestors and has been considered so since systematic research into the species and its behaviour began at Gombe, Tanzania (then Tanganyika) in the 1960s (Goodall, 1986). It has often been argued that knowledge of wild chimpanzee behaviour may provide insights into the behaviour of early humans as behaviours that are exhibited by both chimpanzees and modern humans were probably present in our common ancestor and thus all members of our lineage until the present (Goodall, 1986). Chimpanzees are now regularly featured in models for hominin evolution and are often used by anthropologists to understand behaviour we exhibit today as well as how this may have come from our early history.

Chimpanzees are highly successful hunters. Comparisons are regularly made between the hunting behaviour of chimpanzees and that of large carnivore species that hunt in groups. This is another group of animals that have been suggested as analogous to our early hominin ancestors, creatures that likely lived and hunted in groups (Smith et al., 2012). Studies investigating comparisons between chimpanzees and large social carnivorans hunting behaviour in detail are rare but have proven to be useful in furthering our understanding of chimpanzee behaviour (Gilby & Connor, 2010).

Chimpanzees achieve higher hunting success rates than group hunting carnivores but also hunt prey that are much smaller in relation to their own size. This study aims to first assess the current knowledge of chimpanzee hunting behaviour in relation to what, how and why chimpanzees hunt. Second it aims to determine whether relative prey size is related to the hunting success of large predators that live, breed and hunt in groups. Finally it intends to determine whether this relationship explains how chimpanzees are able to be more successful than large, social, carnivore species.

The Hunters

Some predators hunt in groups and this improves their ability to subdue large prey. Group hunting carnivorans (members of the order Carnivora) most often prey upon animals larger than themselves whereas solitary species often hunt prey smaller than themselves (Griffiths, 1980; Schaller, 1972). Group hunting also helps to reduce pursuit and subduing costs for the predators (Creel & Creel, 1995; Griffiths, 1980; Packer & Caro, 1997). Group hunting can often be cooperative, whereby hunters gain a greater net benefit by hunting with others than by hunting solitarily (Boesch, 1994b; Gilby & Connor, 2010; Packer & Ruttan, 1988). Some of the species that hunt in groups are large, gregarious predators that also live and breed in social groups (Boesch & Boesch-Achermann, 2000; Frame et al.1979; Mech, 1974; Mills, 1990; Schaller, 1972). Chimpanzees are unusual in that they hunt in groups but preferentially target relatively small prey (Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000; Stanford, 1998).

Large mammalian predators often hunt large prey due to their high energetic requirements, with prey size and predator size increasing in concordance (Gittleman, 1985; Radloff & Du Toit, 2004). Carbone et al. (1999) found that animals of the order Carnivora can be classified as either *hunting invertebrates and small animals*, or *hunting large mammals.* This dietary dichotomy relates strongly to predator body weight, with a transition from a diet consisting of small prey (less than half predators mass) to one of large prey (near the mass of the predator) diet at 21.5-25kg predator mass. Chimpanzees are larger than this weighing an average of 32kg and as such it is interesting that they hunt small prey (Butyinski et al, 2013). Of the twelve carnivores above the 21.5kg threshold, four regularly live, breed and hunt in groups: lions *Panthera leo,* spotted hyena *Crocuta crocuta,* African hunting dogs *Lycaon pictus*, and wolves *Canis lupus.* They are termed social carnivores and exhibit an uncommon combination of social behavioural traits for carnivorans (Caraco & Wolf, 1975; Estes & Goddard, 1967; Holekamp et al., 1997; Mech, 1974; Schaller, 1972).

Social predators vary in their hunting success; between 29 – 34% (31% median) for hyena, 47% for hunting dogs, 26% for lion, and between 8% when hunting large prey such as moose or 46% for wolves when hunting smaller prey such as white tailed deer (Creel & Creel, 1995; Holekamp et al., 1997; Kolenosky, 1972; Mech, 1974; Schaller, 1972). Notably, chimpanzees, a large-bodied, social primate also hunt with an exceptionally high success rate when compared to social carnivores, 45% to 70% (Median 54.7% *n*=5) (Mitani & Watts, 1999, 2001; Newton-Fisher, 2014; Stanford et al., 1994; Uehara, 1997).

Chimpanzees are diurnal frugivorous primates weighing on average 32kg (range 26 – 40)(Butyinski et al, 2013). They live, breed and feed in social groups that maintain territories across tropical forest, mosaic woodland, and savannah regions of equatorial Africa (Butyinski et al., 2013; Emery Thompson & Wrangham, 2013; Kingdon, 2012). Similarly to spotted hyenas they live in a fission-fusion social system where sub-groups of the community will separate for feeding or other activities (Aureli et al., 2008; Smith et al., 2008). Evidence of hunting has been found at every site where chimpanzees have been extensively studied (Newton-Fisher, 2014). Prey items comprise a small proportion (4%) of chimpanzee diet although this varies widely between populations (range: 0-28%) (Conklin-Brittain et al., 2001).

Chimpanzees regularly hunt in groups. At some sites they have been observed to hunt collaboratively (“*Hunters perform different complementary actions, all directed toward the same prey*” (Boesch & Boesch 1989 pp. 550)) in a similar manner to some social carnivores, such as lions and hunting dogs in their ability to work collaboratively to capture prey (Boesch, 1994b, 2002). This behaviour is not uniform across populations; chimpanzees at the Taï Forest, Cote d'Ivoire hunt collaboratively and receive a greater net benefit when hunting in groups of 3-4 compared to smaller groups, whereas this has not been observed consistently at other sites (Boesch, 1994b; Gilby et al., 2006; Mitani & Watts, 2001). Distinct hunting roles have been identified in the hunting behaviour of the chimpanzees at Taï: drivers, chaser, blockers and ambushers (Boesch, 2002). This is similar to the findings of Stander (1992) who identified distinct role specialisation in lions hunting on the semi-arid plains of Namibia. Likewise hunting dogs are known to adopt roles of chasers and ambushers when hunting cooperatively (Creel & Creel, 1995).

Unlike the social carnivores that most commonly target ungulates, chimpanzees preferentially hunt arboreal primate prey, particularly colobines (Hayward & O'Brien, 2006; Hayward & Kerley, 2005; Hayward, 2006; Jedrzejewski et al., 2012; Mech, 1974; Newton-Fisher, 2014; Nishida & Uehara, 1983; Stanford, 1998). *Piliocolobus* sp., (red colobus) are the preferred prey (*P. tephrosceles, P. penantii*: East Africa| *P. badius*: West Africa) (Boesch & Boesch-Achermann, 2000; Mitani & Watts, 1999b; Stanford et al., 1994; Stanford, 1998). At sites where no red colobus are present other *Cercopithecidae* are most often targeted. At Budongo, Uganda, the black and white colobus, *Colobus guereza,* is the primary prey species (Newton-Fisher et al. 2002) and at Kahuzi, Democratic Republic of Congo *Cercopithecus sp.* contribute to the majority of the mammalian prey (Basabose & Yamagiwa, 1997).

The prey species that chimpanzees preferentially target are generally small in relation to the predator size. Red colobus can weigh between 5.8 – 10kg (adult females) and 8.4 – 11kg (adult males) depending on the subspecies and at 11 – 23kg, even black and white colobus are much smaller (18 – 71% of predator mass) than the 32kg (average) chimpanzee (Butyinski, et al. 2013). These prey animals are considerably smaller than the prey that social carnivores regularly hunt. African hunting dogs are known to hunt prey weighing an average of 120% their own body mass (29.8 of 25.2kg) and female lions hunt prey 100% of their own mass (Hayward et al., 2006; Hayward & Kerley, 2005). The mean mass of prey species preferred by spotted hyena, when accounting for variations in age class, is 154.7kg, 250% of the predators' 61.1kg mass (Hayward, 2006; Kingdon, 2012). Wolves, weighing an average of 50kg, are known to regularly hunt large prey such as elk, *Cervus elaphus,* and moose, *Alces alces,* weighing between 240 – 800kg (Arjo et al. 2002; Macdonald, 2006; Peterson & Ciucci, 2003).

Chimpanzees are highly successful predators. Success varies between chimpanzee study sites; at Ngogo, chimpanzees hunt with an average success rate of 73%; hunting success is between 40% in the wet season and 60% in the dry season at Gombe, is 54.7% at Taï and 45% at Mahale (Boesch & Boesch, 1989; Mitani & Watts, 1999b; Stanford et al., 1994; Uehara, 1997). This success rate has described as *"considerably higher than those reported for some well-studied African carnivores"* (Mitani & Watts, 1999 pp. 448), an unsurprising statement considering social carnivore average success rates range from 8 – 47%.

Until now there has been no investigation into why chimpanzees have a higher hunting success than large social carnivores. The explanation is likely to be associated with one of the three influencing areas of hunting success: predator, prey or environment-related factors. Differences in factors such as group size, predator condition, and intelligence between chimpanzees and social carnivores may all affect the difference in success. It is possible that differences between the predators in environmental factors such as vegetation cover, seasonality in hunting, or time of day when hunting could provide an answer. Alternatively differences in prey related factors such as: prey size, prey defence and prey accessibility could also provide an explanation.

While these factors almost certainly affect hunting success, Wilson (1975) proposed a simple, negative relationship between hunting success and prey size. Griffiths, (1980) suggested this was caused by an increased difficulty in subduing large prey and higher associated costs. As this determining factor of relative prey size clearly differs between chimpanzees and large social carnivorans and has not been previously tested as an explanation for this phenomenon it is the focus of this research. This study therefore intended to investigate whether variation in an ecological factor, relative prey size, could explain the variation observed in the hunting success of large social mammalian predators. In particular it sought to determine whether the high hunting success of chimpanzees, when compared to large social carnivores, could be explained by the fact that they select relatively small prey.

Objectives:

1.) To determine whether the size of mammalian prey selected by predators influences that predator's ability to succeed in a hunting attempt.
    a. Extract data from the literature on prey species hunted by chimpanzees, *Pan troglodytes*, grey wolves *Canis lupus*, African hunting dogs *Lycaon pictus*, spotted hyena *Crocuta crocuta*, and lion *Panthera leo* (All above mentioned species termed predator species from here on).
    b. Extract prey species-specific data on hunting success for the predator species from the literature and record as a percentage (Successful hunts per species/ total hunts per species).
    c. Extract data from the literature on body mass of the predator species and the prey species identified in objective 1.2.
    d. Convert body mass of prey into a proportion of the predator's mass. Prey/Predator.
    e. Run a linear regression model with hunting success as the dependent variable and proportional body mass (ratio) as the independent variable.

2.) To ascertain whether group-hunting mammalian predators differ in the size of prey that they select and their ability to succeed in hunting attempts of these prey.
    a. Using the data collected in objective 1a and 1b conduct an ANOVA for the predator species (independent) and proportional body mass (dependent) and for predator species (dependent).
    b. Using the above findings to determine which predator species vary in both hunting success and proportional body mass.

3.) To investigate whether chimpanzees' selection of small prey explains their ability to succeed in hunting attempts more often than social carnivores.
    a. Use the data from objective 1a and 2a to conduct a mediation model analysis determining if the difference in proportional body mass of prey explains the difference in hunting success between predator species.
    b. Use the results of the mediation model to determine the extent to which the higher hunting success of chimpanzees is explained by the fact that they select relatively small prey.

Review papers are essential to fully understand the diversity and complexity of chimpanzee hunting behaviour. Furthermore when comparisons are to be drawn between chimpanzee populations or with other predators, a succinct overview greatly eases the process. Until April 2014 only a single review of chimpanzee hunting behaviour existed, published in 2007 (Newton-Fisher, 2007, 2014). Therefore in addition to the objectives stated above and to allow them to be met, this thesis will include a review of published literature that relates to chimpanzees hunting behaviour from all extensively studied sites and where possible lesser studied sites.

Chapters

This thesis is comprised of four chapters. Following this introductory chapter, comprising of the background to the project and the aims and objectives, there are three further chapters.

Chapter two (article 1) is an analysis of the current knowledge relating to chimpanzee hunting behaviour. In this chapter many areas of hunting behaviour and ecology are discussed. The chapter begins by introducing cooperation and the background to hunting by chimpanzees. It contains information on the chimpanzee prey choice and goes on to discuss when and how chimpanzees hunt. Furthermore, it addresses the debate surrounding cooperation in chimpanzee hunting behaviour and how it evolved. It finishes by reviewing the current knowledge on why chimpanzees engage in hunting and critically examines the papers proposing these explanations.

Chapter three (article 2) investigates the relationship between relative prey size and hunting success achieved by large social predators. The results show that the hunting success achieved by large social predators decreases as the relative prey size (recorded as a proportion of the predator's mass) increases. Mediation analysis demonstrated that the higher hunting success of chimpanzees can be partially explained by the fact that they hunt smaller prey than large social carnivorans; wolves, African hunting dogs, spotted hyena and lions. This result held when confounding factors, (vegetation cover and prey preference) were statistically controlled for.

Chapter four discusses the findings of this research alongside the known mechanisms controlling hunting success. It highlights the importance of comparative studies of the hunting behaviour of chimpanzees and large social carnivores. It investigates the impact that this study will have on the understanding of chimpanzee hunting behaviour and how it fits with the current literature. Finally it explores avenues for further research.

Chapter 2 (Article 1)-

Pan as predators: A review of chimpanzees as hunters.

Abstract: All chimpanzee populations that have undergone extensive study have been found to kill and eat mammalian prey yet the nutritional or social explanation for this behaviour has not been determined. Here the current knowledge of chimpanzee hunting is reviewed with a focus on what, how and why they hunt. The prey selected and hunting techniques used to capture them vary between chimpanzee populations with the greatest distinction found between East and West African populations. Hunting can range from simple opportunistic capture of bushbuck fawns to highly coordinated group hunting of colobus monkeys and even 'spear' hunting of prosimians. Hunting of arboreal primates is a male dominated activity with males taking up to twenty years or more to become proficient at the more complex cooperative behaviours that can occur in some populations. Controversy exists in the explanations of the evolutionary process leading to group hunting by chimpanzees and there is a lack of agreement of why it occurs. Only one population seems to hunt "collaboratively" with the chimpanzees of the Taï forest in the Ivory Coast exhibiting more coordination in hunting than other populations. This is most likely due to the density and height of the forest canopy in which they live causing prey capture to be more difficult for solitary hunters. As chimpanzees are primarily frugivorous it is questionable as to why they should undertake a seemingly cognitively complex, energetically costly and risky behaviour to obtain a food item contributing little to their general calorific intake. A number of explanations have been proposed as to why chimpanzees go to such lengths to obtain meat but as of yet no definitive answer has been agreed upon. It is likely that an explanation of why chimpanzees hunt will relate to nutrition rather than sociality.

Introduction

Chimpanzees (*Pan troglodytes*) have been found to hunt at all sites where they have been extensively studied through either observation or faecal analysis (Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2014; Uehara, 1997). Chimpanzees primarily hunt arboreal primates, but prey selection varies depending on site and prey species available. At some study sites chimpanzees have been observed to hunt in groups and thus have been likened to large social carnivores that also hunt in groups (Boesch & Boesch-Achermann, 2000; Boesch, 1994b, 2005; Gilby et al 2008; Newton-Fisher, 2007). A clear distinction in the level of cooperation in group hunting exists between East and West African populations with collaboration, whereby hunters perform different complementary actions directed toward the same prey, only seen regularly at Taï Forest National Park in Cote d'Ivoire, West Africa (Boesch, 2002; Newton-Fisher, 2007). At Taï, chimpanzees perform specific roles within the hunt, each with different purpose (Boesch, 2002). This behaviour is similar to that observed for lions in the Etosha National Park, where hunters performed different roles within the hunt moving pre-emptively in relation to other hunters to improve the chance of capture (Stander, 1992). Hunting group size and frequency of group hunting are known to vary between study sites with the greatest level of group hunting (95%) occurring at Taï Forest (Boesch & Boesch, 1989). As frugivores, chimpanzees primarily rely on fruit for nutrition therefore why they hunt and consume meat is an interesting question and still unanswered. This article reviews chimpanzee hunting preferences, hunting behaviour, levels of cooperation and possible motivation, with the aim of identifying the current status of knowledge with regards to what, how and why chimpanzees hunt.

Chimpanzees are known to hunt nearly 40 species of mammal across their range, (Chapter 3; Basabose, 2002; Newton-Fisher, 1999, 2007, 2014; Nishida & Uehara, 1983). The primary mammalian prey animals of chimpanzees in all populations are arboreal primates and are the only prey regularly hunted in groups. Red colobus monkeys suffer predation by chimpanzees at all study sites where they are sympatric. Hunting pressure varies but chimpanzees are known to kill 6-12% of the red colobus (*Piliocolobus tephrosceles*) annually at Ngogo, Kibale National Park, Uganda, 3 – 7% at Taï Forest, Cote d'Ivoire and 16-32% at Gombe National Park, Tanzania (Boesch & Boesch-Achermann, 2000; Stanford, 1996; Watts & Mitani, 2002). Adult or adolescent male chimpanzees most commonly hunt, particularly when hunting arboreal primates alone or in groups (Boesch & Boesch, 1989; Stanford, 1998).

Chimpanzees at many sites exhibit seasonality in their hunting, often in relation to rainfall patterns. Chimpanzees at Gombe hunt most frequently in the dry season, whilst those at Taï and Mahale hunt most often in the wet season (Boesch & Boesch, 1989; Stanford et al., 1994; Stanford, 1996, 1998; Takahata et al., 1984; Uehara, 1997; Watts & Mitani, 2002). Both study groups of chimpanzees at Kibale hunt most frequently during periods of high fruit availability (Gilby & Wrangham, 2007). Many populations have hunting "binges" where they hunt almost every day for a week or more (Mitani & Watts, 1999b; Stanford et al., 1994).

Although a number of explanations have been given for why chimpanzees might hunt and particularly in groups, none have yet been consistently supported. Nutritional hypotheses such as the “nutrient shortfall” and “nutrient surplus” hypotheses have received only sporadic or inconsistent empirical support and have yet to provide convincing evidence to confirm them across the study sites (Gilby et al., 2006; Gilby & Wrangham, 2007; Mitani & Watts, 2001). Similarly social hypotheses; the “meat-for-sex” hypothesis and the “male social bonding” hypothesis have been refuted by recent literature (Gilby et al., 2006; Gilby et al., 2010; Stanford et al., 1994). The only explanation proposed that has yet to be dismissed and is theoretically well supported is the “meat scrap” hypothesis that posits that chimpanzees hunt to obtain micronutrients rather than simply a caloric benefit (Gilby et al., 2008; Tennie et al., 2009; Tennie et al., 2014).

Chimpanzee Hunting: The details

Chimpanzee Diet

Understanding what chimpanzees eat is critical to understand why they hunt as it gives information on the possible benefit that hunting and consuming mammalian prey may provide. Chimpanzees are considered a ripe fruit specialist, with 64% (in terms of a combination between time and calories) of their diet composed of fruit (Table. 2.1 pp. 20). Leaves comprise 19% of their diet with animal matter (both vertebrate and invertebrate) contributing to an average of 4% with substantial variance among individuals and communities and populations (Boesch & Boesch-Achermann, 2000; Conklin-Brittain et al., 2001; Newton-Fisher, 1999; Nishida & Uehara, 1983). Animal tissue contains essential amino-acids and fats and is calorically rich compared to plant material (Hamilton & Busse, 1978; Milton, 1999). For many predatory animals, mammalian prey represent ephemeral, energy rich food items that are unpredictable in their occurrence (Smith et al., 2012). Considering however, the small amount of animal matter in chimpanzee diet, the great effort undertaken to acquire meat through hunting is highly interesting.

The prey component of chimpanzee diet is highly variable (Table. 2.1), this occurs both geographically and temporally with different populations utilising different prey and techniques of capture (Boesch, 2002; Newton-Fisher, 2007; Stanford, 1998). Chimpanzees prey primarily upon insects and mammals (Basabose, 2002; Bogart & Pruetz, 2011; Conklin-Brittain et al., 2001; Nishida & Uehara, 1983; Pruetz & Bertolani, 2007). Entomophagy by chimpanzees normally occurs through the gathering of large numbers of colonial termites or ants using tools (Bogart & Pruetz, 2008, 2011; McGrew et al., 1979; Pascual-Garrido et al., 2013; Whiten et al., 1999) and hunting generally occurs through group or solo hunting of arboreal primates and opportunistic capture of other animal prey (Boesch & Boesch, 1989; Boesch, 1994a; Nishida et al., 1979; Stanford et al., 1994; Watts & Mitani, 2002).

These two methods of acquiring animal foodstuffs are contrasting in a number of ways. Tool-assisted collection of social invertebrates is gathering or collecting, rather than hunting behaviour; the insect assemblages are stationary and easily obtainable in large numbers once located (Hamilton & Busse, 1978). As chimpanzees and other great apes focus on colonial and sedentary insect species they are able to utilise invertebrates regardless of their large body mass, usually considered a limiting factor in consumption of invertebrates by primates and carnivores (Bogart & Pruetz, 2011; Carbone, et al. 1999; Kay & Simons, 1980). In comparison hunting requires the location, capture and restraint of a prey item to consume it and is therefore dissimilar from gathering of fruit, leaves or insects. To summarise, chimpanzees consume a variety of animal matter, both vertebrate and invertebrate but what is eaten and to what extent varies among sites. However the universal existence of the consumption of animals, particularly meat, suggests that there is likely to be a nutritional benefit to this behaviour.

Table 2.1. Chimpanzee Diet (time & calories combined) adapted from Conklin-Brittain et al., (2001)

	% Fruit (Range)	% Seed (Range)	% Flowers (Range)	% Leaves (Range)	%THV (Range)	% Bark & Misc (Range)	% Prey (Range)
	64	3	2	16	7	4	4
Min	19	0	0	0	0	0	0
Max	99	30	14	56	27	41	28

Data summarized from 24 studies at eleven sites as presented in Conklin-Brittain et al., 2001

(Conklin-Brittain et al., 1998; Galdikas and Teleki, 1981; Ghiglieri, 1984; van Lawick- Goodall, 1968; Hladik, 1977, 1973; Isabirye-Basuta, 1989; Kuroda, 1992; Kuroda et al., 1996; Matsumoto-Oda and Hayashi, 1999; Mc- Grew et al., 1981; Newton-Fisher, 1999; Peters and O'Brien, 1981; Rodman, 1984; Sabater-Pi, 1979; Sugiyama and Koman, 1987; Tutin and Fernandez, 1993; Tutin et al., 1984, 1997, 1991; Wrangham, 1977, 1996; Yamagiwa et al., 1992).

Prey Diversity and Selection

Understanding which species of animal chimpanzees hunt helps to assess the benefits and costs of hunting in terms of prey defence. It also helps to improve understanding of the importance of group hunting relating to this. Furthermore, it is likely that different prey will provide different caloric and nutritional benefits, primarily due to interspecific variation in size. Chimpanzees are diverse in their prey selection; at least 40 species of mammal are targeted across chimpanzee populations (Table 2.2. adapted from Newton-Fisher, 2007). Primates form the majority of prey species accounting for at least 24 species. The most widely preyed upon genus of primates, in terms of species diversity and number of sites where they are hunted is Cercopithecus, guenons with 9 species over nine sites. Another four Cercopithecinae are also preyed upon across four sites; *Cercocebus atys* at one*, Chlorocebus sebaeus* at one site*,* and *Lophocebus albigena* at two, baboons *Papio cyanocaphelus* and *Papio anubis* are also eaten at one site each. Four *Piliocolobus* sp. suffer predation across four sites and three *Colobus* sp. at five sites. Similarly two species of bush baby are hunted at two sites and pottos are hunted at two sites. Chimpanzees occasionally exhibit cannibalism and are known to have killed and eaten other chimpanzees at four sites.

Ungulates are the second most hunted prey of chimpanzees with seven species eaten at seven sites. Of these, three are *Cephalophus sp.,* Duiker are hunted at six sites across chimpanzees range. The bushpig, *Potamochoerus larvatus*, is also eaten however this is only observed at three East African sites. Bushbuck, suni antelope and desert warthog are also eaten at two, one and one sites respectively. Chimpanzees eat at least three rodent species. Three identified species are *Cricetomys eminii*, *Thryonomys swinderionanus* and *Protoxerus stangeri*, unidentified rodent species are recorded as being consumed at two other sites. Two carnivores have been recorded as chimpanzee prey, an unidentified mongoose species and the African civet, *Civetticus civetta*, both at Mahale, three other small mammal species are also hunted at four sites.

Prey diversity is not distributed evenly across chimpanzee populations, the populations with the highest known prey diversity being at Mahale Mountains National Park, Tanzania; the Ngogo Community at Kibale National Park, Uganda; at Gombe Stream National Park, Tanzania and at the Taï forest National Park in Cote d'Ivoire. The variation in these data are likely however to be caused by both ecological differences between sites and variation in study effort and length and research methods (Boesch & Boesch-Achermann, 2000). The sites stated above are long-term research sites, with research at Gombe Stream and Mahale being conducted since the 1960s.

Although prey diversity is high, chimpanzees have a strong preference for *Piliocolobus sp*. particularly red colobus at all long term study sites (Boesch & Boesch-Achermann, 2000; Stanford et al. 1994; Stanford, 1998). At Gombe between 1990 and 1994, 84.5% of all mammalian prey captured were red colobus; at Mahale this number is less, with red colobus contributing 53% of captured prey (Stanford, 1998). At Taï 78% of mammalian prey captured were red colobus (Boesch & Boesch, 1989; Stanford, 1998). The next largest component of the prey base at Taï is black-and-white colobus contributing to 14% of mammalian prey (Boesch & Boesch, 1989). At Gombe, where no black-and-white colobus are sympatric with the chimpanzees, bushpig and bushbuck are the next most frequently captured mammalian prey contributing 8.1% and 5.3% respectively (Stanford, 1998). Chimpanzees at Ngogo exhibited the highest level of prey specialisation as 91% of prey captured were red colobus (Mitani & Watts, 1999). At Budongo, where no *Piliocolobus sp*. are present the primary prey species is the black-and-white colobus *Colobus guereza* contributing to 43.8% of the captured prey, followed by *Cephalophus monticola*, 25% and *Cercopithecus sp*. 18.8% (Newton-Fisher, et al. 2002). At Kahuzi, DRC where no Colobines are sympatric *Cercopithecus* monkeys are heavily hunted, suffering 11-18% mortality of the population to chimpanzees each year (Basabose & Yamagiwa, 1997). Kahuzi has the highest rates of *Cercopithecus* predation of any chimpanzee study site.

Further variation occurs in the age and sex classes of red colobus prey targeted by hunters at Gombe, Mahale and Taï (Table. 2.3). Adults are frequently targeted at Taï with 47% of red colobus captured being fully grown (Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000; Stanford, 1998). Similarly, when Taï chimpanzees hunt black-and-white colobus, 60% of captures were adult monkeys (Boesch, 2002). Conversely at Gombe and Mahale these figures are biased towards the capture of immature red colobus (85% and 70% respectively) (Stanford, 1998). At both Gombe and Ngogo chimpanzees hunt immature red colobus more than expected according to their abundance in the forest (Mitani & Watts, 1999; Stanford, 1998). At Kahuzi, faecal analysis showed that adult and adolescent chimpanzee hunters tended to eat juvenile or sub-adult *Cercopithecus* monkeys (Basabose & Yamagiwa, 1997). Similarly, immature black-and-white colobus are targeted preferentially at Budongo (Newton-Fisher et al., 2002).

In summary there is a broad pattern of prey preference and diversity of target species across populations of chimpanzees. Colobines and particularly *Piliocolobus* sp. where sympatric are the clearly preferred prey. East African chimpanzee populations preferentially target immature monkeys in contrast to West African chimpanzees of the Taï Forest who consume a greater proportion of adult monkeys. Most populations occasionally consume Cercopithecinae, particularly of the genus *Cercoithecus*. The capture and consumption of ungulates, particularly duikers, *Cephalophus* sp., is widespread across East African populations and the occasional opportunistic capture of rodents and other small mammals occur (Newton-Fisher et al., 2002; Nishida & Uehara, 1983; Wrangham & Bergmann-Riss, 1990). The species hunted by chimpanzees are generally small in relation to them, often many times smaller than the large bodied chimpanzee. This preference for small prey highlights the small amount of meat that would be provided by each carcass. Whether this small amount of meat is sufficient to be energetically beneficial for chimpanzees, particularly those hunting in groups has been questioned (Boesch, 1994b).

Table 2.2(a) Primate prey of chimpanzees from 14 study sites adapted from Newton-Fisher (2007).

	Pan troglodytes schweinfurthii							**P.t.troglodytes**		**P.t.verus**				
	Gombe	**Mahale**	**Ngogo**	**Budongo**	**Kahuzi**	**Semliki**	**Kasekati**	**Lope**	**Ndoki**	**Assirik**	**Bossou**	**Tai**	**Tenkere**	**Fongoli**
Species														
<u>Primates</u>														
Procolobus badius tephrosceles	x	x												
Procolobus pennantii			x											
Procolobus b. badius												x		
Procolobus verus												x		
Colobus guereza			x	x		x								
Colobus polykomos												x		
Colobus satanus								x						
Cercopithecus ascanius schmidti	x	x	x	x										
Cercopithecus aethiops centralis		x												
Cercopithecus mitis	x	x	x	x	x									
Cercopithecus L'Hoestii					x									
Cercopithecus diana												x		
Cercopithecus mana											x			
Cercopithecus petourista											x			
Cercopithecus pogonias									x					
Cercopithecus ascanius schmidti	x	x	x	x			x							
Cercocebus atys												x		
Chlorocebus sabaeus														x
Lophocebus albigena			x					x						
Papio cyanocephalus		x												
Papio anubis	x													

Table 2.2(b). Prey of chimpanzees from 14 study sites adapted from Newton-Fisher (2007)

	Pan troglodytes schweinfurthii							P.t.troglodytes		P.t.verus				
	Gombe	**Mahale**	**Ngogo**	**Budongo**	**Kahuzi**	**Semliki**	**Kasekati**	**Lope**	**Ndoki**	**Assirik**	**Bossou**	**Tai**	**Tenkere**	**Fongoli**
Species														
Artiodactyla														
Cephalophus monticola		x	x	x				x						
Cephalophus callipyga			x											
Cephalophus natelensis				x								x		
Cephalophus sp.									x					
Tragelaphus scriptus	x	x												
Nesotragus moschatus		x												
Potamocherous porcus	x	x	x											
Phacocheroerus aethiopicus		x												
Rodentia														
Cricetomys eminii		x												
Thryonomys swinderionanus		x												
Protoxerus stangeri					x									
Other											x	x		
Carnivora														
Viverra civetta		x												
Mongoose *(Bdeogale sp., Mungos s., or Ichn*		x												
Others														
Heterohyrax brucei		x												
Rynochocyon sp.		x												
Manis sp.									x	x	x			

Table 2.2 a & b adapted from Newton-Fisher 2007 with added data from 10 references: Basabose, 2002; Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000; Gaspersic & Pruetz, 2004; Hockings et al., 2012; Nishida et al., 1979; Nishida & Uehara, 1983; Pruetz & Bertolani, 2007; Uehara, 1997; Yamagiwa & Basabose, 2006

**Table 2.3. Age class of chimpanzee prey from Gombe, Mahale and,
adapted from Stanford (1998).**

Age Class	Gombe % Red Colobus Prey	Mahale % Red Colobus Prey	Tai % Red Colobus
Adult	10.6	30	
Male	1.8	-	-
Female	8.8	-	-
Immatures	89.4	70	

Chimpanzees as Hunters

An interesting and important question is whether hunting is unifor group members. This helps us to understand the social environment hunting occurs and whether this influences its prevalence. Hunting ef in fact, evenly distributed among group members: there are differenc sex, individuals, ages and group composition within and between po Hunting is a male dominated behaviour, particularly when Cercopithecidae (Basabose & Yamagiwa, 1997; Newton-Fisher, 2007). dominance of this behaviour varies between sites, at Gombe 91% o made by adult and adolescent males (Stanford et al., 1994). In contra (1986) found that 23% of kills were made by females at the site. At T kills were made by females and 13% of adult hunters are female reg whether they are carrying an infant (Boesch & Boesch, 1989). Likewis captures made were by females at Mahale (Takahata et al., 1984). A chimpanzees at Ngogo contribute to 86% of kills compared to 3% by adolescent females, considerably lower than other sites (Mitani & Watt

Both hunting frequency and success have been found to increase with the number of adult males in a forging party. At Gombe, the number of adult and adolescent males in a hunting party has a significant effect on the success of red colobus hunts with larger parties having higher success and hunting frequency than smaller parties (Gilby et al., 2006). Similarly Taï chimpanzees hunt more often and more successfully when a hunting party has higher numbers of males (Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000). At Ngogo, Kibale chimpanzee hunting frequency is also significantly associated with the number of males in a foraging party (Mitani & Watts, 1999, 2001).

Hunting effort and hunting success differ among individuals within groups (Mitani & Watts, 1999). Certain 'impact hunters' (Gilby et al, 2008), contribute a disproportionate amount to the hunting effort, hunting success, and hunt initiation; individual chimpanzees with particularly high hunting rates have been recorded at Gombe (Stanford, 1998), Taï (Boesch & Boesch, 1989), Ngogo (Watts & Mitani, 2002) and Kanyawara (Gilby et al., 2008). The presence of an impact hunter in a community, group or foraging party may explain the variation in hunting frequency and success (Gilby et al., 2008; Gilby et al., 2013). Upon encountering red colobus monkeys, sub-groups with an "impact hunter" present had higher hunting frequency. This therefore suggests that the correlation between party size and hunting frequency could be due in part to the higher chance of an impact hunter being present as group size increases (Gilby et al. 2008).

Hunting prowess does not necessarily correspond with social standing; both high and low ranking males can be proficient hunters. Males vary in their influence on the success of group hunts within communities and can remain highly influential and successful at hunting into old age (Stanford, 1998). At Taï this is evident due to the role differentiation that occurs within hunts, some males consistently performing the more demanding tactics (Boesch & Boesch-Achermann, 2000; Boesch, 2002). In summary, there are clear demographic influences on how chimpanzees hunt, with variation in the sex, age, individual motivation and impact of hunters, adult males dominating this behaviour.

Seasonality in Hunting

To understand the benefit an animal receives from hunting, it is necessary to understand whether there is any pattern, either seasonally or ecologically, in their hunting effort. Seasonality is important as it highlights the impact of the physical or social environment on the initiation of behaviour. Seasonality or temporal variation in hunting effort has been documented at Gombe, Tai, Mahale and Ngogo, however the times at which this variation is occurring are inconsistent (Boesch & Boesch, 1989; Stanford et al., 1994; Stanford, 1996, 1998; Takahata et al., 1984; Uehara, 1997; Watts & Mitani, 2002).

At Gombe, Mahale, Kanyawara and Taï, hunting peaks correspond to different stages in the annual rainfall cycle (Table 2.4)(Boesch & Boesch-Achermann, 2000; Stanford et al., 1994; Stanford, 1998). At Gombe, hunting is most frequent at the end of the dry season (July – October), peaking in August and September; between 30 and 35% of hunts occurred during these months (Stanford et al., 1994; Stanford, 1998). Similarly, the majority of hunting effort at Mahale is conducted at the start of the wet season in October and November (Takahata et al., 1984). At Taï hunting frequency and success are at their highest during the wet season (mid-August to mid-November), peaking in September and October, when chimpanzees will hunt every day, an increase from around once per week during the rest of the year (Boesch & Boesch-Achermann, 2000). Chimpanzees at Ngogo exhibit a different pattern of seasonality that corresponds with fruit availability rather than rainfall patterns. Watts & Mitani (2002) found a significant relationship between fruit abundance and hunting frequency regardless of the precipitation levels. At Ngogo, Kibale, fruit abundance is unrelated to patterns in rainfall. Similarly hunting frequency at Kanyawara, Kibale increases with the availability of preferred, high calorie fruits (Gilby & Wrangham, 2007).

A number of explanations have been proposed to cause the temporal variation in hunting effort. One suggested explanation is that hunting effort is dependent on prey availability and that seasonality may correspond with the birthing season of the prey species, if this were the case then chimpanzees would be purely reacting to an ecological determinant of an easily obtainable resource (Stanford, 1998). The ease of resource attainment has been further suggested as an explanation for seasonality in hunting at Taï. There, the peak hunting frequency occurs during the two wettest months of the year and it appears that the ease of prey capture is facilitated by the lack of prey stability on branches due to the wet weather. Similarly these months are the primary birthing season for the red colobus monkeys at the site, leading many female colobus to be heavily pregnant or carrying an infant, likely reducing their ability to flee from predators and increasing ease of capture (Boesch & Boesch-Achermann, 2000). At Gombe, where the peak hunting frequency occurs in the dry season, Stanford (1998) suggested a further ecological determined explanation for the phenomenon, that the reduction in foliage allows for increased visibility and thus better prey target selection and thus the higher capture success observed (35% April-May - late rainy season/ 65% July and September - late dry season) (Stanford et al., 1994). Boesch & Boesch-Achermann (2000) state that at Taï there is very low food availability in June and July, this may influence hunting behaviour through encouraging the utilisation of alternative resources before fruit abundance later in the season.

Chimpanzees in multiple populations have been documented to occasionally hunt with very high frequencies independent of seasonality, these periods of increased hunting effort have been described as hunting "binges" and are likely linked to social phenomena (Mitani & Watts, 1999; Stanford et al., 1994). Binges will often entail the chimpanzees hunting on consecutive days for an extended period often capturing multiple colobus during hunting attempts. Hunting success during binges is often very high, possibly in part due to them occurring at time when large numbers of males are grouped together (Stanford, 1998; Watts & Mitani, 2002).

Table 2.4. Seasonality of chimpanzee hunting behaviour.

Site	Season/ Rainfall	Peak Months
Gombe	Dry (late)	August - September
Mahale	Wet (early)	October - November
Taï	Wet	September - October
Ngogo (Kibale)	N/A	*not related to rainfall*
Kanyawara (Kibale)	N/A	*not related to rainfall*

Hunting Methods

Hunting methods are directly related to the costs of hunting and are therefore of relevance when attempting to determine why an animal hunts and the benefit it receives from it. Meat is normally acquired through one of three methods, group hunts, individual pursuits or opportunistic captures (Newton-Fisher et al., 2002). Hunts of arboreal prey are most often initiated after chimpanzees encounter prey within the course of their normal behaviour. Conversely it is known that chimpanzees at some sites will also occasionally hunt with intention, actively searching for prey in a group (Boesch & Boesch, 1989; Mitani & Watts, 1999). These searches involve chimpanzees moving silently through the forest in a directed single file line paying particular notice to any arboreal movement. Searches can continue for several hours (often far shorter) with a hunt ensuing if arboreal primates, particularly colobus, are encountered (Mitani & Watts, 1999). Researchers at Gombe and Mahale have not documented searching behaviour and thus reported hunting as opportunistic (Busse, 1977, 1978; Nishida et al., 1979; Takahata et al. 1984).

Hunting of primates is usually conducted in the forest canopy by adult and adolescent male chimpanzees, this can be both solitary or in groups (Boesch & Boesch, 1989; Busse, 1978; Stanford, 1998; Uehara, 1997). Hunts are fast paced and involve frequent rapid climbing causing them to be energetically expensive (Pontzer & Wrangham, 2004). The technique used for capturing arboreal primates varies depending on the age class, prey species and study site (Boesch & Boesch, 1989; Boesch, 2002; Newton-Fisher, 2014). At East African sites where infant red colobus are targeted, hunters attempt to snatch infant monkeys from their mother. This involves the hunters avoiding mobbing males and getting close to a female with young, enabling them to capture their target (Newton-Fisher, 2014; Stanford, 1998). At Taï in West Africa, where adult monkeys are more frequently captured, hunts involve chasing a group of red colobus in such a manner that the hunter can get close enough to grab a monkey, at which point a kill is made. Although male red colobus will still mob the hunters at Taï they are likely to increase their mortality risk through this behaviour as hunters will occasionally kill males that come too close (Boesch & Boesch-Achermann, 2000). At Gombe less confident hunters will often retreat from mobbing male red colobus and have been reported as being more scared of them when compared to hunters at Taï (Boesch, 1994a; Busse, 1977).

The duration of hunting episodes is highly variable both within and among communities. Chimpanzee hunts last an average of 28 minutes although they may continue for up to 120 minutes (Gilby & Wrangham, 2007; Stanford, 1998). At Taï, hunt duration increases with hunting group size and lone hunters, on average, make a kill for every 39 minutes of hunting, conversely, at Gombe the time taken for solitary hunters to succeed in capturing a monkey is far shorter, only 7.2 minutes (Boesch & Boesch-Achermann, 2000). Boesch and Boesch-Achermann (2000) suggest that because of this there is little pressure to hunt in groups to improve success and thus explaining why group hunting is less frequently observed there.

The killing technique used by the hunters depends on the prey they have captured. Observations from study sites have shown that when neonates are targeted, killing by the hunters is achieved instantaneously through a cranio-cervical bite (Stanford, 1996). When juveniles or adults are targeted killing can occur through a number of different techniques; often hunters begin to eat the prey whilst it is still alive and death follows disembowelment sometimes several minutes later (Gilby pers. comm.). Occasionally hunters will kill adult monkeys through a bite to the back of the neck (Boesch & Boesch, 1989). At Gombe hunters have been observed to flail captured prey on the ground or branches until they are killed (Boesch & Boesch, 1989; Stanford, Wallis, Mpongo, et al., 1994; Stanford, 1996).

When ungulates or small non-primate mammals are captured it is often a result of opportunistic hunting (Newton-Fisher et al., 2002; Nishida et al., 1979; Stanford et al., 1994). Both male and female chimpanzees will capture bush piglets and bushbuck fawns if they chance upon them, often this will occur when chimpanzees find them resting or hiding in the undergrowth (Stanford et al., 1994).

By looking at how chimpanzees hunt, particularly that they will actively hunt arboreal prey, rather than purely capturing prey opportunistically we can assume that the behaviour is likely to be highly beneficial in some context either nutritionally or otherwise. This is further supported, as the behaviour will incur some costs; the pursuit of arboreal prey in the canopy is likely to be energetically expensive.

Cooperation in Hunting

Most predators that hunt cooperatively are thought to do so because it reduces individual hunting costs and maximises benefits through improving their ability to capture large prey etc. (Creel, 1997; Schaller, 1972). Clearly chimpanzees are not hunting large prey in the same manner as many large carnivores, therefore understanding why they hunt in groups and to what extent, is critical for identifying why they hunt.

Cooperative hunting is a widely exhibited social behaviour and has been observed in chimpanzees when hunting arboreal prey (Packer & Ruttan, 1988). Cooperation between hunters can occur both inter and intraspecifically (Bshary et al. 2006; Luhrs et al. 2012) but cooperative hunting is most often exhibited by social groups of predators (Smith, et al. 2012). There is debate as to the level of cooperation that chimpanzees exhibit whilst hunting.

Cooperation within hunting effort is controversial. Some define cooperative hunting economically, stating that cooperation directly relates to fitness benefits and that for hunting to be cooperative then hunters must gain a greater net benefit when hunting as a member of a group than when hunting alone (Packer & Ruttan, 1988). Others suggest that group hunting can be cooperative. They propose that a social definition is suitable, describing cooperation in hunting *"… as concurrent attack by more than one con-specific directed toward a selected prey item regardless of its outcome or fitness consequences"* (Smith et al., 2012 pp. 442). It has been stated that cooperation in hunting can be divided into categories, Boesch & Boesch, (1989) suggest that similarity, synchrony, coordination and collaboration all occur as different levels within cooperation. Regardless of the definition, cooperation in hunting increases the ability to subdue larger prey, allows for increased hunt frequency, and reduced hunting costs (Creel, 1997; Griffiths, 1980; Schaller, 1972).

For cooperative hunting to evolve, a number of key circumstances must occur. First hunting success of solo hunters must be low; otherwise little gain will be made from increasing group size. Second, the increased performance of the hunter must be sufficient to overcome the cost of division of the prey. According to game theoretical models hunting in groups will become an evolutionary stable strategy (ESS) if it improves performance though increasing success or encounter rates, or if it reduces capture costs (Packer & Ruttan, 1988). Boesch (1994) suggested an additional necessity for group or cooperative hunting to become an ESS: that a mechanism limiting access to prey items by non-hunters must be in place.

Chimpanzees hunt in groups, with this more common at some sites than others (Boesch & Boesch-Achermann, 2000; Boesch, 1994b; Newton-Fisher, 2014; Stanford et al., 1994; Watts & Mitani, 2002). This group hunting can be classified as social predation as the frequency of hunting arboreal prey by chimpanzees increases with the chimpanzee party size (Gilby, et al. 2008). The probability chimpanzees will hunt upon encountering red colobus increases with the number of males present in the group (Gilby & Connor, 2010; Gilby, et al. 2006; Gilby & Wrangham, 2007; Mitani & Watts, 2001). However the proportion of hunts that involve multiple hunters is not consistent across sites. Table 2.5. shows the proportion of hunts that are solitary, group and collaborative. Gombe has the highest proportion of solitary hunting, 64% compared to 28% at Mahale and 16% at Taï. Group hunts are common at both Mahale and Taï (72% & 84%) when compared to Gombe (36%) but collaboration, the highest form of cooperation in hunting only occurs frequently at Taï (77%) (Boesch & Boesch-Achermann, 2000).

Levels of cooperation within hunts can vary within and among populations. The extent to which cooperation occurs within chimpanzee hunts has been heavily contested as has the cognitive requirement of this behaviour (Gilby & Connor, 2010). This controversy is likely in part due to the contrasting and varying definitions used when describing cooperative hunting by chimpanzees (Table 2.6.). Due to the inter-study site differences in recording methods, data collection and chimpanzee behaviour, a common definition of cooperation has not been agreed upon (I.C. Gilby pers comm).

The definitions of cooperative hunting are not consistent in the literature (Table 2.6.). A strong working definition of cooperative hunting is that "Hunting is considered to be cooperative if an animal obtains a greater net benefit by hunting with others than by hunting solitarily" (Gilby & Connor, 2010; Packer & Ruttan, 1988), this could be considered functional cooperation. Chimpanzees must be more successful and gain a greater benefit when hunting as a group and individuals must have a greater benefit as part of the group than not part for hunting to be functionally cooperative. At Gombe, Ngogo and Taï, hunting success increases with the number of adult male hunters which is likely to be attributed to more males creating more opportunities for one to make a kill (Mitani & Watts, 1999; Stanford, 1998). This behaviour is therefore functionally cooperative provided the chimpanzees are getting a greater overall benefit of acting as part of the hunt group than that of hunting alone.

For the increase in hunting success from hunting in a group to equate to an increase in individual benefit the access to meat from the hunt must also increase (Boesch, 1994b). The costs of participation also need to be accounted for when looking at the comparative benefits of hunting strategies. Hunting is a costly behaviour for chimpanzees as the capture of agile, fast moving arboreal primates is energetically expensive and risky in part because adult male red colobus mob and attack hunters (Boesch, 1994a, 1994b; Busse, 1977; Stanford, 1995).

Many studies have tried to determine whether hunting by chimpanzees meets the above criteria for being a cooperative act (Boesch, 1994b; Busse, 1978; Gilby et al., 2008; Tennie et al. 2009; Watts & Mitani, 2002). Busse (1978) stated that chimpanzee hunting behaviour is non-cooperative after he looked at the relationship between hunting group size, hunting success and meat consumption. Busse suggested that lone hunters would obtain more meat than group hunters due to the high levels of contest competition over small kills and that group hunts were the incidental result of predator and prey group encounters. In contrast, Boesch (1994b) investigated the cost/benefit of hunting in groups by chimpanzees relating to the amount of meat gained and the energy expended from the hunt. He considered the amount of meat gained per hunt, the amount of hunters and the time taken to capture the prey using a game theoretical model tested empirically with data from Taï. Boesch concluded that hunting at Taï was truly cooperative as hunters benefitted most by working together in groups of four. Gilby et al. (2006) used the definition of ‘joint action for mutual benefit’ for cooperation to investigate evidence for cooperative hunting at Gombe. They found little evidence to support an assertion of cooperative hunting occurring at either Gombe or Ngogo and no evidence of hunting success increase or gains per capita meat availability in large parties compared to small parties even though they did find an increase in the volume of meat captured by larger groups.

Table 2.5. Frequency of group hunting by chimpanzees when predating red colobus monkeys at Taï, Gombe and, Mahale adapted from Boesch & Boesch-Achermann (2000).

Site	Solitary Hunts %	Group Hunts %	Collaboration %
Taï	16	84	77
Gombe	64	36	19
Mahale	14	72	0

Table 6. Definitions of cooperation as found in peer reviewed literature discussing chimpanzee hunting behaviour.

Definition	Author
"...behavior whose outcome is increased fitness of both participants (see Hamilton 1964; Brown 1975;Gadgil 1975)"	Busse, 1978
"Hunting is considered to be cooperative if an animal obtains a greater net benefit by hunting with others than by hunting solitarily”	Gilby & Connor, 2010
"...behaviour of two or more individuals acting together to achieve a common goal"	Boesch & Boesch, 1989
"...positive relationships between hunting party size and success rate have been interpreted as evidence of cooperation (Packer and Ruttan 1988 for lions)."	Stanford, 1996
"...that an individual’s net payoff is higher when hunting with others than when hunting solitarily (Packer and Ruttan 1988; Mesterton-Gibbons and Dugatkin 1	Tennie et al, 2009
"... hunting is cooperative if the payoff to a hunter is higher by hunting with others than by hunting alone (Mesterton-Gibbons & Dugatkin 1992; Clements & S	Gilby et al 2006
"'joint action for mutual benefit’ (Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995)"	Gilby et al 2006

Cooperation vs. Collaboration: Levels of cooperation in social pre

There is evidence that different chimpanzee populations vary in the c of group hunting behaviour that they exhibit. Chimpanzees at Taï are c to act cooperatively when hunting in a group as they received a great than when hunting alone. When studies began at Taï some i differences in hunting behaviour were noted compared to long-term s in East Africa. Researchers at Taï found that not only did chimpan cooperatively, they hunted in larger groups than had been observe sites at that time and with a greater level of coordination. Research assert that chimpanzees hunting at Taï work together to ensure the maximise the likelihood of making a kill (Boesch & Boesch, 1989; Boes 2002). They propose that to define cooperation in hunting appropr account for the variation in definitions given by other authors on cooperation should be considered with four tiers and operationally such (Boesch & Boesch, 1989; Boesch, 1994b).

> Similarity where: “All hunters concentrate similar actions on prey, but without any spatial or time relation between them; h least two hunters always act simultaneously”.

> Synchrony where: “Each hunter concentrates similar actio same prey and tries to relate in time to each other’s actions”.

> Coordination where: “Each hunter concentrates similar actions on the same prey and tries to relate in time and space to each other’s actions”.
>
> Collaboration where: “Hunters perform different complementary actions, all directed toward the same prey”.

These definitions intentionally remove the requirement for a greater benefit when working with others so that highly coordinated actions by hunters are not dismissed as non-cooperative based on the outcome of individual circumstances e.g. an unsuccessful hunt (Boesch & Boesch, 1989).

Further studies from Taï have looked at cooperative hunting in more detail. Boesch (1994a) investigated the level of coordination in hunts at Taï and Gombe and when compared found that solitary hunts were most frequent at Gombe (48%) whereas at Taï collaboration most often occurred (63%). He attributed this difference to the high success rate of solitary hunters in the woodland savannah habitat of Gombe leading to a low selection pressure for higher forms of cooperation. At both sites he found a similar frequency of synchrony (Gombe: 13%, Taï: 11%) and coordination (Both sites: 11%).

The increased rate of collaboration that is said to be exhibited at Taï requires a complicated strategy of capture as the chimpanzees are required to work together to achieve the shared goal of prey capture. A requirement of this strategy is that chimpanzees are able to coordinate their actions and this has led to them performing different roles in the hunt. Hunters at Taï perform four main roles in their hunting attempts, driving, blocking, chasing and ambushing; according to Boesch (2002) these roles require different levels of anticipation and thus cognitive demand. This is a possible explanation for the improvement in hunting ability of chimpanzees with age; older chimpanzees ambush prey significantly more than young chimpanzees (Boesch, 2002).

East African chimpanzees are not known to regularly perform collaborative hunts (Boesch, 1994a). Anticipatory behaviour has however been observed, for example at Ngogo chimpanzees will occasionally run along the ground ahead of fleeing colobus and climb into tree in their path and attempt to capture them (Watts & Mitani, 2002). At Gombe chimpanzees will often follow a hunt from the ground and enter at a later point if they see a monkey attempting to escape in another direction or falling to the ground (Stanford, 1998). This said, no study has conclusively stated that East African Chimpanzees regularly show higher levels of cooperation as described by Boesch & Boesch (1989).

Clearly hunting in groups and seemingly the ability to cooperate are important factors in chimpanzees' hunting behaviour. It may be that hunting in groups or cooperating relates to why chimpanzees hunt, relating to benefits, costs and sociality.

Why do chimpanzees hunt and why in groups?

Four main hypotheses exist attempting to explain why chimpanzees hunt and what factors influence the occurrence of hunting. Initially it was thought that hunting fulfilled a nutritional requirement or shortfall from the chimpanzees' frugivorous diet, this is often termed the 'nutrient shortfall' hypothesis. This hypothesis suggests that chimpanzee hunting with be more frequent when fruit is scarce, the meat fulfilling a nutritional shortfall (Stanford, 1996, 1998; Takahata et al., 1984). A number of studies have investigated whether episodes of carnivory coincide with periods of nutritional shortfall; two studies from Gombe found that hunting frequency was higher during the dry season when body mass is low (Gilby et al., 2006; Stanford et al. 1994). A converse hypothesis exists termed the 'nutrient surplus' hypothesis proposes that chimpanzee hunting frequency will increase at times where diet quality is high. The reasoning behind this explanation is that the energetic costs of hunting are more easily absorbed at times when the chimpanzees have an abundance of energy rich foods (Mitani & Watts, 2001).

At Taï, Cote d'Ivoire, chimpanzees achieve a positive caloric benefit from hunting that is maximised by hunting groups of three or four. At Taï it was found that chimpanzees were not only able to gain a nutritional benefit from hunting when factoring in approximated costs, but also that by hunting in groups this benefit was maximised. As group hunting by male chimpanzees at the site gave a greater benefit than hunting alone, the behaviour could be considered cooperative (Boesch, 1994b).

Further hypotheses on why chimpanzees hunt in groups relate to social benefits of hunting and meat acquisition. A controversial suggestion was the 'meat for sex' hypothesis; that chimpanzee males use meat as a form of currency to improve their access to mating with oestrus females. For this proposal to be valid male chimpanzees must hunt more frequently when oestrus females are present and they must have improved mating rates (Stanford et al., 1994; Stanford, 1998). Data from Gombe has previously been stated as consistent with this idea, a positive correlation exists between the presence of tumescent females and hunting frequency (Stanford et al., 1994).

Another suggested hypothesis is the ‘male social bonding hypothesis’, this proposes a social incentive for hunting where male chimpanzees may use meat to help develop and maintain intra-sexual alliances (Mitani & Watts, 2001; Stanford et al., 1994). This hypothesis predicts that male chimpanzees are more likely to hunt if they are in close proximity with many other males whom they are bonded or allied with. As large parties will be more likely to contain another male with which the hunter holds a strong social bond then it is expected that hunting will occur more frequently when chimpanzees are in larger groups.

Hypotheses testing

A recent attempt has been made to address whether or not these hypotheses are defendable. Researchers have looked to results of older studies and re-analysed the data. The link between nutrition and hunting by chimpanzees is complex and influenced by many factors. A recent study has found little support for a “nutrient shortfall” hypothesis, it was found that Gombe chimpanzees are less likely to hunt and are less successful at hunting in “poor diet” months (Gilby et al., 2006). This has not however led to greater support for the alternative "nutrient surplus" hypothesis. A number of studies have found positive associations between high diet quality and increased hunting yet they failed to control for two confounding factors linked to diet that are known to influence hunting behaviour: party size and presence of swollen females (Mitani & Watts, 2001; Nishida et al., 1979; Takahata et al., 1984; Watts & Mitani, 2002). When these data were tested whilst accounting for confounding factors (particularly group size) then no significant association was found between high diet quality and hunting frequency at Gombe but the relationship remained significant at Kanyawara (Gilby et al., 2006; Gilby & Wrangham, 2007).

Social explanations for chimpanzee hunting have also struggled to find emprical support. The "meat for sex" hypothesis has been largely refuted with recent studies contrasting with the findings of early studies. Although a correlation was found between the presence of tumescent females and frequency of hunting at Gombe, this study used a small data set and unsuitable statistics (Gilby et al., 2010; Stanford et al., 1994). More recent studies found a negative association between the presence of maximally tumescent females and frequency of hunting after controlling for party size the also found no significance when testing for preferential sharing of meat with oestrus females by male meat possessors (Gilby et al., 2006, 2010). Data on this topic appear to imply that hunters must decide between "meat or sex" rather than "meat for sex", as males who hunt are unlikely to be able to deny access to mating by other males through forming or maintaining consortships with oestrus females (Gilby et al., 2006). Similarly, little empirical support for the "male social bonding" hypothesis has been found. Although a positive association between male party size and the likelihood of one male hunting exists, there is no association between party size and the chance of a focal individual hunting (Gilby et al., 2006). Furthermore it has been found that male chimpanzees do not prefferentially share with allied males and that, in fact, a male is not more likely to hunt if his ‘preferred social partner’ is present (Gilby, 2006),

Meat-scrap hypothesis.

Although it has long been known that meat is a good source of micro-nutrients such as: vitamin B12, iron, calcium, and salts (Hamilton & Busse, 1978), this knowledge had not been integrated into a working hypothesis attempting to explain chimpanzee hunting until recently (Hamilton & Busse, 1978; Tennie et al., 2009). The meat-scrap hypothesis posits that chimpanzees hunt and consume mammalian prey to increase their intake of these micronutrients (Tennie et al., 2009). Not only does meat contain these micronutrients, but also it contains them in high concentrations. By eating meat chimpanzees are likely to be able to consume micronutrients, some of which are available in a vegetative diet but contained within a considerable lower volume of food, thus reducing dietary bulk (Milton, 1999). This hypothesis was modelled using over 25 years of data from Gombe. The concept helps to explain why chimpanzees may hunt in groups even though the behaviour may not maximise their per capita caloric intake, calories possibly being the incorrect currency to consider when measuring hunting payoffs (Tennie et al., 2009).

Conclusion

Chimpanzees are regular and successful hunters that can work cooperatively to achieve prey capture (Boesch, 1994b; Newton-Fisher, 2014). Chimpanzee hunters primarily target Cercopithidae. They have a preference for red colobus monkeys. There is among site variation in the age class of prey that are commonly hunted (Stanford, 1998). Chimpanzees normally hunt by pursuing and capturing arboreal primates alone or in groups. Hunting is a male dominated behaviour and normally conducted by adult or adolescents (Newton-Fisher, 2007). Chimpanzees at Gombe preferentially hunt infant or juveniles whilst hunters at Taï capture adults and young colobus equally (Boesch & Boesch-Achermann, 2000; Stanford, 1998). Hunting frequency can vary by season, at some sites hunting occurs most often during the wet season and at others during the dry season (Boesch & Boesch, 1989; Stanford, 1998). It has also been noted that some populations of chimpanzees hunt most often when fruit availability is high rather than during a specific rainfall period (Gilby & Wrangham, 2007).

There is between-site disparity in the level of cooperation that exists in chimpanzee hunting. Chimpanzees at Taï, Cote d'Ivoire, West Africa exhibit cooperative and even collaborative behaviours whilst hunting (Boesch & Boesch, 1989; Boesch, 1994b). Conversely chimpanzees at East African sites do not. Although group hunting has been observed it has not been found to consistently be cooperative and it is thought that these chimpanzees do not regularly exhibit this behaviour (Boesch, 1994a; Busse, 1978).

Current hypotheses explaining why chimpanzees hunt are often supported by equivocal evidence, many are supported at only some of the many sites where chimpanzees are known to hunt (Gilby et al., 2006). Future studies should address the dearth in information about hunting by females, opportunistic or otherwise as well as looking in more detail about the nutritional components and benefits of meat in the chimpanzee’s diet. Further research should be conducted into the opportunistic hunting of ungulate prey across the study sites.

Chapter 3 (Article 2) – Variation in hunting success is mediated by variation in relative prey size: Chimpanzees are more successful because they hunt small prey

Abstract:

Chimpanzees *Pan troglodytes* are highly successful hunters of mammalian prey. All known populations of chimpanzees hunt; their primary prey are medium sizes arboreal primates, particularly *Piliocolobus* sp.. In contrast, other large social carnivore species hunt large prey, primarily ungulates, and achieve lower success rates than chimpanzees. This study aimed to determine whether chimpanzees consistently achieve hunting success rates higher than social carnivorans and whether they truly do hunt relatively smaller prey. Furthermore it aimed to assess whether prey size, a prey related factor that influences hunting success, explained why chimpanzees are more successful hunters than large social carnivores. Data for five predator species, chimpanzees *Pan troglodytes,* grey wolves *Canis lupus,* African hunting dogs *Lycaon pictus,* spotted hyena *Crocuta crocuta,* and lions *Panthera leo* were collected from published literature (69 studies) on hunting success and predation. A mediation analysis was implemented to assess whether relative prey size could explain the difference in hunting success observed between predators using data from published literature. Chimpanzees were found to be more successful hunters and hunt smaller prey than large social carnivorans and that their high hunting success compared to social carnivores (i.e. wolves, African hunting dogs and spotted hyena) is explained by them hunting relatively smaller prey. This study highlights that chimpanzees are similar in their hunting preferences to large social carnivores despite being facultative carnivores: prey size, a simple factor unrelated to intelligence, partly determined the hunting success of both chimpanzees and large social carnivores. Therefore, ecological and not cognitive differences explain the relatively higher hunting success rates of chimpanzees.

Introduction

Although the chimpanzee *Pan troglodytes* is a primarily frugivorous primate an average of 4% (range 0 – 18%) of their diet is composed of animal prey (Conklin-Brittain, et al. 2001). All extensively studied chimpanzee populations show some evidence of hunting, however different populations of chimpanzees vary in their hunting behaviour (Newton-Fisher, 2014)(Chapter 2). Chimpanzees have been observed to hunt over 40 species of mammal although they preferentially capture arboreal primates, particularly colobines (Table 2.2.)(Newton-Fisher, 2007, 2014). The most striking aspect of chimpanzee hunting in comparison to large mammalian non-primate predators is that they have a very high success rate and hunt relatively small prey. This study addresses the debate about whether their high success rates compared to other large social mammalian predators is related to social factors, cognitive abilities or ecological differences.

Chimpanzees often hunt in groups, similar to large (>21.5kg) social carnivores: e.g. wolves *Canis lupus,* African hunting dogs *Lycaon pictus,* spotted hyenas *Crocuta crocuta,* and lions *Panthera leo* (Boesch & Boesch, 1989; Busse, 1978; Estes & Goddard, 1967; Mech, 1974; Mills, 1990; Nishida et al., 1979; Schaller, 1972; Stanford, 1998). From here on the term “carnivoran” will be used to describe members of the order “Carnivora” to remove any implication of dietary habits with the term “carnivore” (McNab, 1989). At some sites, group hunting by chimpanzees can be considered cooperative, with the net benefit of hunting in a group being greater than when hunting alone (Boesch, 1994b; Packer & Ruttan, 1988). Chimpanzees in some populations are able to coordinate their actions in relation to other hunters to maximise their chance of succeeding in a hunt (Boesch & Boesch, 1989; Boesch, 1994b, 2002). At the Taï Forest, Cote d'Ivoire, hunting chimpanzees appear to adopt different roles: drivers, chaser, blockers and ambushers (Boesch, 2002). Lions and African hunting dogs also engage in this type of collaborative by taking on different hunting roles (Creel & Creel, 1995; Stander, 1992).

Like many social carnivorans, chimpanzees are facultative group hunters; in some locations they achieve high hunting success when hunting alone (Boesch, 1994b; Stanford, 1998). Animals are less likely to hunt cooperatively if their chances of success when hunting alone are high (Boesch & Boesch-Achermann, 2000; Packer & Ruttan, 1988; Stanford, 1998). Predators are expected to cooperate when hunting if it increases their net fitness benefit, for example by increasing their ability to subdue large prey, or if it reduces costs, e.g. by reducing the time taken or energy expended to capture a prey animal (Boesch, 1994b; Creel & Creel, 1995; Packer & Ruttan, 1988). Many large social predators exhibit plasticity in cooperative behaviour with different populations varying in their tendencies to hunt in relation to the ecological or social environment in which they live; chimpanzees are no exception (Boesch & Boesch-Achermann, 2000; Holekamp, et al. 1997; Newton-Fisher, 2014; Schaller, 1972). Although theoretically, factors such as intelligence and social dynamic could influence the hunting behaviour of chimpanzees research has found no known factors separating the benefits and mechanisms of group hunting by chimpanzees from those of large social predators (Gilby & Connor, 2010).

Chimpanzees exhibit two key hunting behaviours that appear to contrast with the hunting behaviour of large social carnivorans: they hunt small prey (relative to themselves) in comparison to the mammals captured by the social carnivorans and they have a higher success. Chimpanzees' primary prey are arboreal primates. They have a preference for red colobus *Piliocolobus* sp. wherever they are sympatric. These are medium sized folivorous monkeys weighing between 5 – 11 kg, i.e. 13 – 28% of their own body mass (Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000; Butyinski et al 2013a, 2013b; Stanford, 1998; Struhsaker & Grubb, 2013). At sites where red colobus are not present, smaller cercopithecines, mainly *Cercopithecus* sp. or larger black and white colobus monkeys, *Colobus* sp., are hunted most often (Basabose & Yamagiwa, 1997; Newton-Fisher, et al. 2002). In contrast large carnivorans (>21.5kg) primarily hunt animals that are 45% of their own body mass or greater and those that hunt in groups target prey considerably larger than this, often many times their own size (Carbone, et al., 1999; Radloff & Du Toit, 2004).

The second distinguishing feature of chimpanzee hunting is that they achieve high rates of hunting success (the number of successful hunts as a percentage of the number of hunting attempts). Populations vary in their hunting success, success rates range from a low of 45% to 70% (Median 54.7% *n*=5) (Boesch & Boesch, 1989; Mitani & Watts, 2001; Stanford et al., 1994; Uehara, 1997). Large social carnivorans are often far less successful than this, lions and hyena have average success rates of 26% and 29% respectively (Holekamp et al., 1997; Schaller, 1972). The high hunting success achieved by chimpanzees has led to some researchers stating that chimpanzees are extraordinary in their hunting ability when compared to large African carnivores yet until now there has been no investigation into the factors explaining differences in hunting success observed between these animals (Mitani & Watts, 1999). Why chimpanzees should be more successful hunters than large social carnivorans is not instantly apparent. Various explanations could be given, 1) Chimpanzees' intelligence enable them to use complex, coordinated hunting tactics which increase the probability of success (Gilby & Connor, 2010). 2) Chimpanzees are facultative carnivores and only hunt when they are likely to succeed. 3) Chimpanzee prey is relatively easy to capture because they are small or lack suitable defensive capabilities.

Predator hunting success is influenced by factors of three general types: predator, prey and environment related. Wind orientation, number of hunters, prey species, prey herd size, moon brightness (visibility) and, grass height were all found to significantly influence the hunting success of lions (Funston et al., 2001; Stander & Albon, 1993). It has previously been suggested that a general, intraspecific relationship, between relative prey size and capture success exists (Wilson, 1975). Data from studies on avian predators such as the American kestrel (*Falco sparverius*) have shown that predators can experience a dramatic increase in capture success when shifting from vertebrate to invertebrate i.e. smaller prey (Griffiths, 1980). Furthermore it is generally agreed upon that many predators hunt in groups to improve their ability to subdue large prey, therefore it can be inferred that hunting larger prey is more difficult than hunting small prey as it requires more individuals to do it effectively. This may lead to a lower rate of success for predators hunting large rather than small prey (Gilby & Connor, 2010; Radloff & Du Toit, 2004; Schaller, 1972).

This study investigates whether the two key differences between chimpanzees hunting behaviour and that of large social carnivorans i.e. the size of prey a predator hunts (prey-related factor) and the hunting success, are related (Wilson, 1975). Other predator, prey and environmental related factors are likely to have some influence on hunting success of the predators but relative prey size is of particular interest as it relates intrinsically to the caloric benefit of prey. Furthermore as it has been previously hypothesised that relative prey size affects hunting success of predators and that this factor is a key difference between chimpanzees and large social carnivorans, an investigation into whether this can explain the differences in hunting success was therefore appropriate. Data on vegetation cover type (environmental factor) and prey preference (predator factor) were collected to control for as possible confounding factors.

Predictions and Hypotheses:

1.) There is a negative relationship between the proportional size of prey (Ratio of Predator mass: Prey mass) and the hunting success a predator can achieve.

2.) Two confounding factors that will affect the hunting success achieved by the predator species are the preference of the predator for the prey and the level of cover available in the habitat. Prey specialisation will cause predators to achieve a higher hunting success rate when they hunt their preferred prey species (predator factor). Cover type (environmental factor) will influence the ability of predators to succeed in hunting attempts, semi-open habitats will allow improve hunters chance of success.

3.) Chimpanzees, wolves, African hunting dogs, spotted hyenas, and lions will hunt prey of different relative sizes. These different predator species will also differ in their ability to successfully capture prey. Chimpanzees will hunt proportionally smaller prey and have a higher hunting success rate than the other predators.

4.) The variation in hunting success amongst predator species is explained by the variation in the size of prey that they hunt. The higher hunting success achieved by chimpanzees compared to, wolves, African hunting dogs, spotted hyenas and lions is explained by their selection of smaller prey.

5.) When considering all mammalian prey species hunted by each predator species there will be a greater distinction between chimpanzees and the large social carnivorans than among the large social carnivorans. This will differentiate chimpanzees from large social carnivorans on the basis of relative prey size. Lions relative prey sizes will overlap the other predators' profiles to the greatest extent due to their large size.

Methods

Data collection for this study was conducted through an extensive literature review using a semi-systematic methodology of acquiring the data from literature. Standard search terms were used (Appendix I) and further papers were included if they were cited in the literature collected and appeared useful. The review focussed solely on five large mammalian predator species: chimpanzees *Pan troglodytes,* grey wolves *Canis lupus*, African hunting dogs *Lycaon pictus,* spotted hyenas *Crocuta crocuta* and lions *Panthera leo.*

Hunting Success

The review process returned 28 papers, books or book chapters that gave unique data on hunting success on the five predator species: chimpanzees, wolves, African hunting dogs, spotted hyenas and lions. Data on hunting success were included only when they were available for each prey species captured. Success data were either given as a percentage or as a number of hunts leading to capture out of total hunts attempted. Average success rates (percentages from multiple prey species) were not included. Literature was included when the sample size was greater than 3 and provided data were prey species specific. Data on hunting success for certain prey species were available from multiple studies and multiple study sites; these repeats were included separately in the database. Some studies provided multiple success rates for a single prey species, these were included as separate data entries provided they were unique from a previous success rate e.g. temporally unique, variation in hunting group size, different age class of prey etc.

Prey Profile

A literature search returned 41 papers, chapters or books that gave unique data on prey profile for the five predator species investigated. Papers were included if they provided data on the prey species hunted by any of the five predator species investigated. If reference to a verified hunt was made in the literature then this prey species was included in the predator's profile. This study focuses on the mammalian prey of these predators therefore only accounts of mammal predation were included. To build complete predation profiles of mammalian prey for the predators, all verified predation events found in the literature were included. Recordings of predation on domestic species were not included (full prey profiles are presented in Appendix III).

Prey Size

To approximate the average size (mass) of a prey animals hunted, three-quarters of the weight of an adult female was used as the weight measurement for each species (Hayward & Kerley, 2005; Schaller, 1972). This accounted for variation in the size and age class of prey captured from infants to adult males and gave an approximate average weight of prey. This also allowed data collected through faecal analysis to be used in conjunction with direct observation of prey captured.

Prey Mass:

$$P = \tfrac{3}{4} M$$

P = prey mass in kilograms (kg)

M = average female mass in kilograms (kg)

To assess how body weight related prey selection varies between predator species mass measurements were converted into a predator:prey mass ratio (R). This ratio shows the prey mass as a proportion of the mean predator mass (Radloff & Du Toit, 2004) and was the standardised empirical measure necessary for comparative analysis between species.

Predator:Prey Ratio:

$$R = {}^{C}/_{P}$$

R = Ratio

C = mean predator mass in kilograms (kg) (*both sexes*)

P = prey mass in kilograms (kg)

Prey Preference:

The predator species' preferences for particular prey species was recorded from the literature to determine whether it was a confounding factor in a relationship between relative prey size and hunting success (Hypothesis 2) in three ways:

1. When a prey species was hunted more frequently than would be expected in relation to its occurrence in the predators environment it was classified as preferred. All other species were classified as 'not preferred' (M. Hayward et al., 2006; M. W. Hayward & Kerley, 2005; M. Hayward, 2006).
2. If a species was simply stated as being a preferred or not-preferred (avoided, expected) species within a study or other literature without thorough analysis of the relative prey abundance it was still classified as such. Although more subjective, this manner of classification was important as there is a dearth of studies collecting quantifiable data on prey preference by large social predators exists within the literature.
3. If no reference to whether a prey species was preferred could be found then the prey preference was classified as unknown.

Vegetation Cover Categorisation

Habitat type data were taken from site descriptions in the predator studies. This was conducted to ascertain whether vegetation cover influenced hunting success and if it did to account for this confounding factor in the future analysis (Hypothesis 2). Although uncommon, if a situation occurred where no site description was given then the site location was used and a search was conducted to find the habitat type of the site in other literature. Assigning a vegetation cover categorisation was conducted by assigning each study site (site at which success results were recorded) a habitat classification as taken from the IUCN Habitat Classification Scheme V.3.1. (IUCN, 2012) (Appendix II). A habitat classification was given to each hunting success result by comparing the site description given in the literature with the descriptors given in the scheme and assigning the best fit. Each Habitat Classification was then assigned to a vegetation cover category according the descriptors in the scheme: dense, semi-open, open and, mixed.

Analysis:

Analytical Strategy

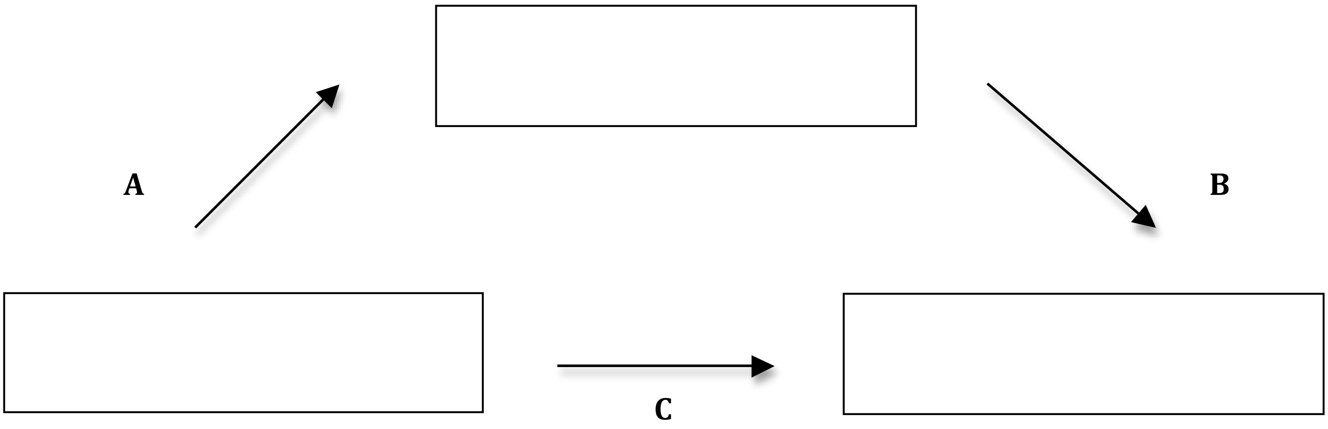
All data were analysed using SPSS Statistics 22.0. An (OLS) linear regression model was used to determine whether a relationship existed between hunting success (dependent variable (DV)) and both predator species (independent variable (IV)) and Predator:Prey ratio (IV). Ratio data were log10 transformed to normalize the data (Elston et al., 1996; Gittleman, 1985). Success data from studies with very small sample sizes (*n < 3*) were excluded.

ANOVA was used to determine whether success (DV) varied with predator species (IV) and whether ratio (DV) varied with predator species (IV). This was conducted to fulfil the requirements below.

Hypotheses 3 & 4 of this study are mediation (explanatory) hypotheses and as such analyses were completed according to the recommendation of Baron & Kenny (1986) and Wu & Zumbo (2007) on mediation analysis. This approach recommends to first show that there is a significant association between the independent variable (*predator species*) and the proposed dependent variable (*hunting success*) (**C**). Second, one must show that the independent variable is significantly associated with the proposed mediator (*ratio*) (**A**). Thirdly the proposed mediator (*ratio*) must be significantly associated with the proposed dependent variable (*success*) (**B**). To test the indirect effect of species on hunting success through *ratio* the PROCESS macro for SPSS developed by Hayes (2014) was used. Simply put this analysis tests whether the differences in hunting success among predators (**C**) is mediated (explained) by them hunting different sized prey (**A & B**), see figure 3.1.

Post-hoc tests were conducted on both ANOVAs to ascertain which pairs of predators were significantly different in both their hunting success and their predator:prey ratio.

1. Mediation model diagram; Baron and Kenny's three steps.



Prey Profile Data

ANOVA was used to test prey profile data. This was conducted to determine the variation among the relative prey size of the predator species when accounting for all mammalian species that are hunted by them (Hypothesis 5). *Ratio* data were Log10 transformed (Gittleman, 1985).

Results

Ratio predicting hunting success – Hypothesis 1

A linear regression (OLS) analysis with *ratio* and *predator species* (dummy coded) as the independent variables and *hunting success* as the dependent variable indicated a significant negative effect of *ratio* (whilst controlling for the effect of species)($\beta = -.33$, $t(77) = -2.28$, $p = .03$; Figure 3.2). The lack of negative relationship seen for the chimpanzee data is due to the small size range (*ratio* = 0.09 – 0.23) of prey hunted.

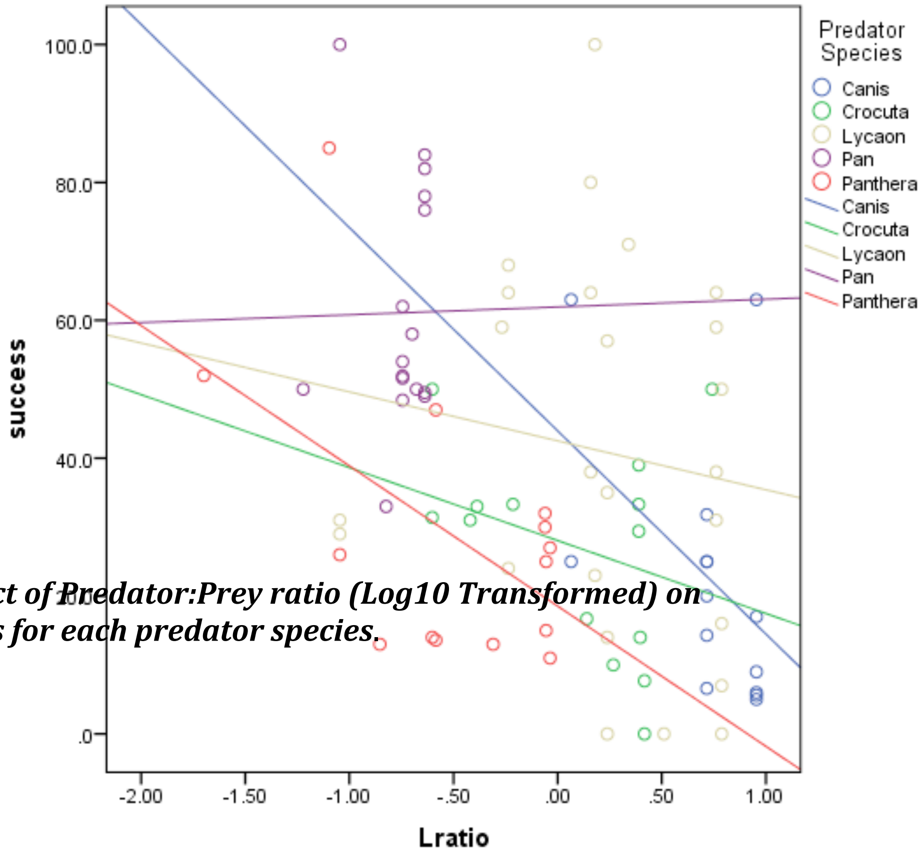


Figure 3.2. Effect of Predator:Prey ratio (Log10 Transformed) on hunting success for each predator species.

Confounding Factors – Hypothesis 2

To determine whether cover type was a confounding variable of hunting success a two way ANOVA was conducted with *cover* (IV), *preference* (IV) and *hunting success* (DV). No significant effect of *cover* type or *prey preference* on *hunting success* was found *F*(6, 78) = .468, *p* = .83, η^2_p = .038).

Hunting Success – Hypothesis 3

It was predicted that different predator species have different hunting success and that chimpanzees would have a higher hunting success than wolves, African hunting dogs, hyenas and lions. An ANOVA with *predator species* as the independent variable and *hunting success* as the dependent variable showed a significant main effect of *predator species* on *hunting success* (F[4, 78] = 8.10, p < .001, η_p^2 = .29) (Hypothesis 3). Additional post-hoc tests were conducted to test whether the *hunting success* differences among species were significant. Five out of ten pairs tested were found to differ in their *hunting success*; wolves and African hunting dogs were the only carnivoran pair that differed, chimpanzees differed from all other predator species (Table 3.1.).

Table 3.1: Mean hunting success per species

	M(*SD*)	Canis	Crocuta	Lycaon	Pan
Canis	22.59 (19.19)	--			
Crocuta	27.06 (15.25)	*p* = .58	--		
Lycaon	40.88 (27.21)	*p* = .01	*p* = .06	--	
Pan	61.09 (17.69)	*p* < .001	*p* < .001	*p* = .004	--
Panthera	28.83 (20.61)	*p* = .44	*p* = .83	*p* = .10	*p* < .001

Predator:Prey Ratio – Hypothesis 3

It was expected that different predator species hunt prey of different relative sizes as they hunt different prey animals. Consequently this causes variation in Predator:Prey mass ratio. An ANOVA with predator species as the independent variable and ratio as the dependent variable showed a significant difference between a number of species (*F*[4, 78] = 29.18, *p* = .001, η^2_p = .60)(Hypothesis 3). Additional post-hoc tests were conducted to test between which species there was a significant difference in the ratio of prey; eight of the ten pairs tested were found to have significantly different Predator:Prey ratios. No difference was found between African hunting dogs and spotted hyena, or, lions and chimpanzees (Table 3.2.).

Table 3.2: Mean Predator:Prey ratio per species

	M (median)	*Canis*	*Crocuta*	*Lycaon*	*Pan*
Canis	6.25 (2.82)	--			
Crocuta	1.84 (1.45)	*p* < .001	--		
Lycaon	2.79 (2.31)	*p* = .001	*p* = .34	--	
Pan	.19 (.05)	*p* < .001	*p* < .001	*p* < .001	--
Panthera	.50 (.37)	*p* < .001	*p* < .001	*p* < .001	*p* = .12

Note: True mean (M) and median ratios given. Log10 transformed ratios were used in the analyses

Mediation Analysis – Hypothesis 4

It was expected that the predators hunting prey of different relative sizes caused differences in the hunting success among the predator species. When the correct assumptions were met for mediation analysis (significant [*p* <0.05] IV~DV/ IV ~ Mediator/ Mediator ~ DV [significance Tables 3.1 & 3.2.]) then pairs were tested against each other. The indirect effect of predator species through ratio on hunting success was tested, to see if it significantly differed from 0. The indirect analysis, using the PROCESS macro (Hayes, 2014; 5000 bootstrap samples), indicated that the indirect effect of predator species through ratio on hunting success was significantly different from 0 for all pairs tested (Table 3.3).

Mediation effects were found for all pairs of predators tested (Table 3.3). The only pair of carnivorans that showed significant difference in both hunting success and relative prey size was the African hunting dog *Lycaon pictus* and the grey wolf *Canis lupus*. This showed that African hunting dogs have a higher hunting success than wolves partly due to them hunting species with lower ratios and therefore proportionally smaller prey (*b* = 6.23, S.E. = 2.91, 95% C.I.: [1.49; 13.28]).

Chimpanzees *Pan troglodytes* were found to differ in success and ratio between three carnivorans, wolves, African hunting dogs and spotted hyena. Ratio mediates hunting success for these pairs; chimpanzees are more successful than wolves, African hunting dogs and hyena because they hunt smaller prey. Chimpanzees had a higher hunting success and this is explained in part by them hunting proportionally smaller prey relative to their own body mass:

chimpanzees/wolves (*b* = 18.59, S.E. = 9.08, 95% C.I.: [2.71; 38.47]) ***chimpanzees/spotted hyena*** (*b* = 10.65, S.E. = 5.31, 95% C.I.: [2.15; 23.47]) ***chimpanzees/African hunting dogs*** (*b* = 12.36, S.E. = 6.85, 95% C.I.: [1.55; 28.89]).

When hunting smaller prey, predators had a higher hunting success than when hunting larger prey. Furthermore, the effect of predator species on hunting success was mediated by the Predator:Prey ratio, with species that hunt proportionally smaller prey generally experiencing a higher hunting success than those that hunt larger prey. Chimpanzees were found to be more successful hunters than wolves, African hunting dogs, hyena and lions; this was found to be because they hunt smaller prey.

Table 3.3. The predator pairs tested for mediation: Direct & Indirect Effects

Predator Pair	Indirect	Direct
Pan - Canis	(*b* = 18.59, S.E. = 9.08, 95% C.I.: [2.71; 38.47])	(*b* = 19.91, *t*(77) = 1.78, *p* = .08)
Pan - Crocuta	(*b* = 10.65, S.E. = 5.31, 95% C.I.: [2.15; 23.47])	(*b* = 23.38, *t*(77) = 2.61, *p* = .01)
Pan – Lycaon	(*b* = 12.36, S.E. = 6.85, 95% C.I.: [1.55; 28.89])	(*b* = 7.85, *t*(77) = .91, *p* = .36)
Lycaon - Canis	(*b* = 6.23, S.E. = 2.91, 95% C.I.: [1.49; 13.28])	(*b* = 12.06, *t*(77) = 1.61, *p* = .11)

If zero does not fall between the confidence intervals (C.I.) of the bootstrapping then it can be concluded that there is a significant mediation to report.

Prey Profiles - Hypothesis 5

This study also intended to investigate whether large, social predators vary in the proportional size of prey that they hunt when taking into account all known prey for each species. This gives an account of the true variation in the size of prey hunted among chimpanzees, wolves, African hunting dogs, hyenas and lions. The data highlight bias that may exist in the hunting success data. The hunting success data may be biased as it only considers those prey species for which success data has been collected; it does not consider the entire prey range (profile).

Data were collected from literature on the prey species that the predators eat and each prey-predator dyad was assigned a Predator:Prey ratio value. An ANOVA with predator species as the independent variable and Log10 ratio from the complete prey profiles as the dependent variable was used to test for an association between these variables. This showed a significant effect between a number of species ($F[4, 185] = 7.819$, $p = .001$, $\eta_p^2 = .147$). Between groups, pairwise comparisons revealed significant differences between the prey profiles of wolves and African hunting dogs, spotted hyena and chimpanzees, and, African hunting dogs and chimpanzees. (Table 3.4.).

Table 3.4. Mean Predator:Prey ratio per species and interspecies comparisons for the complete prey profiles of all predator species.

	Canis	*Crocuta*	*Lycaon*	*Pan*
Canis	--			
Crocuta	$p = .480$	--		
Lycaon	$p = .003$	$p = .661$	--	
Pan	$p = 1.00$	$p = .006$	$p < .001$	--
Panthera	$p = 1.00$	$p = 1.00$	$p = .070$	$p = .077$

Although differences between the means of the prey profiles were only found to vary for two predator pairs, both including chimpanzees, the range of relative prey size within the profiles varied between predators but the carnivorans exhibited greater diversity in relative prey size (Figure 3.3.). Figure 3.4. shows the contrast between the lower range of the chimpanzees prey profile and the higher of the other predators prey profiles, body mass data here were log transformed.

Figure 3.3. Range
predator species.

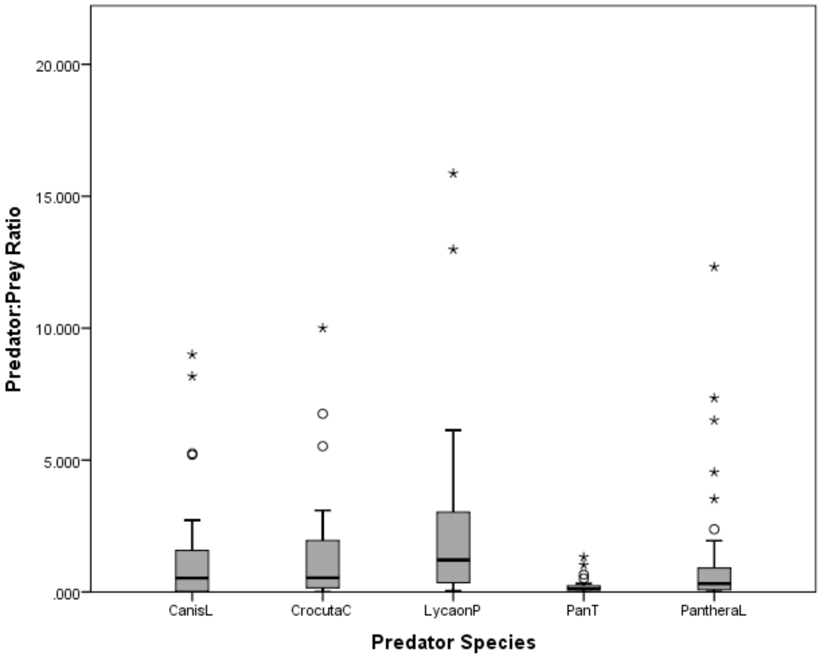
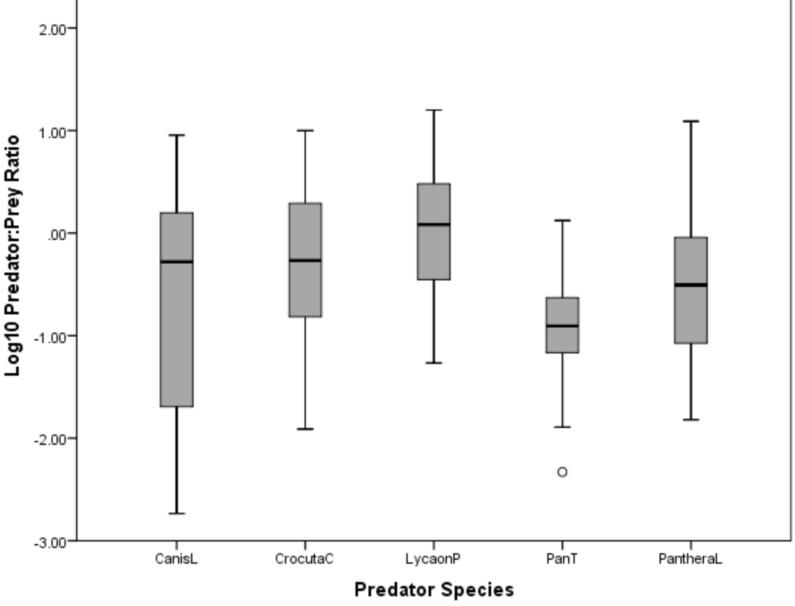


Figure 3.4. Log10 Ratio of complete prey profiles for predator species.



Discussion

This chapter investigated whether the higher success rate of chimpanzees compared to other large, social, mammalian predators is associated with the size of prey that they hunt. The results support the assertion that hunting success decreases as a function of increasing relative prey size across the large social mammalian predators tested (chimpanzees *Pan troglodytes*, wolves *Canis lupus*, African hunting dogs *Lycaon pictus*, spotted hyena *Crocuta crocuta* and lions *Panthera leo*). Both *relative prey size* (Predator:Prey ratio) and *predator species* were significantly associated with hunting success. Habitat type and prey preference were found to have no significant effect on the hunting success of the predators. Consequently the average success rate of hunting a particular prey species is not a good predictor of whether that prey species will be preferentially hunted or not. Hypothesis 2 is therefore unsupported as cover type and prey preference are not confounding factors.

Predator species was predicted to be a major influencing factor on hunting success. Pairwise comparisons revealed that wolves had a significantly lower hunting success rate than African hunting dogs and chimpanzees; chimpanzees had a significantly higher success rate than all other predators tested. Furthermore, when only considering prey species for which hunting success data were available, the size of the mammalian prey hunted by the predators also varied significantly among predator species as predicted in hypothesis 3. Further pairwise comparisons showed that most predator pairs tested with the exception of African hunting dogs and spotted hyena, and, chimpanzees and lions, significantly differed in the proportional size of prey that they hunted.

Relative Prey Size and Hunting Success.

Chimpanzees hunt small prey when compared to many other large predators; they also have a high hunting success rate (Mitani & Watts, 1999; Newton-Fisher, 2014; Owen-Smith & Mills, 2008). It was found that the higher hunting success exhibited by chimpanzees when compared to all large social carnivorans tested here is partially mediated and thus in part explained by their predation of smaller prey relative to their own body mass. Similarly it was found that the higher hunting success of African hunting dogs than wolves was partially mediated by their predation of smaller prey relative to their own body mass.

The results indicate that not only does the proportional size of prey hunted influence a predators ability to succeed in a hunting attempt, but also that the differences observed between the hunting successes of different predators, are partly explained through the predators selection of different sized prey. This supports earlier theoretical work suggesting that relative prey size affects the hunting success of predators (Wilson, 1975).

The results of this study are in agreement with the idea that predator hunting success is influenced by factors relating to prey (Funston et al., 2001). Prey size, a prey related factor, was found here to significantly influence the ability of a predator to succeed at hunting. Vegetation cover type (environment related factor) and prey preference (predator related factor) were not found to significantly impact on the hunting success of the predators. This result may be due to a lack of precision in the method of assigning cover types from site descriptions and lack of available data on prey preference. More detailed and accurate data on the vegetation cover, particularly relating to the vegetation cover types of individual hunts rather than study site may yield significant results as predicted by Funston et al (2001). Chimpanzees hunting at woodland/savannah sites have been found to be more successful solo hunters than at sites with continuous and lower canopy, and lions in areas of tall grass have are known to have a higher hunting success (Funston et al., 2001; Gilby et al., 2006) Similarly prey that are preferred or avoided may vary in their defensive capabilities, therefore avoided prey may be better at defending themselves or avoiding capture which may cause predators to be less successful at hunting them. If more data were available on this factor then it may be found to have a significant affect on hunting success (Funston et al., 2001).

Interspecific Variation in the Range of Relative Prey Size.

When considering all species (prey profile data) that the predators hunt the predators differed in the size of prey they hunted. There was a distinction in the mean relative size of prey (predator: prey ratio) between two carnivoran species, wolves and African hunting dogs. (Table 3.4 and Fig. 3.3/3.4). Chimpanzees differed significantly from hyena and African hunting dogs in the relative size of prey they hunted but not from wolves or lions partially supporting hypothesis 5. Although lions were predicted to have the greatest range in relative prey size as predicted in hypothesis 5, wolves rather than lions were found to have the greatest range in relative prey size using Log10 transformed Predator:Prey ratio data of all species recorded as hunted by each predator. African hunting dogs were found to have the greatest overlap in relative prey size rather than lions when considering the untransformed data, these findings do not support hypothesis 5.

Previously female lions have been found to have the largest range of prey size when compared to other sympatric large carnivores (Radloff & Du Toit, 2004). Radloff & Du Toit used actual (net) prey mass rather than relative (ratio) prey mass to test this, differing from this study. Due to the lions' large mass their relative prey size range is reduced when looking at Predator:Prey mass ratios and overtaken by smaller predators that hunt prey with a high net mass (Figure 3.3/3.4) The large mass of lions is also likely to cause the lack of significant difference between the relative size of prey lions and chimpanzees hunt. As lions have a large net mass, the size of their prey in relation to them will be lower than for sympatric predators that hunt the same prey species. Many prey species hunted by lions are close to or below their own body weight (see Appendix III) thus reducing their mean relative prey size closer to that of the chimpanzee, a predator that hunts prey smaller than itself.

Previous research looking at the prey profiles of sympatric large African carnivores found that the prey profiles of predators skew towards prey that is smaller than the predator. An exception to this was the African hunting dog (Radloff & Du Toit, 2004). The results presented here support prior findings that most large carnivore prey profiles skew towards prey smaller than themselves (Radloff & Du Toit, 2004). They also support previous findings that African hunting dogs hunt proportionally larger prey than other large carnivores (Figure 3.3; Woodroffe & Lindsey, 2007).

Comparisons in Carnivory

Very few studies have investigated chimpanzees hunting using comparative methodologies with carnivorans. Gilby & Connor (2010) compared the benefits and mechanisms of group hunting by chimpanzees and large social carnivores. They investigated whether chimpanzees' high levels of intelligence explained their group hunting behaviour. Gilby & Connor could find no major factor separating chimpanzees from other social predators through examination of the mechanisms and benefits of group hunting. They found little evidence that chimpanzees directly apply their advanced intelligence to the process of acquiring prey. In support of their findings this study showed that the high hunting success of chimpanzees is explained by their selection of small prey relative to themselves rather than their superior cognitive abilities. Relative prey size mediates the difference in hunting success between chimpanzees and large social carnivorans. The hunting success of all predators investigated here is controlled by the same mechanism, hunting success negatively relates to the relative size of prey hunted.

Chimpanzees were found to consistently hunt smaller prey than social carnivorans (except lions) when looking at both complete prey profiles and when considering the prey species that corresponding success data were available for. This shows that chimpanzees hunt relatively smaller prey than hyena and African hunting dogs but not wolves or lions (Table 3.4).

This study aimed to investigate whether chimpanzees are able to achieve high hunting success because they hunt prey that is small relative to them. The findings presented here support the assertion that chimpanzees are highly successful hunters because they hunt small prey in relation to their body mass. Funston et al. (2001) stated that three types of factor determine the hunting success a predator can achieve. These factors are predator related, prey related and environment related. The results of this study show that chimpanzee's high hunting success is partially determined by the prey related hunting success factor: relative prey size.

Conclusion

The ability for large, social living, predators to succeed in capturing prey is undoubtedly influenced by many factors at both a species, individual and hunting party level. Nutrition or fitness level, experience, age, and motivation amongst other factors will likely influence individual hunters. At a hunting party level, the number of hunters, the presence of certain catalyst individuals and the habitat in which a hunt takes place may well also influence the outcome of a hunt for predatory species. Although these factors and others such as intelligence and ability to cooperate may impact on the hunting success of chimpanzees, this study shows that their ability to be highly successful hunters is explained at least in part by a simple ecological pattern; hunting small prey relative to themselves allows predators to be highly successful. The results presented here demonstrate that the size of mammalian prey relative to the predator in is an important determining factor on the hunting success of large, predatory, social, mammals.

Chimpanzees primarily hunt arboreal primates such as the red colobus monkey; when compared to the ungulate prey most often hunted by large, social, carnivorans these animals are small. By hunting small prey, chimpanzees are able to be very successful in their hunting attempts, normally achieving success rates over 50%. The study showed that the higher hunting success that chimpanzees achieve when compared to large carnivorans: wolves, spotted hyena, and African hunting dogs is explained, in part, by them hunting prey of a smaller size relative to their own body mass.

Chimpanzees do not appear to have a unique intrinsic ability that allows them to be successful hunters but instead they are successful, in part, because they hunt small prey. The negative relationship between relative prey size and hunting success influences the hunting success of all large social carnivorans investigated in this study. This being true, there is only one key difference between the hunting behaviour of chimpanzees and large social carnivorans, they hunt small prey (<45% of the predator’s body mass.)

Chapter 4 – Discussion & Conclusions

This study aimed to investigate three key areas relating to hunting by chimpanzees: the extent of knowledge of chimpanzee hunting behaviour published in literature, relating to what, how and why chimpanzees hunt, whether relative prey size is an influencing factor on the hunting success of large predators that live, breed and hunt in groups, and if this relationship explains how chimpanzees are able to have a higher hunting success rate than large, social, carnivore species. In this chapter, the information in the previous chapters will be brought together and explained in conjunction.

The research presented in chapters 1, 2 and 3 provides information on chimpanzee hunting behaviour and how this compares with hunting by large, social, mammalian carnivorans, as well as insight into the most important factors that explain the higher hunting success achieved by chimpanzees, *Pan troglodytes,* when compared to a number of other large mammalian predators: wolves, *Canis lupus,* African hunting dogs, *Lycaon pictus,* spotted hyena, *Crocuta crocuta*, and lions, *Panthera leo.*

An overview of the findings.

Animal matter, both from invertebrates and vertebrates, comprises, on average, 4% of wild chimpanzees' diet and all populations that have been extensively studied hunt and consume mammals (Conklin-Brittain et al., 2001; Newton-

Fisher, 2014). Chimpanzees hunt nearly 40 species of mammal but primarily target arboreal primates, particularly the sympatric red colobus monkey, *Piliocolobus* sp., animals that are small relative to chimpanzees (18-34%) (Chapter 3). Male chimpanzees contribute greatest to the hunting effort, dominating hunting behaviour both in frequency and percentage of captures (Goodall, 1986; Stanford, 1998). Occasionally the hunts will be conducted by groups of chimpanzees, chasing the monkeys in the canopy. Groups of chimpanzees at Taï in West Africa have been reported as working together, cooperating or collaborating to fulfil different hunting roles and increase their likelihood of capture (Boesch, 1994b). Chimpanzees, as group and occasional cooperative hunters, as well as social animals, are similar to a number of large, social, mammalian carnivorans: wolves, African hunting dogs, hyenas and lions.

It is not yet agreed upon as to why chimpanzees hunt, but proposed explanations relating to social causes of the behaviour, such as the meat-for-sex hypothesis, have been dismissed. With these explanations no longer viable, the remaining hypotheses relate to nutritional causality, therefore the answer to the still undecided question "Why do chimpanzees hunt?" is likely to rest in this area. Whatever the motivation behind chimpanzees hunting it is certain that they are highly successful hunters.

Hunting requires predators to locate, pursue and subdue their prey. Different predators must expend different amount effort of each of these activities based on their hunting behaviour and foraging technique. These three hunting components have associated costs. Large predators normally have foraging tactics with greater pursuit and subduing costs than small predators, whose costs are often greater in the location of prey. Each foraging behaviour can be carried out with varying success, the term capture success or hunting success is generally applied to the pursuit and capture components of predation (Griffiths, 1980). The ability of large predators to succeed in a hunting attempt is influenced by predator, prey and environment related factors (Funston et al., 2001). In chapter 3 a comparative approach was used to determine the effect of several predator-, prey- and environment-related factors on the hunting success of large, social, mammalian terrestrial carnivores. Predator-related factors include individual differences such as body condition, group size, age, and sex. Prey-related factors include: prey species and size, prey group size, and prey age class etc. Environment-related factors include; vegetation cover, visibility, topography etc. Differences in the factor types above can cause considerable variation in hunting success rates (Funston et al., 2001; Kunkel & Pletscher, 2001; Radloff & Du Toit, 2004).

Prey selection and hunting success.

Prey selection (prey related factor) relates strongly to both hunting success and the benefit of a hunt. Relative prey size is a controlling factor of hunting success. The first objective of this study, as seen in the results presented in chapter 3, was to show that increasing relative prey size is associated with a reduction in hunting success of large, social, mammalian predators, This was shown to be correct. Likewise, the third objective of this study was shown to be correct as this relationship mediates the differences in the hunting success among them.

Different prey animals have different benefits and costs associated with them: these costs are based on factors that increase or decrease the cost of pursuit and subduing and benefits based on nutritional value. Prey size is a major contributor to the caloric value and therefore benefit of different prey, with prey weight almost directly associated with this (Griffiths, 1975). Furthermore relative prey size influences the cost of subduing a prey animal, a number of predators hunt in groups, aiding their ability to subdue large prey (Creel & Creel, 1995; Packer & Ruttan, 1988). Predators must balance the costs against the benefits (cost:benefit ratio) whilst also accounting for risks of failure and meeting their energetic needs when selecting their prey; prey size is an important factor in this selection (Dugatkin, 1997; Gilby & Wrangham, 2007; Griffiths, 1980).

Prey size differences among large social mammalian predators.

Net prey size increases with the size of the predator for most carnivoran predators. Large carnivorans (>21.5kg) are known to primarily prey upon animals 45% of their own body size or greater. This relationship is limited by the high absolute energetic requirements of larger animals and that 21.5kg (predator mass) is the mass at which carnivoran predators are predicted to shift from hunting small to large prey (Carbone et al., 1999; Gittleman, 1985). Wolves *Canis lupus,* African hunting dogs *Lycaon pictus,* spotted hyena *Crocuta crocuta*, and lions *Panthera leo* are large, social, carnivorans that live, hunt and breed in groups. By hunting in groups these predators are able to increase their ability to subdue prey often larger than the predators themselves (Hayward, 2006; Macdonald, 1983). Unlike large social carnivorans, chimpanzees only hunt prey that are small relative to themselves such as red colobus monkeys. Chimpanzees weigh, on average, 32kg whereas their preferential prey only weigh an average of 5 – 11kg, far smaller than the predicted ≥45% of the predators mass for carnivorans (Butyinski et al. 2013; Carbone et al., 1999).

Although it was predicted that chimpanzees hunt prey of smaller relative size than the large social carnivores tested, they were found to have no significant difference in the relative size of prey hunted when compared to lions (Chapter 3, Table 3.2; Figure 3.3 – 3.4). Variation was found between the relative sizes of prey hunted by chimpanzees and the other carnivorans; wolves, African hunting dogs and hyenas. Chimpanzees hunted smaller prey. Wolves also significantly differed from African hunting dogs in the size of prey that they hunted, hunting larger prey. Chimpanzees were found to have no significant difference in relative prey size compared to wolves when considering only prey profile data, although this was not used in the analysis alongside the hunting success data (Table 3.4; Figure 3.3 – 3.4). The similarity in average prey size from the prey profile data is likely to be caused by the methodology and analysis used. For this dataset, each prey species was considered a data point, this means that small prey relative to the predator are likely to be over represented when compared to large prey relative to the predator as large predators are predicted to hunt a wider variety of small prey (Wilson, 1975).

Hunting relatively small prey helps chimpanzees to hunt with unprecedented success for a large social predator. The high success predators can achieve when hunting small prey relative to themselves may, in part, explain how chimpanzees are able to utilise small prey as a supplementary food source to their frugivorous diet. By hunting small prey with a low failure risk, low subduing costs and possibly low pursuit costs, it may benefit omnivores and facultative carnivores such as chimpanzees to hunt prey when they encounter them (Chapter 3; Griffiths, 1980). Alternatively, provided the small prey are in high density and thus causing a high encounter rate, it will likely benefit predators to actively search for and hunt them.

Alternative Foraging Strategies

Although not common, some large social carnivorans have been found to regularly hunt (relatively) small prey animals in some circumstances. African hunting dogs are able to utilise prey small relative to them, provided that it is highly abundant. In areas devoid of large prey, packs of African hunting dogs have been observed to hunt dik-dik (*Madoqua kirkii*) extensively. Dik-dik are small ungulates ≤15% of the dog's body mass and have been found to compose 70% of the dogs prey in parts of northern Kenya. An explanation given for this behaviour was that the dogs are able to use this prey resource, regardless of the animals small size and thus small caloric benefit, because the prey were very abundant in the area and thus encountered and hunted frequently (Woodroffe & Lindsey, 2007). The findings of chapter 3, combined with the findings of

Woodroffe & Lindsey, show that this might also be explained in part, by the high success the dogs would be expected to achieve whilst hunting these small prey compared to larger prey, quite possibly reducing the associated failure risk. Similarly the costs of hunting (pursuit costs/subduing costs) increase with prey size and so hunting smaller prey will likely incur less costs for the predator (Griffiths, 1975).

Small prey may have a smaller absolute energy value (energy value = energy content – cost of capture/handling) than large prey but are lower risk (in terms of failure) (Chapter 3; Griffiths, 1975). It can therefore be asserted that if small prey animals are highly abundant then it may be preferential for carnivorans to subsist on such a resource due to the high hunting success and reduced hunting cost they would achieve when compared to hunting of larger prey in relation to them. This should be possible provided they achieve a better cost to benefit ratio whilst continuing to meet the energetic needs of the predator (Chapter 3; Griffiths, 1975; Woodroffe & Lindsey, 2007). Similarly, chimpanzees as facultative carnivores, may be able to utilise relatively small prey when encountered as an alternative/supplementary resource to their frugivorous diet as there is a low risk of failure, consuming meat to acquire protein, fat, calories, and micronutrients (Gilby et al., 2006; Hamilton & Busse, 1978; Tennie et al., 2009). The results from chapter 3 show that when considering the cost: benefit ratio of different prey and how this relates to prey selection, hunting success/ risk of failure and the association with prey size as demonstrated in chapter 3 should also be considered alongside other factors.

It has been proposed that the ability to utilise small prey was a factor that allowed our early human ancestors to survive periods where large prey were unavailable or scarce. Similarly, the inability of some members of our lineage, namely neanderthals, to adapt in this way may have limited their survival in similar times. Fa et al. (2013) suggest that early humans were able to utilse a relatively small, yet superabundant mammalian prey, the European rabbit *Orcytolagus cuniculus* after a severe reduction in the megafaunal prey in the upper palaeolithic. In contrast little evidence of utilisation of the these prey have been seen from the Mousterian, a time dominated by *Homo neanderthalensis.* They posit that, therefore, neanderthals were large prey specialists and unable to adapt to utilise a prey source comprised of relatively small animals.

The idea that early *Homo sapiens* could utilise this resource would also be supported by the finding of Chapter 3 alongside those of Woodroffe & Lindsey, (2007). A small but superabundant prey (rabbits) could have allowed early humans, as large social mammalian predators, to obtain mamalian prey with a high rate of success and low subduing costs. In an environment where encounter rates with large mammalian prey would be low, a superabundant resource with a good cost:benefit ratio could become vastly important if it was available in such an extent as to meet the absolute energetic/nutrient needs of the human hunters. It can be suggested that, provided this was the case, rabbits could have provided an important resource to humans in a similar manner to extant predators such as the African hunting dog and possibly the chimpanzee.

Implications

The findings presented in this study will be important for future studies looking at understanding chimpanzee hunting behaviour. Chimpanzees do not rely on meat as their only source of calories; it is likely that meat is consumed to provide both calories, and/ or micronutrients (Boesch, 1994b; Hamilton & Busse, 1978; Mitani & Watts, 2001; Tennie et al., 2009). Through the high success they can achieve whilst hunting small prey relative to themselves they may be able to heavily utilise this resource provided encounter rate is high, similarly to African hunting dogs preferentially hunting dik-dik over larger prey species. Furthermore, the utilisation of small prey by omnivores and facultative carnivores may be a response to opportunistic encounters with prey animals, whereby when small prey are encountered it is beneficial to hunt them provided the costs of pursuit and capture are sufficiently low. It can be suggested that this can occur as the chance of success is likely to be high (risk of failure low) compared to hunting large prey when encountered that may also have higher associated pursuit and subduing costs (Funston et al., 2001; M. Hayward, 2006). Future studies looking at omnivore hunting should investigate whether relatively small prey or large prey is preferred by large omnivorous species and whether this is affected by hunting success, particularly omnivores from the order Carnivora such as Ursidae as these were noted as common exception to the findings of Carbone et al. (1999).

It will be necessary for future research to look into whether a negative relationship continues to exist between relative prey size and hunting success for non-social (solitary) mammalian predators. The scope of this study was limited to large social mammalian predators and did not investigate hunting success or relative prey size in solitary predators. Furthermore it will be of interest to determine whether this continues to apply for small carnivores (<21.5kg) that hunt large prey such as the dhole *Cuon alpinus* and the Bush dog *Speothos venaticus* (Carbone et al., 1999).

Areas for Future Research into Chimpanzee Hunting

This study highlights the importance of comparative studies between chimpanzees and other mammalian species, particularly large social carnivorans when investigating hunting behaviour. Rarely are comparative interspecific methodologies used in wild chimpanzees research, with studies often opting to focus more on aspects of chimpanzee cognition, sociality or ecology. Similarly to the findings of Gilby & Connor (2010) this study could find no differences in the benefits or mechanisms of chimpanzee and large social carnivoran hunting behaviour and thus validates the usefulness of comparative methodologies in this context. Future studies may benefit from taking a similar approach where appropriate, possibly in the context of carnivory and its nutritional benefits.

The nutritional benefit of chimpanzee carnivory is not yet known; this area requires serious future research effort and is key to understanding chimpanzee hunting patterns, including success rates. It is important to determine which nutrients chimpanzees gain from meat if we are to understand why they hunt.

Understanding which parts of mammal carcasses are most coveted will be a way of learning more on this topic. Chimpanzees may consume the most nutritionally important components of prey animals first and may also be less likely to share these with group members. There is evidence that sharing of different body parts does not occur with equal propensity, the head of infants being rarely shared and often consumed first (Boesch & Boesch, 1989). The head contains high concentrations of fat (the brain) and it can be suggested that chimpanzees are preferentially consuming this body part to access this resource. Fat is essential for cognitive development and helps in the development of complex brains (Aiello & Wheeler, 2014). If fat is the targeted nutritional component if the prey hunted, then this may explain why infant and juvenile animals are targeted preferentially at some sites. The brain contributes to approximately 10% of neonate primates body mass, a considerably higher proportion than for adult primates (Matsuzawa, 2007). Access to this concentrated fat source from juvenile primates is likely to be easier due to their skulls being more fragile and the cost of subduing them being lower. The answer to why chimpanzees hunt may well relate to the improved access hunter will get to this fat source. Regardless of whether chimpanzee hunting behaviour is eventually explained by social or nutritional hypothesis it is highly likely that meat is a high value and important resource for chimpanzees and is nutritionally valuable in some aspect.

Little to no research has yet focussed on the hunting behaviour of solitary female chimpanzees beside that conducted at Fongoli, Senegal on bush baby predation. Understanding the carnivorous behaviour of female chimpanzees will increase the ability of future research to determine the proximal causes and benefits of the behaviour through intersex comparisons, similar to interspecific comparisons that we have shown to be valuable. It has been stated that females are more opportunistic in their hunting behaviour, often capturing more ephemeral animals that occur less predictably in the environment such as young bushbuck or bushpigs, rather than hunting arboreal primates (Stanford, 1998). It would be interesting to determine whether female chimpanzees have less mammalian prey in their diet than males or whether they are utilising alternative resources of similar nutritional benefit. If female chimpanzees are found to consume approximately equal amounts of animal matter as males then it highlights the possible disparity between the proximate causes of carnivory by chimpanzees and the causes of group/ cooperative hunting.

Summary

The ability for large, social living, predators to succeed in capturing prey is undoubtedly influenced by many factors at both an individual and hunting party level. Nutrition or fitness level, experience, age, and motivation amongst other factors will likely influence individual hunters. At a hunting party level the number of hunters, the presence of certain catalyst individuals and the habitat in which a hunt takes place may well also influence the outcome of a hunt for predatory species. Although these factors and others such as intelligence and ability to cooperate may affect the hunting success of chimpanzees, this study shows that their ability to be highly successful hunters is explained at least in part by a simple ecological pattern, that increasing relative prey size is associated with decreasing hunting success. The results presented here demonstrate that the size of mammalian prey relative to the predator in is an important determining factor on the hunting success of large, predatory, social, mammals.

There are many aspects of chimpanzee hunting behaviour that are yet to be understood. For research to move forward in a meaningful and productive manner focus must be given to two key areas, the nutritional benefit that chimpanzees gain from mammalian prey and, the prevalence of hunting and meat consumption by female chimpanzees whether solitarily, using tools or as part of a group. Here it has been shown that interspecific comparison studies can produce meaningful results in the context of chimpanzee hunting behaviour, future research into this area may benefit from similar interspecies or intersex comparative methodologies.

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Appendix I - Review Methodology

To select suitable literature for the review and analysis a standardised methodology was used. This methodology ensured that the majority of suitable papers and books were used in the review and the process of data acquisition was as exhaustive as possible.

Literature Sources

Literature searches were made through a number of online search engines and databases as well as through the Bournemouth University library catalogue.

Table A1.1. Literature sources used.

Catalogues	Search Engines	Databases	Social Media
BU Library	Google Scholar	JSTOR	ResearchGate
-	Web of Science	Wiley Online Library	-
-	-	Elsevier	-
-	-	Springer	-

Standardised search terms were used when locating literature from the above sources. This was done to provide a near exhaustible reference list of relevant literature and ensure replicability of the review process.

Search Terms

1) “(*species) prey selection”.
2) “(*species) prey diversity”.
3) “(*species) diet”.
4) “(*species) predation patterns”.
5) “(*species) hunting behaviour”.
6) “(*species) prey species”.
7) “(*species) feeding habits”.
8) “(*species) foraging ecology”.

1) “(*species) hunting success”.
2) “(*species) hunting rate”.
3) “(*species) capture success”.
4) “(*species) capture rate”.
5) “(*species) kill rate”.
6) “(*species) predation success”.
7) “(*species) predation rate”.
8) “(*species) predation patterns”.

* All common names and scientific names of the predator species researched were used.

Papers from references and citations

When I reviewed a paper found using one of the above search terms care was taken to note any citations likely to lead to further literature sources of relevance. If a reference appeared useful it was the reviewed and included if contained appropriate data.

Paper Inclusion and Selection

A strict inclusion/ exclusion policy was implemented in the literature search. Initial inclusion began with the title; papers or books that included the common species name or scientific name and a key phrase (e.g. prey selection, foraging habits) were read through for relevant data. Secondly if no key phrases were included in the title but key words or phrases (e.g. hunting, predator, prey, hunting patterns) were present in the abstract then the paper/ book was read for relevant data or information.

The final inclusion came through citation in literature that had been selected from the above criteria. If a paper or book was cited in a way it implied it contained relevant data or specific information of interest it was acquired and read. Although this method was more subjective, ‘point inclusion’ was necessary to obtain data from older sources that may not be online (e.g. Schaller, 1972).

Papers that did not meet the above criteria or were not found through ‘point inclusion’ were not included in the review. Although some papers may have been missed and this review is non-exhaustive, using a semi-systematic methodology improves the replicability and thus scientific merit of the review process.

Table A.1.2. The key phrases and words for use in the inclusion/exclusion method.

Key Phrase	Key Word
Prey Selection	Prey
Prey Preference	Foraging
Prey Diversity	Hunting
Prey Species	Hunt
Predation Patterns	Predation
Predatory Behaviour	Feeding
Hunting Behaviour	Diet
Foraging Behaviour	Food
Foraging Ecology	Capture
Foraging Habits	Kill
Feeding Ecology	Eat
Feeding Habits	-
Dietary Preference	-

Appendix II -IUCN Habitat Classification Scheme

Using the descriptors in the literature (shown below) data were allocated an IUCN habitat category taken from the IUCN Habitat Classification Scheme (2012).

These categories were the assigned to a density rating based on the description given in IUCN (2012).

1 Forest
- 1.1 Boreal Forest
- 1.2 Subarctic Forest
- 1.3 Subantarctic Forest
- 1.4 Temperate Forest
- 1.5 Subtropical/Tropical Dry Forest
- 1.6 Subtropical/Tropical Moist Lowland Forest
- 1.7 Subtropical/Tropical Mangrove Forest Vegetation Above High Tide Level
- 1.8 Subtropical/Tropical Swamp Forest
- 1.9 Subtropical/Tropical Moist Montane Forest

2 Savanna
- 2.1 Dry Savanna
- 2.2 Moist Savana

3 Shrubland
- 3.1 Subarctic Shrubland
- 3.2 Subantarctic Shrubland
- 3.3 Boreal Shrubland
- 3.4 Temperate Shrubland
- 3.5 Subtropical/Tropical Dry Shrubland
- 3.6 Subtropical/Tropical Moist Shrubland
- 3.7 Subtropical/Tropical High Altitude Shrubland
- 3.8 Mediterranean-type Shrubby Vegetation

4 Grassland
- 4.1 Tundra
- 4.2 Subarctic Grassland
- 4.3 Subantarctic Grassland
- 4.4 Temperate Grassland
- 4.5 Subtropical/Tropical Dry Lowland Grassland
- 4.6 Subtropical/Tropical Seasonally Wet/Flooded Lowland

Grassland
4.7 Subtropical/Tropical High Altitude Grassland

5 Wetlands (inland)
- 5.1 Permanent Rivers, Streams, Creeks [includes waterfalls]
- 5.2 Seasonal/Intermittent/Irregular Rivers, Streams, Creeks
- 5.3 Shrub Dominated Wetlands
- 5.4 Bogs, Marshes, Swamps, Fens, Peatlands [generally over 8 ha]
- 5.5 Permanent Freshwater Lakes [over 8 ha]
- 5.6 Seasonal/Intermittent Freshwater Lakes [over 8 ha]
- 5.7 Permanent Freshwater Marshes/Pools [under 8 ha]
- 5.8 Seasonal/Intermittent Freshwater Marshes/Pools [under 8 ha]
- 5.9 Freshwater Springs and Oases
- 5.10 Tundra Wetlands [includes pools and temporary waters from snowmelt]
- 5.11 Alpine Wetlands [includes temporary waters from snowmelt]
- 5.12 Geothermal Wetlands
- 5.13 Permanent Inland Deltas
- 5.14 Permanent Saline, Brackish or Alkaline Lakes
- 5.15 Seasonal/Intermittent Saline, Brackish or Alkaline Lakes and Flats
- 5.16 Permanent Saline, Brackish or Alkaline Marshes/Pools
- 5.17 Seasonal/Intermittent Saline, Brackish or Alkaline Marshes/Pools
- 5.18 Karst and Other Subterranean Inland Aquatic Systems

6 Rocky Areas [e.g. inland cliffs, mountain peaks]

7 Caves and Subterranean Habitats (non-aquatic)
- 7.1 Caves
- 7.2 Other Subterranean Habitats

8 Desert
- 8.1 Hot
- 8.2 Temperate
- 8.3 Cold

Habitat Classification Scheme – Designations used:

1.1. Boreal Forest
1.6. Subtropical/Tropical Moist Lowland Forest

2.1. Dry Savannah
3.3. Boreal Shrubland
3.5. Subtropical/ Tropical dry shrubland
4.5. Subtropical/ Tropical dry lowland grassland
4.6. Subtropical/ Tropical seasonally wet/ flooded lowland grassland

Habitat Density Categorisation:

Dense:
1.1
1.6

Semi-Open:
2.1
3.3
3.5

Open:
4.5
4.6

Mixed:
More than one of the above in different catagories. e.g. 1.1./3.3.

Habitat types:

Chimpanzee

Moist tropical forest – (1.6)
Boesch, C., 1994. Chimpanzees-red colobus monkeys: a predator-prey system. *Animal Behaviour*, 47, pp.1135 – 1148.
Miombo woodland – (2.1.)
Stanford, C.B., 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*, London: Harvard University Press.
Moist evergreen forest – (1.6)
Mitani, J. & Watts, D., 1999. Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, 109(4), pp.439–454.

Wolf

Boreal Forest N.Am– (1.1)
NPCA Center for Park Research, 2007. *National Parks of the Great Lakes*. Fort Collins, CO.
Boreal Forest/ Mixed Hardwood Forest – (1.1)

Kolenosky, G., 1972. Wolf Predation on Wintering Deer in East-Central Ontario. *The Journal of Wildlife Management*, 36(2), pp.357–369.

Mixed Sagebrush/ Boreal Forest/ High alpine – (1.1/3.3)

National Park Service, 2009. *Yellowstone BioBlitz 2009 Habitat Types*. U.S. Department of the Interior: Washington.

Boreal Forest / Alpine Scan – (1.1)

Sand, H. et al., 2006. Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, 72(4), pp.781–789.

Hyena

Open Grassland – (4.6)

Holekamp, K.E. et al., 1997. Hunting rates and hunting success in the spotted hyena (Crocuta crocuta). *Journal of The Zoological Society of London*, 242, pp.1–15.

Riverine shrub and grass plains <5%/ Dune habitat, tall grass and scattered shrub, Kalahari - (3.5)

Mills, M.G.., 1990. *Kalahari hyaenas: comparative behavioural ecology of two species* 1st ed., Caldwell: The Blackburn Press.

Lions

Semi-Arid Plains – (4.5)

Stander, P., 1992. Foraging dynamics of lions in a semi-arid environment. Canadian Journal of Zoology, 70, pp.8 – 21.

Grassland Plains – (4.6)

Schaller, G.B., 1972. *The Serengeti Lion*. University of Chicago Press. Chicago.

Grassland Plains – (4.6)

Stander, P. & Albon, S., 1993. Hunting success of lions in a semi-arid environment. *Symposia of the Zoological Society of London*, (65), pp.127–143.

Dry Riverine Beds/ Bushveld/ Duneveld – (3.5.)

Eloff, F.C., 1984. Food Ecology of the Kalahari Lion. Koedoe, pp.249–258./

Van Rooyen, M.W., Van Rooyen, N. & Van Den Berg, H.M., 2008. Landscapes in the Kalahari Gemsbok National Park, South Africa. *Koedoe*, 50(1), pp.99–112.

Mixed Bushveld – (3.5.)

Power, R.J., 2002. Prey selection of lions Panthera leo in a small , enclosed reserve. *Koedoe*, 45(2), pp.67–75.

Hunting dogs

Miombo/ Chipya Woodland – (2.1.)

Creel, S. & Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. *Animal Behaviour*, 50(5), pp.1325–1339.

Zululand Thornveld (tropical forest) + Lowveld (tropical bush and savannah – (3.5.)

Krüger, S., Lawes, M. & Maddock, A., 1999. Diet choice and capture success of wild dog (Lycaon pictus) in Hluhluwe-Umfolozi Park, South Africa. *Journal of Zoology*, 248, pp.243–551.

Grassland, Acacia Bushland – (2.1)

Fuller, T. & Kat, P., 1993. Hunting Success of African Wild Dogs in Southwestern Kenya. *Journal of Mammalogy*, 74(2), pp.464–467.

Grassland Plains – (4.6.)

Schaller, G.B., 1972. *The Serengeti Lion: A study of predator: prey relations.* University of Chicago Press. Chicago.

Grassland Plains + Acacia Woodlands – (2.1)

Frame, L. et al., 1979. Social Organization of African Wild Dogs (Lycaon pictus) on the Sernegeti Plains, Tanzania 1967 - 1978). *ZEITSCHRIFT FUR TIERZUCHTUNG UND ZUCHTUNGSBIOLOGIE*, 50, pp.225 – 249.

Appendix III - Mammalian prey profiles:

Chimpanzee

Table A3.1. Chimpanzee *Pan troglodytes* mammalian prey profile.

Chimpanzee *Pan troglodytes* Prey Profile

Prey Species	Preference (Preferred, Not Preferred, Unknown)	3/4 Mean Female Body Weight	Ratio
Procolobus badius tephrosceles	P	5.9	0.18
Procolobus rufomitratus thephrosceles	U	4.4	0.14
Procolobus pennantii	P	7.5	0.23
Procolobus verus	U	3.2	0.10
Colobus guereza	NP	6.9	0.21
Colobus polykomos	U	6.2	0.19
Colobus satanus	U	6.2	0.19
Cercopithecus ascanius schmidti	NP	2.1	0.07
Chlorocebus aethiops centralis	U	2.1	0.07
Cercopithecus mitis	NP	2.9	0.09
Allochrocebus L'Hoestii	U	2.7	0.09
Cercopithecus diana	U	2.9	0.09
Cercopithecus mona	U	2.5	0.08
Cercopithecus petaurista	U	2.2	0.07
Cercopithecus pogonias	U	2.1	0.07
Cercopithecus cambelli	U	2.0	0.06
Lophocebus albigena	NP	4.8	0.15
Cercocebus atys	U	4.7	0.15
Chlorocebus sabaeus	U	3.3	0.10
Papio cynocephalus	U	10.2	0.32
Papio anubis	NP	9.2	0.29
Otolemur crassicaudatlls crassicalldatus	U	0.6	0.02
Galago senegalensis	U	0.2	0.00
Perodictus potto	U	0.8	0.03
Cephalophus monticola	U	4.0	0.12
Cephalophus natelensis	U	8.9	0.28
Cephalophus callipyga	U	16.4	0.51
Cephalophus rufilatus	U	7.5	0.23
Tragelophus scriptus	U	21.0	0.66
Nesotragus moschatus	U	4.1	0.13
Potamocherus porcus	U	32.6	1.02
Phacochoerus aethiopicusi	U	42.4	1.32
Ichneumia albicauda	U	3.1	0.10
Civettictis civetta	U	8.7	0.27
Heterohyrax brucei	U	2.2	0.07
Rhynchocyon sp.	U	0.4	0.01
Protoxerus stangeri	U	0.5	0.02

Data from nine studies: Basabose, 2002; Gaspersic & Pruetz, 2004; Newton-Fisher, 2007; Nishida, Uehara, & Nyundo, 1979; Nishida & Uehara, 1983; Uehara, 1997; Watts & Mitani, 2002; Yamagiwa & Basabose, 2006.

Grey Wolf

Table A3.2. Grey Wolf, *Canis lupus* mammalian prey profile.

Wolf *Canis lupus* prey profile

Prey Species	Preference (Preferred, Not Preferred, Unknown)	3/4 Mean Female Body Weight	Ratio
Alces alces	P	450.0	9.00
Bison bison	U	408.8	8.18
Ovibus moschatus	U	262.5	5.25
Cervus canadensis	P	260.0	5.20
Rangifer tarandus	P	136.1	2.72
Sus scrofa	NP	93.8	1.88
Odocoileus hemionus	U	90.0	1.80
Ovis dalli	U	78.8	1.58
Odocoileus virginianus	U	57.8	1.16
Ovis canadensis	U	51.0	1.02
Odocoileus hemionus columbianus	U	48.5	0.97
Oreamnos americanus	U	42.8	0.86
Cervus nippon	U	36.0	0.72
Dama dama	U	31.1	0.62
Ovis aries	U	30.0	0.60
Antilope cervicapra	U	26.3	0.53
Rupicapra rupicapra	U	24.8	0.50
Castor fiber	U	15.4	0.31
Castor canadensis	U	15.4	0.31
Capreolus capreolus	P	15.0	0.30
Lepus timidus	U	2.3	0.05
Lepus americanus	U	2.3	0.05
Lepus arcticus	U	2.3	0.05
Sylvilagus nuttalli	U	1.0	0.02
Martes americana	U	0.8	0.02
Tamiasciurus hudsonicus	U	0.2	0.00
Mustela frenata	U	0.1	0.00
Thomomys talpoides	U	0.1	0.00
Ochotoma princeps	U	0.1	0.00
Cervus elaphus	P	90.0	1.80
Tamias amoenas	U	0.4	0.01
Spermophilus columbianus	U	0.4	0.01
Peromyscus maniculatus	U	0.2	0.00

Data from seven studies: Arjo, Pletscher, & Ream, 2002; Barja, 2009; Holleman & Stephenson, 1981; Jedrzejewski et al., 2012; Kunkel, Ruth, Pletscher, & Hornocker, 1999; Mech, 1974; Peterson & Ciucci, 2003.

Spotted Hyena

Table A3.3. Spotted Hyena *Crocuta crocuta* mammalian prey profile

Hyena *Crocuta crocuta* prey profile

Prey Species	Preference (Preferred, Not Preferred, Unknown)	3/4 Mean Female Body Weight	Ratio
Oryx gazella	P	151.9	2.49
Connochaetes taurinus	U	150.0	2.45
Taurotragus oryx	U	337.5	5.52
Antidorcas marsupialis	U	23.6	0.39
Alcelaphus buselaphus	P	112.9	1.85
Struthio camelus	U	75.0	1.23
Tragelaphus strepsiceros	U	125.6	2.06
Raphicerus campestris	U	8.6	0.14
Lepus sp.	U	2.3	0.04
Pedetes capensis	U	2.6	0.04
Hystrix sp.	U	13.9	0.23
Mouse	U	0.8	0.01
Equus quagga	U	159.4	2.61
Kobus kob	P	51.4	0.84
Kobus ellipsiprymus	U	135.0	2.21
Hippotragus equinus	U	188.6	3.09
Ourebia ourebia	U	12.8	0.21
Sylvicapra grimmia	U	14.1	0.23
Redunca sp.	U	42.8	0.70
Damaliscus lunatus	U	84.4	1.38
Gazella rufifrons	U	15.0	0.25
Aepyceros melampus	U	37.5	0.61
Giraffa camelopardalis	U	611.3	10.00
Gazella granti	U	39.4	0.64
Madoqua sp.	U	3.6	0.06
Phacochoerus africanus	P	45.0	0.74
Papio anubis	U	15.4	0.25
Syncerus caffer	P	412.5	6.75
Cephalophus rufilatus	U	7.5	0.12
Genetta genetta	U	1.3	0.02
Tragelaphus scriptus	U	31.5	0.52
Civectittus civetta	U	10.1	0.17
Papio papio	U	11.6	0.19
Erythrocebus patas	U	7.9	0.13
Panthera pardus	U	33.0	0.54
Tragelaphus angasii	U	57.0	0.93
Oreotragus oreotragus	U	6.8	0.11
Raphicerus sharpei	U	8.6	0.14
Hippotragus niger	U	157.5	2.58

Data from six studies: Breuer, 2005; Hayward, 2006; Holekamp, Smale, Berg, & Cooper, 1997; Mills, 1990; Silvestre, Novelli, & Bogliani, 2000; Trinkel, 2009.

African hunting dog

Table A3.4. African hunting dog *Lycaon pictus* mammalian prey profile.

Hunting dog *Lycaon pictus* prey profile

Prey Species	Preference (Preferred, Not Preferred, Unknown)	3/4 Mean Female Body Weight	Ratio
Damaliscus dorcus phillipsi	U	54.0	2.08
Connochaetes taurinus	NP	150.0	5.77
Syncerus caffer	NP	412.5	15.87
Equus burchellii	NP	159.4	6.13
Tragelaphus scriptus	P	31.5	1.21
Taurotragus oryx	NP	337.5	12.98
Gazella granti	P	39.4	1.51
Cephalophus rufilatus	U	7.5	0.29
Sylvicapra grimmia	U	14.1	0.54
Alcelaphus buselaphus	NP	112.9	4.34
Aepyceras melampus	P	37.5	1.44
Oreotragus oreotragus	NP	13.0	0.50
Tragelaphus strepsiceros	P	125.6	4.83
Redunca fulvorufula	NP	20.3	0.78
Tragelaphus angasii	U	57.0	2.19
Ourebia ourebia	U	12.8	0.49
Hippotragus niger	U	157.5	6.06
Lepus saxatilis	U	2.3	0.09
Raphicerus sharpei	U	8.6	0.33
Redunca arundinum	U	50.6	1.95
Antidorcas marsupialis	NP	23.6	0.91
Raphicerus campestris	U	8.6	0.33
Gazella rufifrons	P	15.0	0.58
Damaliscus lunatus	NP	84.4	3.25
Phacochoerus africanus	U	45.0	1.73
Kobus ellipsiprymus	U	135.0	5.19
Lepus capensis	U	2.3	0.09
Redunca arundinum	U	42.8	1.64
Potamocherus porcus	U	73.1	2.81
Mungos mungos	U	1.4	0.05
Ichneumia albicauda	U	2.7	0.10
Papio cyanocephalus	U	9.8	0.38
Madoqua kirkii	U	3.6	0.14
Procavia capensis	U	5.5	0.21
Hystrix cristata	U	14.6	0.56

Data from nine studies: Creel & Creel, 1995; Estes & Goddard, 1967; Hayward & O'Brien, 2006; Krüger, Lawes, & Maddock, 1999; Owen-Smith & Mills, 2008; Pole, Gordon, Gorman, & MacAskill, 2004; Radloff & Du Toit, 2004; Woodroffe & Lindsey, 2007.

Lion

Table A3.5. Lion *Panthera leo* mammalian prey profile.

Lion *Panthera leo* Prey Profile

Prey Species	Preference (Preferred, Not Preferred, Unknown)	3/4 Mean Female Body Weight	Ratio
Oryx gazella	P	151.9	0.88
Connochaetes taurinus	P	150.0	0.86
Taurotragus oryx	NP	337.5	1.95
Antidorcas marsupialis	NP	23.6	0.14
Alcelaphus buselaphus	NP	112.9	0.65
Tragelaphus strepsiceros	NP	125.6	0.72
Raphicerus campestris	NP	8.6	0.05
Equus quagga	P	159.4	0.92
Kobus kob	NP	51.4	0.30
Kobus ellipsiprymus	NP	135.0	0.78
Hippotragus equinus	NP	188.6	1.09
Ourebia ourebia	NP	12.8	0.07
Sylvicapra grimmia	U	14.1	0.08
Redunca sp.	NP	42.8	0.25
Damaliscus lunatus	NP	84.4	0.49
Gazella rufifrons	NP	15.0	0.09
Aepyceros melampus	NP	37.5	0.22
Giraffa camelopardalis	P	611.3	3.52
Gazella granti	NP	39.4	0.23
Phacochoerus africanus	P	45.0	0.26
Syncerus caffer	P	412.5	2.38
Tragelaphus scriptus	NP	31.5	0.18
Tragelaphus angasii	NP	57.0	0.33
Oreotragus oreotragus	NP	13.0	0.07
Raphicerus sharpei	U	8.6	0.05
Hippotragus niger	NP	157.5	0.91
Rusa unicolor	U	187.1	1.08
Hippopotamus amphibius	NP	1128.8	6.51
Axis axis	U	64.5	0.37
Loxodonta africana	U	2137.5	12.32
Papio anubis	U	15.4	0.09
Ceratotherium simum	NP	1275.0	7.35
Diceros bicornis	NP	787.5	4.54
Potamochoerus larvatas	U	73.1	0.42
Colobus guereza	U	12.4	0.07
Civectittus civetta	U	10.1	0.06
Hystrix cristata	U	14.6	0.08
Orycteropus afer	U	45.8	0.26
Otocyon megalotis	U	3.1	0.02
Pedetes capensis	U	2.6	0.02

Data from four studies: Breuer, 2005; Eloff, 1984; M. W. Hayward & Kerley, 2005; Loveridge et al., 2006.