INCORPORATING PREY DEMOGRAPHICS AND PREDATOR SOCIAL STRUCTURE INTO PREY SELECTION AND CARRYING CAPACITY ESTIMATES FOR CHEETAH

By

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DECLARATION

I, Hayley Susan Clements (s211197092), hereby declare that the dissertation for the degree of Master of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

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ABSTRACT

There is a need for a refined understanding of large carnivore prey preference and carrying capacity (K). To date, K estimates for large carnivores have been developed from predictions of carnivore diet at a prey and predator species-level. These predictions therefore assume that all social classes within a carnivore species display similar prey preferences and that all demographic classes within a prey species are equally preferred or avoided. The objective of this study was to investigate the importance of including prey demographics and carnivore social class in carnivore diet descriptions and thereby K estimates, using cheetah *Acinonyx jubatus* as a study species. It was predicted that prey sex, prey age and cheetah social class influence cheetah prey preferences, when they influence the risk and ease of prey capture, and that their inclusion in a K model would improve its predictive strength. Based on an analysis of 1290 kills from South Africa, male coalition cheetah were found to prefer a broader weight range of prey than solitary cheetah. Prey demographics further influenced cheetah prey preference, when it corresponded to differences in prey size and the presence of horns. The current species-level K regression model for cheetah is based on preferred prey and thus omits highly abundant antelope that often comprise the majority of the diet, an artefact of the way in which preferences are calculated. A refinement of the species-level K regression model, to account for prey demographic- and cheetah social class-level differences in diet and the biomass of accessible prey (defined in this study as all non-avoided prey) instead of just preferred prey, doubled the predictive strength of the K model. Because group-hunting enabled predation on a broader weight range of prey, cheetah K was influenced by the ratio of male coalition cheetah to solitary cheetah in the population. The refined K regression model is derived from ecosystems supporting an intact carnivore guild. A mechanistic approach to estimating K, based on Caughley's (1977) maximum sustainable yield model, therefore better predicted cheetah K in systems devoid of lion *Panthera leo* and African wild dog *Lycaon pictus*, which were found to suppress cheetah density. This study improves our understanding of the relationships between prey demographics, cheetah social classes and intra-guild competition in determining cheetah prey preferences and K. This study therefore paves the way for similar work on other large carnivores.

Key Words: prey demographics; carnivore social classes; intra-guild competition; prey preference; carrying capacity; cheetah *Acinonyx jubatus*

CHAPTER 1: GENERAL INTRODUCTION

To-date, carrying capacity estimates for large carnivores have been developed from predictions of predator diet at a prey and predator species-level (Mladenoff & Sickley 1998; Hayward *et al.* 2007d; Hetherington & Gorman 2007). The aim of this study is to improve our understanding of predator diet and carrying capacity by investigating prey preference at a prey demographic- and predator social class-level. This chapter highlights the need for accurate large carnivore diet predictions and carrying capacity guidelines by outlining the current conservation status of large carnivores, the value of reintroductions as a conservation tool and the situations under which predictions of predator diet and carrying capacity are imperative. Potential short-falls in the current predator diet predictions and carrying capacity models are addressed. Cheetah *Acinonyx jubatus* will be used as a study species and this chapter justifies the use of this carnivore as a tool to explore the determinants of predator prey preference and carrying capacity.

1.1 <u>Carnivore conservation status and reintroduction as a conservation tool</u>

Carnivore numbers are declining globally (Weber & Rabinowitz 1996; Hayward *et al*. 2007b) with a reduction in distribution and abundance leading to almost a quarter of species now threatened with extinction (Ginsberg 2001). As a result of their size and trophic position, the rate of elimination of large carnivores from most areas is disproportionately high in comparison with species of lesser trophic levels (Miller *et al.* 1999; Johnsingh & Madhusudan 2009; Carbone *et al.* 2011). Major threats to large carnivores include depletion of prey, hunting, persecution due to human-wildlife conflict, as well as loss and alteration of habitat (Weber & Rabinowitz 1996). In South Africa, agricultural and economic development drove large carnivores to extinction (Skead 2007, 2011) in all but the least habitable areas, such as the tropical and subtropical lowveld (Kruger National Park and north-east KwaZulu Natal), and the arid Kalahari (Hayward *et al.* 2007a).

Carnivore reintroductions have become an important conservation approach globally, with the gray wolf *Canis lupis,* red wolf, *Canis rufus,* Canadian lynx *Lynx canadensis* and black bear *Ursus americanus* being reintroduced in North America, and wildcat *Felis silvestris,* Eurasian lynx *Lynx lynx* and brown bear *Ursus arctos* being reintroduced in Europe (Breitenmoser & Breitenmoser-Würsten 1990; Fritts *et al.* 1997; Breitenmoser *et al.* 2001; Hedrick & Fredrickson 2008; Clark 2009; Smith & Bangs 2009; Linnell *et al.* 2009). Reintroductions have also been considered for tiger *Panthera tigris* in India and snow leopard *Uncia uncia* across their range in Asia (Jackson & Ale 2009; Johnsingh & Madhusudan 2009). In southern Africa, there has been recent growth in the ecotourism industry (Hayward *et al.* 2007a). The resultant surge in the development of small (< 30 000 ha) nature reserves has led to an increase in the area managed for conservation, and thus an increase in reintroduced mammals, including carnivores, that had previously been extirpated from the region (Hayward *et al.* 2007a,b). Cheetah are a good example, having been reintroduced into 48 reserves throughout South Africa (van der Merwe 2012). This has increased the number of cheetah populations and thereby increased the number of cheetah in South Africa by at least 22% (Lindsey *et al.* 2011). Similarly, lion *Panthera leo* have been reintroduced into 37 reserves, and African wild dog *Lycaon pictus* into at least 14 reserves in South Africa (Lindsey *et al.* 2009; Lindsey *et al.* 2011).

1.2 The merits and potential problems associated with conserving carnivores

Conservation areas in South Africa where reintroductions have occurred are mostly fenced (Lindsey *et al.* 2009). The fencing of reserves appears crucial for long-term conservation in Africa by separating wildlife from the local processes which threaten it (Norton-Griffiths 2007; Hayward & Kerley 2009). However, by preventing dispersal of individuals from populations, fences can hinder the natural processes that regulate these populations in response to resource availability (Hayward & Kerley 2009). As a result of this, carnivore numbers on such reserves can increase rapidly (Pettifer 1981; Hunter 1998; Tambling & du Toit 2005; Hayward *et al.* 2007a). In small, fenced reserves ungulates are unable to escape predation (Sinclair *et al.* 1985; Fryxell *et al.* 1988; Sinclair & Arcese 1995; Hayward 2009) and therefore the consequence of carnivore population growth can be ungulate population declines, and even collapses (Hunter 1998; Power 2002b; Tambling & du Toit 2005; Hayward *et al.* 2007d). There is also evidence to suggest that an overpopulation of carnivores encourages emigration and thus increases reserve break-outs, which can cause conflict with neighbouring farmers (Anderson 1981; Maddock *et al.* 1996; Castley *et al.* 2002). Furthermore, fencing that prevents carnivore emigration also prevents carnivore immigration, which can compromise gene flow (Hayward & Kerley 2009). Inbreeding and genetic drift in isolated populations may threaten the future of reintroduced carnivores (Caughley 1994; Hayward & Kerley 2009). There is therefore a need to recognize and mitigate these risks of carnivore overpopulation and inbreeding on enclosed reserves.

1.3 The mitigation of risks facing carnivore conservation on fenced reserves

Risks associated with the isolation of small carnivore populations can be offset by intensive management. In order to mitigate inbreeding a ‘managed metapopulation’ can be established, whereby a series of small, isolated subpopulations are managed as a single population by moving carnivores between areas. Such a technique has been used for African wild dog and cheetah in South Africa (Davies-Mostert *et al.* 2009; van der Merwe

2012). The risk of rapid carnivore population growth can be mitigated by intensive carnivore population regulation. Such regulation can include carnivore translocation, contraception, and culling (Slotow & Hunter 2009). In order to effectively regulate carnivore numbers, and thereby improve the likelihood of a successful reintroduction into one of the subpopulations, an estimate of the number of carnivores that the reserve can sustain.

Knowledge regarding how many large carnivores a given system can sustain is, however, limited and not wide-spread (Hayward *et al.* 2007a). Many reserves have managed their carnivore populations without reference to scientific guidelines (Hayward *et al.* 2007a). According to the Eastern Cape South Africa's Department of Economic Development and Environmental Affairs' Certificate of Adequate Enclosure and Dangerous Game Fencing Specifications, in order to be legally allowed to reintroduce large carnivores onto a property, it must be adequately fenced and 1000 ha in size for cheetah, or 2000 ha in size for lion, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta* and African wild dog. This is in contrast to the 2000 ± 400 ha and 7000 ± 3000 ha found to be required by a single cheetah in the absence and presence of lion, respectively, based on a species-level cheetah diet analysis (Lindsey *et al.* 2011). The scientific rationale behind the area requirements of current legislation is not evident. In the absence of scientifically-based guidelines regarding carnivore numbers, reserves are faced with a potential overabundance of reintroduced carnivores, and the concomitant decline in prey populations (Hayward *et al.* 2007d). There is therefore a need for accurate and applicable models, by which to determine how many carnivores a system can sustain. This study refers to such models as "carrying capacity" models, as has been done in the past (Hayward *et al.* 2007d). Carnivore carrying capacity in this study is used to describe the maximum number of carnivores that a given reserve can sustain at a given time, dependent on available resources. It does not therefore imply that each reserve will have one constant carrying capacity, or 'equilibrium state' at which the predator-prey relationship should always be stable. Such a concept has largely been replaced with that of stochasticity, where a system fluctuates in response to climate and resource availability (Wu 1995). Therefore, while the carnivore carrying capacity of a reserve does vary based on resource availability, models which predict carrying capacity can provide a useful guideline for managers looking to both introduce large carnivores and effectively manage their numbers (Hayward *et al.* 2007d). Another perspective of carrying capacity models is that they can be used to test predictions of the relationships between predators and their resources, depending on the availability of relevant data.

1.4 _Current carrying capacity models and their potential short-falls_

The density of carnivores that a natural ecosystem can sustain is determined largely by the abundance of available prey (East 1984; Fuller & Sievert 2001; Carbone & Gittleman 2002; Hayward *et al.* 2007d). Recent carnivore carrying capacity models have used the abundance of prey species assumed to represent the predator's diet to determine either the number of carnivores that a given area can sustain (Boshoff *et al.* 2002; Lindsey *et al.* 2004, 2011) or the number of carnivores that a given prey population can sustain (Mladenoff & Sickley 1998; Hayward *et al.* 2007d; Hetherington & Gorman 2007). The success of such models is therefore dependent on accurately predicting, within a given prey community, which prey will be targeted by the predator (Hayward *et al.* 2007c; Hayward 2009).

Understanding which prey a predator is likely to target is more complex in African systems than those of North America or Europe, given the greater diversity of both predators and prey (Mills & Shenk 1992). This understanding can be improved using the concepts of prey preference and avoidance, or the selection or avoidance of a specific prey item independent of its availability (Johnson 1980). By analyzing which prey are consistently preferred and avoided by a predator across ecosystems, insights can be had into what prey characteristics are favoured by the predator (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). Relating carnivore density to the biomass of preferred prey is believed to result in more robust carrying capacity estimates than a model which indiscriminately relates carnivore density to the biomass of all available prey (Hayward *et al.* 2007d). However, an artefact of the way in which prey preference is calculated means that when a prey species occurs at a high abundance in the prey community, it will not be found to be preferred, even if it constitutes a large proportion of the predator's diet (Jacobs 1974; Strauss 1979; Lechowicz 1982). In contrast, prey species that usually occur at low densities may be found to be preferred even if they constitute a minimal proportion of the predator's diet (Jacobs 1974; Strauss 1979; Lechowicz 1982). This suggests that the concept of "preferred prey" does not necessarily describe the majority of a predator's diet. The utility of a carrying capacity model based on preferred prey will therefore be a function of the relationship between preferred prey and what is actually eaten (defined as accessible prey in this study; the term includes all non-avoided prey). There is therefore a need to explore the implications of using preferred versus accessible prey to predict carnivore carrying capacity.

Furthermore, large African carnivore prey preferences have only been described at the species-level of the prey and the predator (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). The application of a carrying capacity model based on these preference predictions therefore makes the assumption that, within each prey species, all demographic classes will be equally preferred or avoided by the predator. Under such an assumption, a preferred prey species may be found to have a population size theoretically sufficient to sustain a predator, and yet still suffer population declines, and even collapse, if that predator is systematically eliminating females (Festa-Bianchet *et al*. 2006) or the population's annual recruitment (Lovari *et al.* 2009). According to optimal foraging theory, a predator should prefer prey which offers maximum energetic benefits in terms of size, with minimum energetic costs and risks incurred during prey capture (MacArthur & Pianka 1966; Griffiths 1975; Pyke *et al.* 1977). Prey size and level of risk can be dependent on prey sex and age (Ginsberg & Milner-Gulland 1994; Estes 1999), and sex- and age-biased prey preferences have been observed in several large carnivores (Fitzgibbon 1990; Mills 1990; Ginsberg & Milner-Gulland 1994; Fuller *et al.* 1995; Karanth & Sunquist 1995; Mills *et al.* 2004). There is therefore a need to refine the predictions of predator diet and carrying capacity to incorporate variability in predator preference for different prey demographic classes.

Species-level diet predictions and carrying capacity models further assume that, for a given carnivore, all social classes have similar hunting abilities. However across the order Carnivora, sexual dimorphism and variation in hunting group size have been found to influence both the average size and maximum size limitations of prey killed (Gittleman 1985; Cohen *et al*. 1993; Caro 1994; Hunter 1998; Marker *et al.* 2003; Mills *et al.* 2004; Radloff & du Toit 2004; Bissett & Bernard 2007). Omitting the influence of hunting group composition on predator diet and prey preference may not be important for a large reserve with a substantial carnivore population equally representing all carnivore social classes. In such a case the impact of predation on the prey population could be reasonably estimated by calculating diet averages for the carnivore population. However, several nature reserves in South Africa have reintroduced very small carnivore populations (Hayward *et al.* 2007a). On such reserves, where it is unlikely that all social classes will have equal representation, individual predator performance will determine the impact of the predator population on the prey population. There is therefore a need to refine the predictions of predator diet and carrying capacity to incorporate variability in prey preferences and accessibility between different carnivore social classes.

1.5 Cheetah as a study species

Once distributed throughout non-forested Africa, South Asia and the Middle East (Nowell & Jackson 1996), the decline in the distribution and abundance of cheetah is largely as a result of illegal trade, unregulated captive breeding and persecution (Marnewick *et al*. 2007). The cheetah is one of 36 species worldwide in the Family Felidae and one of seven species in southern Africa (Sunquist & Sunquist 2002; Stuart & Stuart 2007). Five sub-species of cheetah have been recognized (Caro 1994) and the conservation status of all five sub-species, according to the International Union for Conservation of Nature (Durant *et al.* 2010), is either Vulnerable (sub-Saharan Africa) or Critically Endangered (North Africa and Asia). The sub-species that occurs throughout southern Africa is *A. j. jubatus* (Skinner & Chimimba 2005).

The cheetah is highly specialized as a rapid pursuit cursorial predator and, as the fastest living land mammal, is capable of speeds up to 112 $km.h^{-1}$ for short distances (Sharp 1997; Mills & Harvey 2001). In southern Africa cheetah historically occurred in the Grassland, Savanna, Nama Karoo and Succulent Karoo biomes (Skinner & Chimimba 2005), suggesting that they are capable of hunting in a relatively wide range of habitats. As adult cheetah weigh between 40 and 60 kg (Stuart & Stuart 2007) they prey on large (30 to 60 kg) vertebrates (> 45% of their own body mass) in order to satisfy their energetic demands (East 1984; Carbone *et al.* 1999). Within this niche, cheetah have been found to prefer prey species with a body mass between 23 and 56 kg (Hayward *et al.* 2006b).

Cheetah form part of the large African carnivore guild, including leopard, lion, spotted hyaena and African wild dog, which is still intact on many reserves in South Africa (Lindsey *et al.* 2011). The diet of the five large African carnivores overlaps to varying degrees, with cheetah diet overlapping most extensively with that of leopard and African wild dog (Hayward & Kerley 2008; Lindsey *et al.* 2011). Cheetah are inferior competitors to lion and spotted hyaena, who compete with them for food as well as kill them and displace them from optimal foraging areas (Laurenson 1995; Durant 2000; Hayward & Kerley 2008).

Cheetah display a certain degree of sociality. Females are solitary unless they have cubs, which remain with their mother until independence (Skinner & Chimimba 2005). Males are either solitary, or male litter-mates form coalitions of up to four or five individuals (Caro & Collins 1986; Skinner & Chimimba 2005). Male coalitions are considered stable, remaining through adolescence into adulthood (Caro & Collins 1986). Male coalition cheetah have been observed to hunt cooperatively (Caro 1994; Hunter 1998; Bissett & Bernard 2007). Male cheetah weigh 25% more than female cheetah (Skinner & Chimimba 2005).

1.6 <u>Research aims and general predictions</u>

This study aims to improve the current understanding of the drivers of predator prey selection and carrying capacity, at a prey demographic- and predator social class-level. Cheetah have been selected as a study species for two primary reasons. Firstly, the drivers of predator prey selection are perhaps most important when they directly influence the predator's ability to run down, seize and kill prey (Gittleman 1985). As a large-bodied predator evolved for rapid pursuit hunting, cheetah select prey species which offer least risk of injury during capture (Hayward *et al.* 2006b), while still fulfilling the energetic demands imposed by large carnivore body size (Carbone *et al.* 1999). Since the risk of injury to the predator can vary between demographic classes in a prey species (Fitzgibbon 1990; Mills 1990; Ginsberg & Milner-Gulland 1994; Fuller *et al.* 1995; Karanth & Sunquist 1995; Mills *et al.* 2004), I predict that cheetah prey preference and carrying capacity are driven by demographic-level prey characteristics. Secondly, predator size and hunting group size can influence predator diet (Kruuk 1966, 1970; Bothma & le Richie 1984; Gittleman 1985; Fanshawe & Fitzgibbon 1993; Creel & Creel 1995; Funston *et al.* 1998; Carbone *et al.* 1999; Radloff & du Toit 2004; Knopff *et al.* 2010). Since cheetah display sexual dimorphism (Marker & Dickman 2003) and their hunting style (solitary or coalition) can vary between the sexes (Caro 1994), I predict that cheetah prey preference and carrying capacity is further driven by differences in cheetah hunting ability between social classes.

1.7 Key research questions

In Chapter 3 I investigate the drivers of cheetah prey preference, beyond the species-level of the predator and the prey. In order to calculate robust preference results that are not biased by observations from one particular area and are therefore not overly influenced by the available community of prey species, a multi-site analysis is performed (as was done by Hayward *et al.* 2006b). In order for a prey item to be significantly preferred or avoided in a multi-site analysis, it must be so across diverse communities throughout its range. Chapter 3 is designed to answer the following key research questions:

- Do cheetah display prey preferences at a prey demographic class level?
- Do demographic-level differences in prey preference correspond with differences in prey size and thus risk of injury?
- Do demographic-level differences in prey preference correspond with differences in prey weaponry and thus risk of injury?
- Do demographic-level differences in prey preference correspond with differences in prey herding behaviour and thus ease of capture?
- Do cheetah prey preferences differ between predator social classes?
- Do solitary male cheetah prefer larger prey than solitary female cheetah?
- Do male coalition cheetah prefer larger prey than solitary cheetah?

In Chapter 4 I develop a refined cheetah carrying capacity model, based on an improved understanding of cheetah diet and prey preference. As was done by Hayward *et al.* (2007d), a multi-site approach is used to relate the biomass of prey to the density of cheetah, thereby developing a regression-based carrying capacity model. Potentially tenuous assumptions associated with a regression model are then tested by developing a more mechanistic carrying capacity model, based purely on cheetah dietary requirements. Chapter 4 is designed to answer the following key research questions:

- Is accessible prey or preferred prey a better predictor of cheetah density in a natural system?
- Do prey demographic class- and predator social class-level diet predictions improve the predictive strength of a carrying capacity model, compared with a model based on species-level predictions?
- Does the carrying capacity model based on species-level predictions of cheetah diet underestimate cheetah carrying capacity by not accounting for differences in diet between cheetah social classes?
- Does the social class composition of the cheetah population influence cheetah carrying capacity?
- Does intra-guild competition reduce cheetah carrying capacity?
- Do carrying capacity models, developed from prey demographic class- and cheetah social class-level predictions of cheetah diet, accurately predict cheetah carrying capacity across diverse reserves?

In the concluding chapter, my findings are summarized in a conceptual framework, and the implications of my findings for improving our understanding of predator-prey relationships are discussed, within an evolutionary and conservation context.

CHAPTER 2: STUDY SITES

2.1 Research approach

In order to investigate the importance of prey demographics and cheetah social class in shaping cheetah diet and prey preferences (Chapter 3), a multi-site cheetah diet analysis was performed. This analysis used both data which I collected at Samara Private Game Reserve, as well as similar data which I acquired from other sites in South Africa. In order to develop and test a refined carrying capacity model for cheetah (Chapter 4), two groups of datasets were analyzed with different objectives, namely: developing a cheetah carrying capacity regression model and using the model to predict carrying capacity at prediction sites. Two sites were then used to test both a regression and mechanistic carrying capacity model (test sites). This study site chapter therefore includes a detailed description of the field-work study site (Samara Private Game Reserve), followed by tabulated descriptions of the sites from which additional data were obtained. These additional datasets are divided into three tables, Table 2.1 (Chapter 3: diet analysis sites), Table 2.2. (Chapter 4: carrying capacity regression model development sites) and Table 2.3 (Chapter 4: carrying capacity prediction sites). The two carrying capacity test sites used in Chapter 4 (Mountain Zebra National Park and Phinda Private Game Reserve) are both used in a previous analysis (carrying capacity prediction and cheetah diet analysis, respectively), and are therefore included in Table 2.3 and Table 2.1, respectively.

2.2 Field work study site

2.2.1 Location

Samara Private Game Reserve (32º34'S, 24º84'E; hereafter referred to as Samara) is located 20 km south-east of the town of Graaff Reinet in the Eastern Cape, South Africa (Fig. 2.1). Spanning 280 km^2, it is located in the Great Karoo, on the southern edge of the Great Escarpment (Watkeys 1999). The predominant land-use in the region is livestock farming and the reserve is surrounded by privately-owned farmland on the majority of its boundary, except in the north-east where it borders Mount Camdeboo Private Game Reserve. Samara, made up of what were previously a number of livestock farms, was established as a conservation area in 1998. Internal fences divide the reserve into an electrified, game-fenced section and a stock-fenced section of approximately equal size (Fig. 2.2).

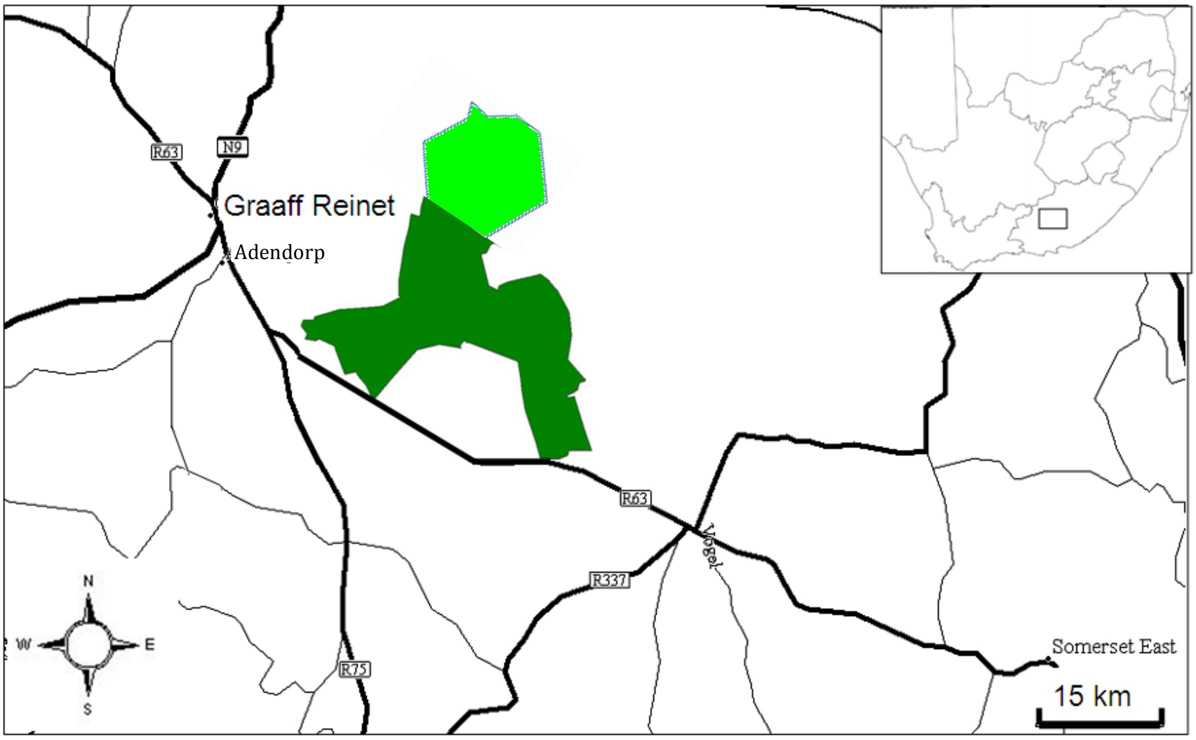


Figure 2.1. Location of Samara Private Game Reserve (dark green) in South Africa (top right), and in relation to Graaff Reinet and Mount Camdeboo Private Game Reserve (light green).

2.2.2 *Geology and topography*

Samara is situated on the shale-dominated bedrock of the Beaufort Group within the geological entity known as the Karoo Supergroup (Visser 1986; Meadows & Watkeys 1999). This bedrock has been intensively intruded by Karoo dolerite which is more resistant to weathering in the dry climate (Visser 1986) and has therefore resulted in a landscape of mountain plateaus and extensive flat Karoo plains. The altitude on the property varies from 760 m.a.s.l. to 1450 m.a.s.l. In the center of Samara a valley containing the Apieskloof / Melk River drainage system separates the escarpment in a north-south direction, for the length of the property (Fig. 2.2). The rivers were ephemeral during the study period, flowing only after heavy rainfall or snow-melt, but holding pools of water throughout the study period.

2.2.3 *Vegetation*

Samara supports four of South Africa's nine biomes (van Cauter 2004; Mucina & Rutherford 2006). Thicket is a dense, woody, semi-succulent, thorny vegetation type (Mucina & Rutherford 2006) and is the predominant biome on Samara, covering 71% of the reserve and occurring on a large portion of the plains as well as in the valleys (van Cauter 2004; Fig. 2.2). Nama Karoo is characterized by low (dwarf) shrubs intermixed with grasses, succulents, geophytes and annual forbs (Mucina & Rutherford 2006) and occurs in the southern section of the reserve (van Cauter 2004; Fig. 2.2). Grassland is structurally simple, characterized by a strong dominance of grasses, usually of the family Poaceae (Mucina & Rutherford 2006). While in South Africa this biome occurs mainly on the high central plateau (highveld), it is also present in the central parts of the Eastern Cape and a patch of grassland occurs on Samara's mountain plateaus (van Cauter 2004; Mucina & Rutherford 2006). Savanna is defined as a co-dominance of grasses and trees (Scholes 1997) and on Samara, savanna vegetation is localized along the major drainage lines of the Apies and Melk Rivers (van Cauter 2004; Fig 2.2). There is a further azonal vegetation type on Samara, occurring on the edges of the mountain plateaus and comprising a mosaic of thicket and grassland (van Cauter 2004; Fig 2.2).

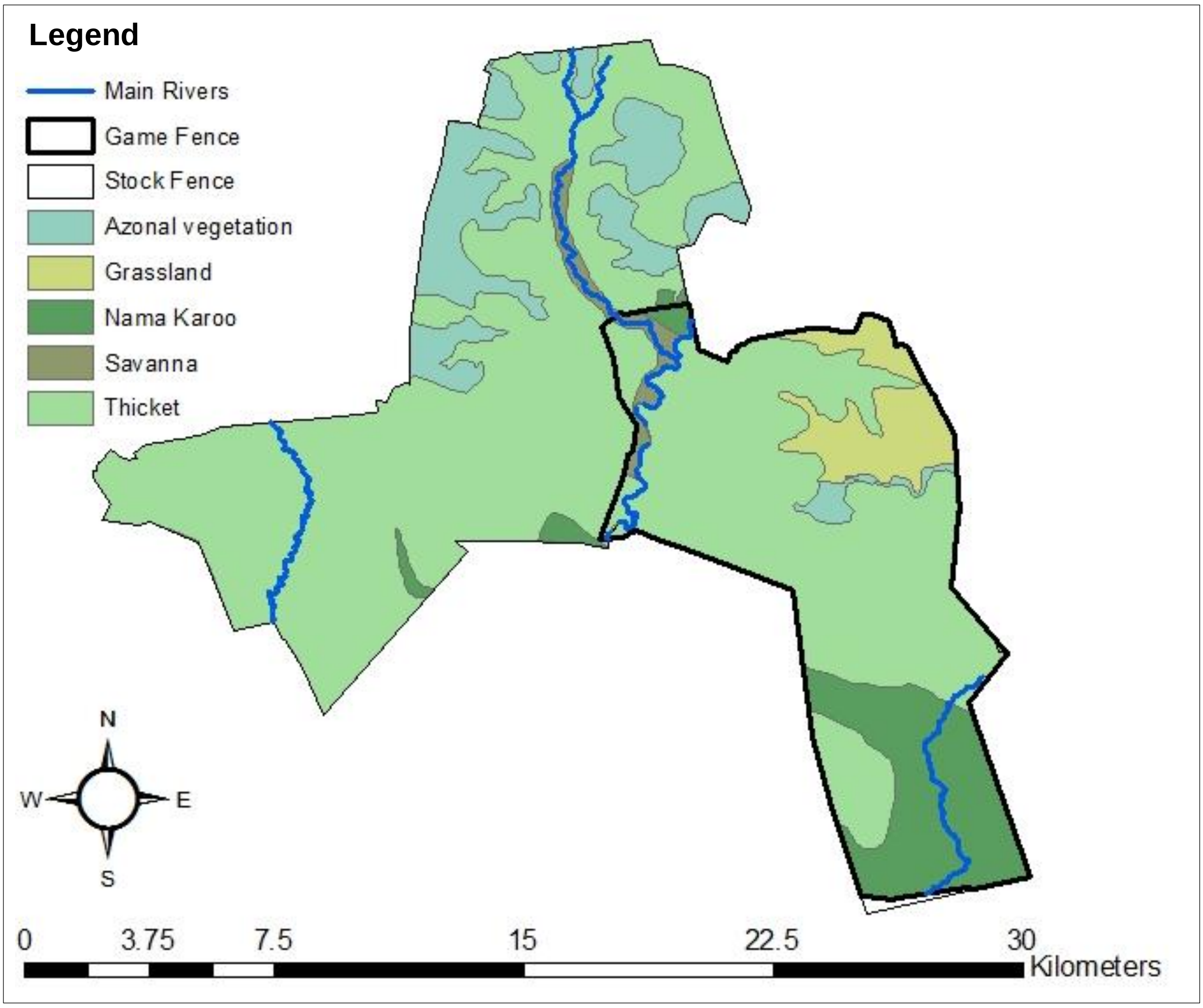


Figure 2.2. Distribution of biomes on Samara Private Game Reserve, as well as major river systems and fences (map from van Cauter 2004).

2.2.4 *Climate*

Samara is located in a semi-arid region (Venter *et al.* 1986), receiving an average annual rainfall of 315 ± 26 mm, with almost two thirds of this rainfall falling between November and March (Fig. 2.3). Summer rainfall is largely due to tropical disturbances, with the lesser winter rainfall derived from occasional deep cold fronts (Desmet & Cowling 1999). The Karoo is subject to extended periods of drought (Venter *et al.* 1986), resulting in high variability in mean monthly rainfall. Mean daily minimum temperature ranges from 3 ± 0.6 ºC in July to 16 ± 0.4 ºC in February (Fig. 2.3). Mean daily maximum temperature ranges from 20 ± 0.5 ºC in July to 32 ± 0.5 ºC in January (Fig. 2.3).

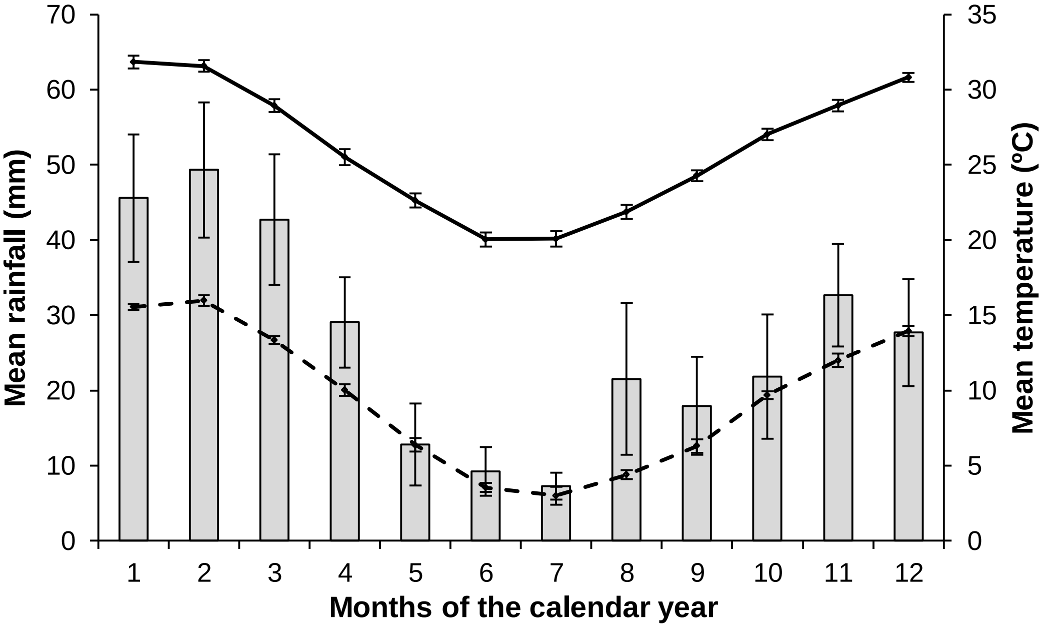


Figure 2.3. Mean monthly rainfall (bars) and daily temperatures (maximum – solid line, minimum – dashed line) ± standard error (SE) for the 12 calendar months, for the Graaff Reinet region from 1981 to 2012 (South African Weather Services).

2.2.5 Mammalian fauna

As a result of conflicting land-use in the past, the majority of indigenous large mammals had been extirpated from the area (Skead 2007). Ungulates that were still present in 1998, when the reserve was established, included black wildebeest *Connochaetes gnou*, bushpig *Potamochoerus larvatus*, blesbok *Damaliscus pygargus phillipsi*, common duiker *Sylvicapra grimmia*, greater kudu *Tragelaphus strepsiceros*, klipspringer *Oreotragus oreotragus*, grey rhebok *Pelea capreolus*, mountain reedbuck *Redunca fulvorufula*, springbok *Antidorcas marsupialis* and steenbok *Raphicerus campestris*. An alien ungulate, fallow deer *Cervus dama*, and an extralimital ungulate, impala *Aepyceros melampus*, were also present on the property. Fallow deer has subsequently been eradicated and a small population (< 20) of impala still exists on the property.

Subsequent to reserve establishment large indigenous mammals were reintroduced onto the property, including buffalo *Syncerus caffer*, eland *Tragelaphus oryx*, gemsbok *Oryx gazella*, red hartebeest *Alcelaphus buselaphus*, mountain zebra *Equus zebra* and plains zebra *Equus quagga*. Two extralimital species, namely giraffe *Giraffa camelopardalis* and white rhinoceros *Ceratotherium simum*, were also reintroduced. Very small (< 20) populations of three additional extralimital ungulates, namely nyala *Tragelaphus angasii*, waterbuck *Kobus ellipsiprymnus* and warthog *Phacochoerus africanus*, exist on the property due to movement from a nearby game reserve (Asante Sane), prior to electric fencing. Other common animals present on Samara include chacma baboon *Papio ursinus*, vervet monkey *Cercopithecus pygerythrus*, scrub hare *Lepus saxatilis* and springhare *Pedetes capensis* (refer to Appendix Table A for scientific names and common names of Samara's mammalian fauna).

Cheetah were the only large carnivore to be reintroduced onto Samara, though several smaller carnivores, insectivores and omnivores were already present on the property. These include aardvark *Orycteropus afer*, aardwolf *Proteles cristatus*, African wild cat *Felis silvestris lybica*, bat-eared fox *Otocyon megalotis*, black-backed jackal *Canis mesomelas*, Cape fox *Vulpes chama*, caracal *Caracal caracal* and small spotted cat *Felis nigripes*. Buffalo, cheetah, giraffe and white rhinoceros were only introduced into the game-fenced section of the property (Fig. 2.2).

2.2.6 *Study animals*

In 2004, four cheetah, two females (F1 & F2) and two males in a coalition (M1 & M2), were fitted with VHF radio collars (Africa Wildlife Tracking) and reintroduced onto Samara. Between 2005 and 2007 F1 had three litters, totaling 18 cubs, of which 17 survived and were relocated by the end of 2008. Subsequent to the third litter, F1 was contracepted. In June 2012, subsequent to the completion data collection for this study, F1 had a fourth litter of two cubs. F2 had two litters of four cubs, in 2006 and 2008. Six of these cubs were relocated by mid-2010. F2 and her remaining cubs (males) were not well habituated and I was unable to monitor them. M1 died in 2009 and M2 died mid-2010. There was therefore one trackable cheetah (F1) from June 2010 until May 2012. An additional female cheetah from the Waterberg was collared and reintroduced onto the property in April 2012 and was subsequently monitored. Although only one cheetah could be reliably monitored for the majority of the study period, a total of 64 kill data points were obtained. Importantly for this study these were all known female cheetah kills and these data supplemented data from other sites, to allow a multi-site cheetah diet analysis (Chapter 3).

2.3 Additional study sites

Table 2.1. Descriptions of the nature reserves from which data were obtained for the cheetah diet analysis in Chapter 3.
(NOTE: hereafter study sites are referred to by their abbreviation. * In 1993 the game fence along the 29 km boundary between Sabi and the KNP to the east was removed. ** Mala Mala is one of the private reserves that comprise the Sabi. *** Phinda is also a model test site in Chapter 4. [X] initial reserve establishment does not reflect subsequent expansions).

Reserve name	**Amakhala Game Reserve**	**Kwandwe Private Game Reserve**	**Mount Camdeboo Private Game Reserve**	**Phinda Resource Reserve *****	**Shamwari Private Game Reserve**	**Kruger National Park**	**Sabi Sand Wildtuin**	**Mala Mala****
Abbreviation	Amakhala	Kwandwe	Camdeboo	Phinda	Shamwari	KNP	Sabi	Mala Mala
Co-ordinates	33º31’S, 26º06’E	33º09’S, 26º37’E	32º54’S, 24º54’E	27°40’S, 31°12’E	33°20’S, 26°01’E	23º06’ to 25º25’S, 31º00’ to 31º57’E	24º50'S, 31º30'E	24º50'S, 31º30'E
Province	Eastern Cape	Eastern Cape	Eastern Cape	KwaZulu Natal	Eastern Cape	Mpumalanga/Limpopo	Mpumalanga	Mpumalanga
Nearest town	Port Elizabeth	Grahamstown	Graaff Reinet	Mkuze	Port Elizabeth	Hazyview/ Phalaborwa	Hazyview	Hazyview
Size (km^2)	50	160	140	170	187	20000	570*	570*
Reserve establishment[x]	1999	2001	1990's	1990	1994	1926	1948	1948
Average annual rainfall (mm)	475	435	315	875	500	600	600	600
Predominant rainfall season	Spring and summer	Spring and summer	Summer	Summer	Spring and summer	Spring and summer	Spring and summer	Spring and summer
Minimum annual temperature (ºC)	7.1	5	4	10	4	8	8	8
Maximum annual temperature (ºC)	32.4	35	32	33	31	30	30	30

Table 2.1. cont.

Reserve name	**Amakhala Game Reserve**	**Kwandwe Private Game Reserve**	**Mount Camdeboo Private Game Reserve**	**Phinda Resource Reserve *****	**Shamwari Private Game Reserve**	**Kruger National Park**	**Sabi Sand Wildtuin**	**Mala Mala****
Predominant vegetation type	Subtropical thicket, savanna	Valley and xeric succulent thicket	Thicket, nama karoo	Natal lowveld bushveld/ coastal bushveld-grassland	Subtropical thicket, savanna	*Mopane*-dominated woodlands and open savanna/grassland in the north*;* *Acacia* and *Combretum* thickets and *Scherocarya birrea/Acacia nigrescens* plains in the south	*Acacia* and *Combretum* thickets and *Scherocarya birrea/Acacia nigrescens* plains	*Acacia* and *Combretum* thickets and *Scherocarya birrea/Acacia nigrescens* plains
Cheetah reintroduction	2004	2001	2007	1992	2000	Never extinct in the area	Never extinct in the area	Never extinct in the area
Current cheetah density (#.km^{-2})	0.04	0.08	0.01	0.08	0.01	0.02	0.03	0.03
Other large carnivore reintroductions	2004: lion; post-2004: leopard, spotted hyaena	2001: lion, leopard; 2004: wild dog	None	1992: lion; never extirpated: leopard, spotted hyaena, transient wild dog	2000: lion; 2001 to 2003: leopard, wild dog	Never extirpated: lion, leopard, spotted hyaena, wild dog	Never extirpated: lion, leopard, spotted hyaena, wild dog	Never extirpated: lion, leopard, spotted hyaena, wild dog
Source for additional information	Odindi & Kakembo (2009); Hayward *et al.* (2007a)	Bissett (2004)	E. Larson pers. comm.	Hunter (1998)	O'Brien (2000)	Mills & Biggs (1993)	Radloff & du Toit (2004)	Radloff & du Toit (2004)

Table 2.2. Descriptions of the nature reserves that served as regression model development sites in Chapter 4.
(NOTE: hereafter study sites are referred to by their abbreviation; ^{x} initial reserve establishment does not reflect subsequent expansions).

Reserve Name	**Hluhluwe-Imfolozi**	**Kalahari Gemsbok National Park**	**Kruger National Park**	**Pilanesberg National Park**	**Sabi Sand Wildtuin**
Abbreviation	Hluhluwe	Kalahari	refer to Table 2.1	Pilanesberg	refer to Table 2.1
Co-ordinates	28°00'S, 31°43'E	25º00’ to 26°28'S, 20°00' to 20º30’E		25°08’S, 26°57’E	
Province	KwaZulu Natal	Northern Cape		North West	
Nearest town	Hluhluwe	Upington		Rustenburg	
Size (km^{2})	960	9591		500	
Reserve establishment^{x}	1895	1931		1979	
Average annual rainfall (mm)	660	255		630	
Predominant rainfall season	Spring and summer	Summer and autumn		Summer	
Minimum annual temperature (ºC)	13	-10		1	
Maximum annual temperature (ºC)	35	40		31	
Predominant vegetation type	Woodland savanna & shrub thicket	Kalahari thornveld		Mixed *Acacia* and broad-leaf bushveld	
Cheetah reintroduction	1965	Never extirpated		Post-1993	
Current cheetah density (#.km^{-2})	0.10	0.01		0.04	
Other large carnivore reintroductions	1965: lion; 1981: wild dog; never extirpated: leopard, spotted hyaena	Never extirpated: lion, leopard, spotted hyaena		1993: lion; post-1993: leopard, wild dog	
Source for additional information	Gussett *et al.* (2008); Graf *et al.* (2009)	Mills (1990)		Slotow & van Dyk (2001); van Dyk & Slotow (2003)	

Table 2.3. Descriptions of the nature reserves that served as carrying capacity model prediction sites in Chapter 4. (NOTE: hereafter study sites are referred to by their abbreviation. * GANP refers to a proposed park expansion; ** MZNP is also a test site in Chapter 4; ^{X} initial reserve establishment does not reflect subsequent expansions).

Reserve name	**Greater Addo National Park Project***	**Addo Elephant National Park – Main Camp Section**	**Addo Elephant National Park – Darlington Section**	**Addo Elephant National Park – Nyathi Section**	**Karoo National Park**	**Madjuma Lion Reserve**	**Mountain Zebra National Park****	**Phinda Resource Reserve**	**Shamwari Private Game Reserve**
Abbreviation	GANP	Addo	Darlington	Nyathi	Karoo	Madjuma	MZNP	refer to Table 2.1	refer to Table 2.1
Co-ordinates	33°58'S, 25°31'E	33°26’S, 25°44’E	33°09'S, 25°08'E	33°26'E, 25°44'E	31°18'S, 22°23'E	24°42’S, 27°58’E	32˚13’S, 25˚28’E		
Province	Eastern Cape	Eastern Cape	Eastern Cape	Eastern Cape	Eastern Cape	Limpopo Province	Eastern Cape		
Nearest town	Kirkwood	Addo	Kirkwood	Addo	Graaff Reinet	Bela Bela	Cradock		
Size (km^2)	3410*	134	90	70	700	15	185		
Reserve establishment^{x}	*	1931	2002-2005	2000	1979		1937		
Average annual rainfall (mm)	250 to 722	400	250	550	260	602	400		
Predominant rainfall season	Autumn and spring	Autumn and spring	Autumn and spring	Autumn and spring	Summer	Summer and autumn	Summer		
Minimum annual temperature (ºC)	0 to 5	5	0	5	3.5	0	0		
Maximum annual temperature (ºC)	45 to 48	45	48	45	32	38.5	28		

Table 2.3. cont.

Reserve name	**Greater Addo National Park Project***	**Addo Elephant National Park – Main Camp Section**	**Addo Elephant National Park – Darlington Section**	**Addo Elephant National Park – Nyathi Section**	**Karoo National Park**	**Madjuma Lion Reserve**	**Mountain Zebra National Park****	**Phinda Resource Reserve**	**Shamwari Private Game Reserve**
Predominant vegetation type	Thicket, savanna, grassland, fynbos, nama karoo and forest	Spekboom thicket	Nama karoo	Spekboom thicket	Nama karoo	Mixed bushveld	Nama karoo		
Cheetah reintroduction	None	None	None	None	None	None	2008		
Current cheetah density (#.km^{-2})	0	0	0	0	0	0	0.04		
Other large carnivore reintroductions	See respective park sections	2003 to 2004: lion, leopard, spotted hyaena	2007: lion	None	2010: lion	1996: lion	None		
Source for additional information	Kerley & Boshoff (1997); Boshoff *et al.* (2002)	Landman *et al.* (2008); SANParks (2008a)	Hayward *et al.* (2007d)	Hayward *et al.* (2007d)	Hayward *et al.* (2007d); SANParks (2008b)	Power (2002b)	Hayward *et al.* (2007d); SANParks (2008c)		

2.4 Relative location of all study sites

The sites used in this study, detailed in sections 2.2 and 2.3, are distributed throughout South Africa (Fig. 2.4).

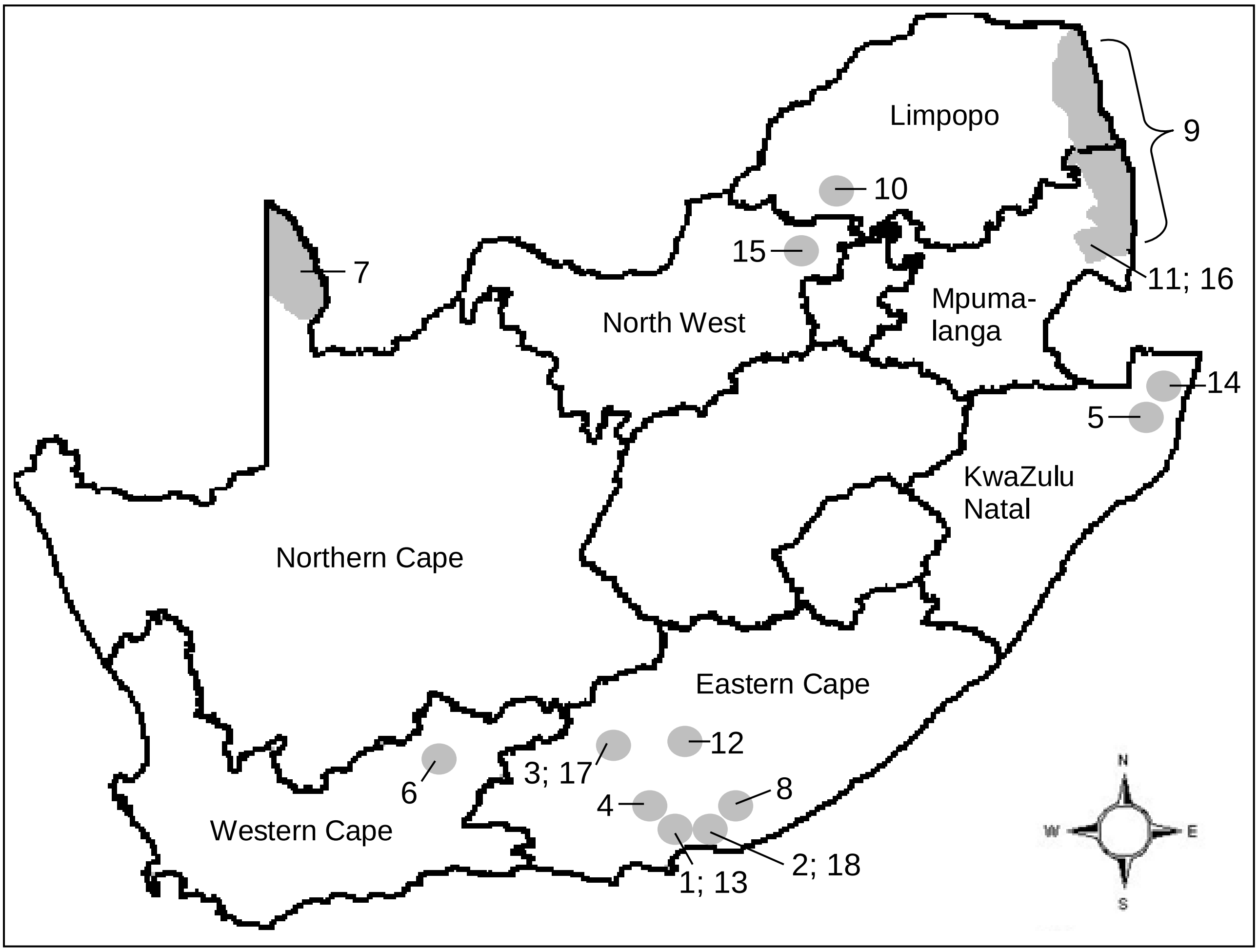


Figure. 2.4. Map of South Africa showing the relative locations (shaded areas) of all sites used in this study (1. Addo; 2. Amakhala; 3. Camdeboo; 4. Darlington 5. Hluhluwe; 6. Karoo; 7. Kalahari; 8. Kwandwe; 9. KNP; 10. Madjuma; 11. Mala Mala; 12. MZNP; 13. Nyathi; 14. Phinda; 15. Pilanesberg; 16. Sabi; 17. Samara; 18. Shamwari). Sites in close proximity to each other are represented by a single shaded area.

CHAPTER 3: THE INFLUENCE OF PREY DEMOGRAPHICS AND PREDATOR SOCIAL STRUCTURE ON CHEETAH PREY SELECTION

3.1 Introduction

3.1.1 Recent research regarding large carnivore prey preferences

Across a myriad of carnivores including copepods, insectivorous birds, raptors and mammals, prey size, relative to predator size, is an important determinant of a predator's prey selection (Rosenzweig 1966; Schoener 1968; Wilson 1975; Gittleman 1985; Hayward & Kerley 2005; Hayward 2006, Hayward *et al.* 2006a,b,c; Andheria *et al.* 2007). Among terrestrial carnivores there is a body mass limit (c. 22 kg) above which a carnivore's energy requirements necessitate predation on vertebrate prey weighing greater than 45% of the predator's body mass (Carbone *et al.* 1999). Thus for larger predators there is a need to feed on larger prey in order to acquire sufficient energy. In India, tiger were found to prefer larger prey than did leopard which are smaller in size (Karanth & Sunquist 1995). Similarly, prey size was found to increase with increasing predator size in the five large African carnivores (Radloff & du Toit 2004).

The relationship between predator size and prey size is perhaps most critical when it directly influences the predator's ability to run down, seize and kill larger prey (Gittleman 1985). According to optimal foraging theory, a predator should prefer prey which offer maximum energetic benefits in terms of size, with minimum energetic costs and risks incurred during prey capture (MacArthur & Pianka 1966; Griffiths 1975; Pyke *et al.* 1977). For cheetah, dhole *Cuon alpinus*, leopard (African and Asian) and African wild dog, cost of prey capture relates to risk of injury from the prey individual during capture, and the observed preferred prey weight ranges are believed to offer least risk of injury (Karanth & Sunquist 1995; Hayward *et al.* 2006a,b,c), while still fulfilling the energetic demands imposed by large predator body size (Carbone *et al.* 1999). There are, however, species within the weight ranges predicted to be preferred by cheetah, dhole, leopard and African wild dog that are not preferred (Karanth & Sunquist 1995; Hayward *et al.* 2006a,b,c). These discrepancies have been justified by variation in risk of injury and ease of capture through prey morphology (e.g. horns); ecology (e.g. prey vegetation preferences and prey scarcity) and behaviour (e.g. large herd size and increased vigilance) (Karanth & Sunquist 1995; Hayward *et al.* 2006a,b,c; Hayward 2011). Similarly, the finding that lion, spotted hyaena and African wild dog prefer larger prey relative to their body mass than do cheetah and leopard has been justified by their more social hunting behaviour (Owen-Smith & Mills 2008).

Research regarding prey preferences of the large African carnivores has been based on across-ecosystem assessments of predator diet at a prey and predator species-level (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). The influence of variation in size, level of risk and ease of capture between different prey sex and age classes is therefore unaccounted for, as is variation in size and hunting behaviour between different social classes within a predator species. This chapter therefore focusses on investigating the influence of prey demographics and predator social class on predator prey preference, using cheetah as a study species.

3.1.2 The influence of prey demographics on predator prey preference

Ungulate juveniles, as a result of their size and lack of defense and speed, are relatively easy targets for predators (Schaller 1968; Karanth & Sunquist 1995; Lovari *et al.* 2009). In over half the studies investigated by Ginsberg & Milner-Gulland (1994), predators selected juvenile prey. If solely the juveniles of a species are preyed upon, predation on that prey species may be low relative to the total prey population size, despite high juvenile predation. This would result in a species-level preference calculation finding the prey species to be avoided, masking a preference for the juvenile age class. For example, species-level diet predictions for cheetah suggest that, in antelope weighing above 56 kg, large prey size and its associated high risk of capture result in the entire species being avoided by cheetah (Hayward *et al.* 2006b). However, the young of large antelope can form an important component of cheetah diet before reaching 56 kg (Gros *et al.* 1996; Marker-Kraus *et al.* 1996; Hunter 1998; Mills *et al.* 2004; Bissett & Bernard 2007).

The risk of injury and ease of capture of a prey item can further vary with prey sex. African wild dog and cheetah have been found to prefer females of the large antelope kudu, which may reflect the higher risks associated with attempting to kill male kudu, which have long horns in contrast to the females which lack horns (Ginsberg & Milner-Gulland 1994; Bissett 2004). In smaller prey species, horns do not appear to infer the same protective advantage, with cheetah and African wild dog selecting male Thomson's gazelle *Eudorcas thomsonii* and impala; and tiger, leopard and dhole selecting male chital *Axis axis* (Fitzgibbon 1990; Mills 1990; Fuller *et al.* 1995; Karanth & Sunquist 1995; Mills *et al.* 2004). In all three of these prey species only the males have horns or antlers (Clutton-Brock 1982; Stuart & Stuart 2007). As these prey species form large breeding herds, male-biased predation is believed to be the result of the male's increased vulnerability and thus ease of capture due to occurring on the periphery of groups, having greater nearest-neighbour distances, being less vigilant and found in smaller groups than females (Fitzgibbon 1990; Karanth & Sunquist

1995). There is therefore a need to include both prey age and prey sex in predator diet and prey preference analyses.

3.1.3 The influence of predator sex and social class on predator prey preference

In sexually dimorphic predators, larger males have been found to kill both larger prey, and a broader size range of prey, than females (Bothma & le Richie 1984; Gittleman 1985; Funston *et al.* 1998; Carbone *et al.* 1999; Radloff & du Toit 2004; Knopff *et al.* 2010). Prey size is further influenced by predator hunting group type, with group-hunting predators killing larger prey relative to their own size than solitary predators (Kruuk 1975; Karanth & Sunquist 1995; Courchamp & Macdonald 2001; Radloff & du Toit 2004; Owen-Smith & Mills 2008). Group versus solitary hunting is variable both across the order Carnivora (Hayward & Kerley 2005), as well as within specific species (Kruuk 1966, 1970; Funston *et al.* 1998). Male cheetah, being 25% larger than female cheetah, have been shown to hunt larger prey (Radloff & du Toit 2004). Male coalitions also display a higher hunting success rate (Eaton 1974; Bissett 2004) and take larger prey than solitary cheetah (Caro 1994; Hunter 1998; Marker *et al.* 2003; Mills *et al.* 2004; Bissett & Bernard 2007). There is therefore a need to include predator social class in predator diet and prey preference analyses.

3.1.4 Objectives, hypotheses and predictions

This chapter aims to investigate predator prey preferences beyond the species-level of the prey and the predator, using cheetah as a study animal. This chapter therefore aims to use cheetah diet information from throughout South Africa in a multi-site analysis in order to investigate if, and under what circumstances, prey demographics and cheetah social structure influence prey preference.

1. It is hypothesized that cheetah will preferentially hunt animals which offer maximum energetic benefits in terms of size, with minimum costs in terms of risk of injury and ease of capture (MacArthur & Pianka 1966; Griffiths 1975; Pyke *et al.* 1977). I therefore predict that:
   - prey age will influence cheetah prey preference when degree of risk and ease of capture vary between prey age classes. Therefore in large prey, predation will be juvenile-biased. There will be a decrease in the proportion that adults constitute of prey killed in a species, as the size of the prey species increases.
   - prey sex will influence cheetah prey preference when degree of risk and ease of capture vary between prey sexes. Therefore:
     - in large prey, the combination of the risks of large size and horns will result in female-biased predation in prey displaying sexual weaponry dimorphism (i.e. only males have horns). Predation will be even across the sexes in large prey which

display no such sexual weaponry dimorphism. In prey with a small or medium mass, horns will not pose a sufficient risk, and therefore sexual weaponry dimorphism will not result in female-biased predation by cheetah.

- in prey which form large breeding herds, males are easier to capture as a result of occurring on the periphery of groups and being less vigilant than females. Therefore in medium and small prey species, in which sexual weaponry dimorphism will not influence predation, predation will be male-biased in prey which form large breeding herds, and will be even across sexes in prey which do not form large breeding herds.

2. It is further hypothesized that predator size and hunting group type influence prey size. Therefore cheetah are limited in what they can capture by both their size and whether they hunt alone or in groups. I predict that:
    - the size dimorphism between cheetah sexes will result in solitary male cheetah killing larger prey and a broader weight range of prey than female cheetah.
    - as a result of group-hunting, male coalition cheetah will kill larger prey and prefer a broader weight range of prey than solitary cheetah of either sex.

3.2 Methods

3.2.1 Field data collection and manipulation

3.2.1.1 Cheetah diet

The field work element of this study was carried out over a 24 month period, from June 2010 to May 2012 at Samara (Chapter 2). From June 2010 until May 2012, a radio-collared female without cubs was monitored using a Communications Specialists R-1000 receiver and an H-bar antenna. From April 2012 to May 2012 an additional radio-collared female without cubs was also monitored. The radio-location method of data collection is known to underestimate the contribution of small kills to the diet since predators are likely to spend less time on smaller kills (Mills 1992, 1996). Frequent location of the predator has been found to reduce this bias (Hunter 1998; Radloff & du Toit 2004). I therefore attempted to locate collared cheetah daily, in the early morning or late afternoon: the times when cheetah are most active (Schaller 1972; Eaton 1974; Pettifer 1981; Caro 1994). When a cheetah was found on a kill, it was assumed that the cheetah on the carcass made the kill as cheetah rarely scavenge (Schaller 1972; Caro 1994). The prey item was identified to species, age (juvenile or adult) and sex if adult. Prey less than a year old were classified as juvenile. Discriminating between age and sex classes was assisted by knowledge of horn and body size development, as well as birth peaks in seasonally breeding animals (Skinner & Chimimba 2005).

3.2.1.2 *Prey abundance*

Ungulate abundance data for Samara for the period June 2010 to May 2011 were provided by an aerial game count performed on 12 August 2010 using a two-seater helicopter. The counter/recorder sat next to the pilot and recorded the species and number of all sighted ungulates. I applied standardized visibility correction factors to these census data, as per Owen-Smith & Mills (2008). In May 2011, there was a large game off-take. Prey abundance for the period June 2011 to May 2012 was therefore estimated by accounting for both recruitment and off-take since the 2010 census (Appendix Table B). Recruitment was estimated by the average percentage of juveniles in each species between August 2010 and May 2011, obtained from ground surveys detailed in section 3.2.1.3. As there was a notable change in prey abundance subsequent to the 2011 game capture (Appendix Table B), the Samara cheetah kill data were divided into two time periods: pre- and post-off-take (Samara 10-11 and Samara 11-12, respectively; Table 3.1). Such partitioning has been used previously in studies of carnivore feeding ecology (Creel & Creel 2002; Hayward *et al.* 2006b). It is not believed to result in autocorrelation since a fundamental determinant of whether a prey item is captured is the probability of the predator encountering that prey item, which varies with prey density (Hayward *et al.* 2006b).

3.2.1.3 *Prey demographics*

Ground surveys were used to establish ungulate species' demographics, as was done to monitor sex and age ratios of ungulates in the Kruger National Park (Mason 1990). The surveyed route, comprising a total of 72.8 km, consisted of three transects (Fig. 3.1). Transects were selected to cover as much of the reserve as possible, while reducing the risk of pseudoreplication (of counting the same animal more than once) by separating transects spatially and topographically. Surveys were performed in an open Toyota Land Cruiser with elevated seats, once a month from August 2010 to May 2011 and twice a month from June 2011 to May 2012. Each survey was performed over a three day period, with one transect driven per day, commencing at sunrise. Transects were driven on consecutive days to avoid substantial animal movement between transects and thus reduce the risk of animals being counted more than once. When a road had to be driven twice during a transect, animals were recorded only once for that section. The same two observers performed all surveys and binoculars were used to assist counting and classification. Wherever possible, ungulates were identified to species and classified into two age classes: juveniles (less than 12 months old) and adults (more than 12 months old). Adults were further classified as male or female, wherever possible. Knowledge of birth periods and peaks was useful for discriminating between age classes in seasonally breeding animals (Skinner & Chimimba 2005).

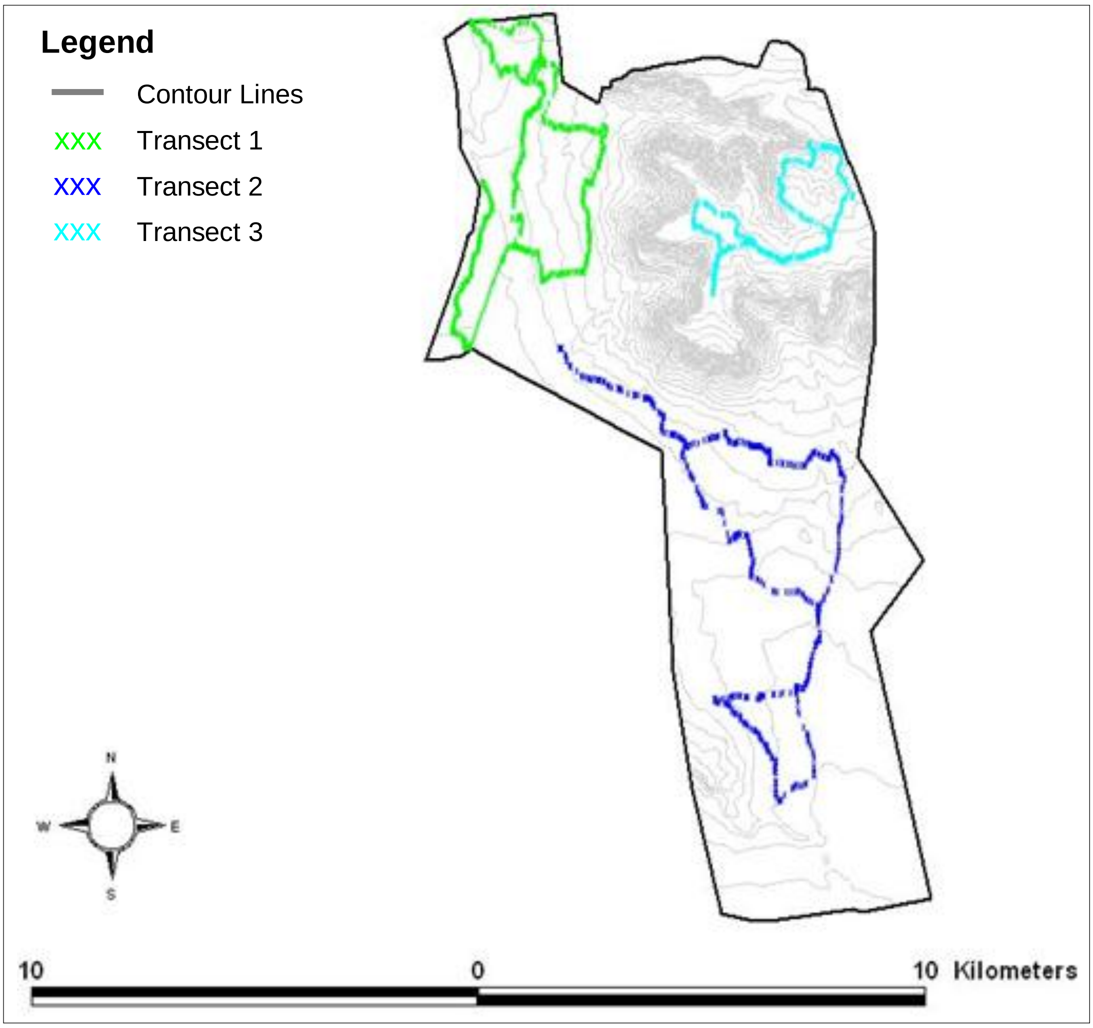


Figure 3.1. Map of the game-fenced section of Samara Private Game Reserve showing the three transects driven during ground surveys, overlaid on a contour map.

Based on the assumption that animals did not move between transects over the three consecutive survey days, ungulate counts from the three transects were pooled for each survey in order to increase the proportion of the population sampled. The average ratio of males to females and of adults to juveniles was calculated for each prey species between August 2010 and May 2011, and between June 2011 and May 2012. A weighted average was used, so that surveys which counted more individuals contributed more to the average ratio.

3.2.2 Additional dataset selection and manipulation

3.2.2.1 Cheetah diet

Cheetah kill data were obtained from a number of sites across South Africa for which appropriate data were available (Table 3.1; Table 2.1 for additional site information). Data were separated into three cheetah social class categories: female cheetah, solitary male cheetah and male coalition cheetah, though not all sites had data for all categories (Table

3.1). As a result of insufficient data classification at sites with both solitary female cheetah and female cheetah with cubs, at each site all female kill data were pooled to represent the female cheetah category.

3.2.2.2 *Prey abundance*

Wherever possible, prey abundance data and kill data coincided, with prey abundance data averaged over the years in which kills were recorded (Table 3.1). Where prey abundance data for kill years were not available, abundance data from the most closely corresponding time period available were used (Table 3.1). At Amakhala and Kwandwe, changes in prey abundance and sufficient kill data allowed the data to be divided into two time periods (Table 3.1). Temporal partitioning of kill data is common practice in studies on carnivore feeding ecology (Creel & Creel 2002; Hayward *et al.* 2006b). For sites representing more than one dataset (time period), each dataset is referred to by the name of the site followed by the last two digits of the years in which data collection commenced and finished (Table 3.1). I applied standardized visibility correction factors to abundance data obtained from aerial censuses (Table 3.1), as per Owen-Smith & Mills (2008).

3.2.2.3 *Prey demographics*

Published or unpublished data that detailed prey demographic ratios for the years most closely corresponding to kill years were obtained for each site (Table 3.1). In the Eastern Cape, prey demographic data were not available for Shamwari, and only available for kudu at Kwandwe (Bissett 2004). It was therefore assumed that both these reserves had prey demographic ratios corresponding to those observed on Amakhala, which neighbours Shamwari and is only 87 km from Kwandwe, all falling within the thicket biome and having similar management histories (Table 2.1). Sex ratios, but not age ratios, were available for Camdeboo, which neighbours Samara and shares similar habitat types and management histories (section 2.2.3 & Table 2.1). Prey age ratios at Samara were therefore assumed to be representative of prey at Camdeboo (Table 3.1).

Table 3.1. Sites, sources and details of cheetah kill, prey census and prey demographic data used in this study.
(F – female cheetah; M – solitary male cheetah; MC – male coalition cheetah; * aerial plus recruitment minus off-take; NOTE: When data from a site were divided temporally into two distinct datasets, the dataset is identified by the name of the site followed by the last two digits of the years in which data collection commenced and finished).

	Kill Data			**Census data**			**Demographic data**	
Site	**Source**	**Cheetah**	**Years**	**Source**	**Method**	**Years**	**Source**	**Years**
Amakhala 07-09	1	F; M	2007 – 2009	1	Road	2007 – 2009	1	2007 – 2009
Amakhala 10-11	1	F; M	2010 – 2011	1	Road	2010 – 2011	1	2010 – 2011
Camdeboo	5	F; M	2009 – 2012	5	Aerial	2009 & 2011	5 (sex) ; 8 (age)	2010 ; 2010 – 2012
KNP	2	F; MC	1987 – 1990	2	Aerial	1987 – 1989	10	1980 -1993
Kwandwe 03-04	3	F; M; MC	2003 – 2004	3	Aerial	2003 – 2004	1	2007 – 2011
Kwandwe 05-07	3	F; MC	2005 – 2007	3	Aerial	2005 & 2007	1	2007 – 2011
Mala Mala	4	F; MC	1988 – 2000	4	Aerial	2006 – 2011	10	1980 -1993
Phinda	6	F; M; MC	1998 – 2010	6	Aerial	2001 – 2010	11	09/1992 – 08/1995
Sabi	7	F; M; MC	2005 – 2011	7	Aerial	2006 – 2011	10	1980 -1993
Samara 10-11	8	F	06/2010 - 05/2011	8	Aerial	2010	8	08/2010 – 05/2011
Samara 11-12	8	F	06/2011 -05/2012	8	Aerial*	2011	8	06/2011 – 05/2012
Shamwari	9	F; M; MC	2004 – 2007	9	Aerial	2010 - 2011	1	2007 – 2011

[1]Amakhala (unpubl. data); [2]Mills *et al.* (2004); [3]Bissett (2004 & unpubl. data); [4]Radloff & du Toit (2004); [5]Mount Camdeboo (unpubl. data); [6]Phinda (unpubl. data); [7]Sabi Sand Wildtuin (unpubl. data); [8]This Study; [9]Shamwari (unpubl. data); [10]Mason (1990); [11]Hunter (1998).

3.2.3 *All sites – data categorization*

3.2.3.1 Prey mass and life-history categorization

As per Hayward *et al.* (2006b), each potential prey species listed as present at a site was allocated a standard "species-mass" of 75% of the adult female mass. Prey species were categorized into three weight ranges based on these masses (Mills *et al.* 2004). Hayward *et al.* (2006b) found cheetah to prefer species whose species-mass fell between 23 to 56 kg. This weight range was therefore classified as "Hayward's preferred" and represents medium-sized prey, with prey smaller than 23 kg classified as "small" and prey larger than 56 kg classified as "large" (Appendix Table C). Within each prey species, adult males, adult females and juveniles (hereafter referred to as species-demographic-classes) were each allocated a standard "species-class-mass", assuming juvenile mass to be 30% of the adult female mass (Appendix Table C). A value of 30% of the average adult mass was used by Radloff & du Toit (2004), however this is likely to overestimate juvenile mass in species where the adults display large sexual size dimorphism (e.g. eland), and thereby influence preferred prey weight analyses. Masses were obtained from Skinner & Chimimba (2005) for ungulates and primates, and Bissett (2004) for rodents and birds (Appendix Table C).

While Hayward *et al.* (2006b) classified prey species into five herding/social categories, these were consolidated into two categories for the purposes of this study: species which form large breeding herds and those that do not (Stuart & Stuart 2007; Appendix Table C). Each species was further categorized by sexual weaponry dimorphism, as either dimorphic (only males have horns), or non-dimorphic (both sexes have or lack horns; Appendix Table C). Males and females of each species were also individually categorized as horned or not horned (Stuart & Stuart 2007), and all juveniles were categorized as not horned (Appendix Table C).

3.2.3.2 Categorizing prey availability at each site

The total prey population available at each site was calculated by summing the census data for all prey species at that site. Both rhinoceros species (black *Diceros bicornis* and white) were omitted due to the reluctance of reserves to release count data on these ungulates. Given their large size and the low prospect of them serving as prey, this omission is not likely to affect cheetah diet analyses. Prey weighing more than 1200 kg was omitted, since a giraffe was the largest prey species recorded to have been killed in Hayward *et al.* (2006b). Carnivores occasionally appear in the kill records, but are rarely consumed (Radloff & du Toit 2004), and are therefore omitted.

3.2.4 Data analysis

While an ideal cheetah diet analysis would be one that simultaneously assessed the influence of prey demographics and cheetah social structure on cheetah prey preferences, dataset limits precluded this multi-factorial option. Instead the following analyses were undertaken.

3.2.4.1 Size and age of prey killed

For this analysis, kill data from the three cheetah social classes were pooled. Prey was divided into the following categories:

1. Prey weight
2. Prey age

The proportion that each prey category comprised of the (a) total kills and (b) total population at each site was calculated. Mean proportions across sites were then calculated. The proportion of adults versus juveniles killed in each prey species was also calculated, and a mean obtained across sites.

3.2.4.2 Size and sex of prey killed

For this analysis, kill data from the three cheetah social classes were pooled. Prey was divided into the following categories:

1. Prey weight
2. Prey sex
3. Prey sexual weaponry dimorphism

The proportion that each prey category comprised of the (a) total kills and (b) total population at each site was calculated. In both the Hayward's preferred and small prey weight categories, adult prey was also divided into the herding categories and the proportion that each category comprised of the (a) total kills and (b) total population at each site was calculated. Mean proportions across sites were then calculated.

3.2.4.3 Species and demographic class of prey killed

For this analysis kill data from the three cheetah social classes were analysed separately. For each site I calculated the proportion that each species-demographic-class constituted of the (a) total kills and (b) total population at that site.

3.2.4.4 Comparison of kill sizes across sites

In order to compare the size distribution of kills between sites, for each cheetah social class the proportion of kills that fell within each of eight mass categories was calculated for each site, based on species-class-masses. Despite Hayward *et al.* (2006d) finding cheetah to prefer prey below 56 kg, on average, 51% (±5%) of kills across study sites were larger than 56kg. Eight categories were therefore used in order to adequately differentiate kills of different sizes without differentiating data so finely that comparisons were between very small sample sizes. The eight categories, each comprising a mass range of 39 kg, were selected to encompass the total mass range of prey killed. The eight categories were 1 to 39 kg; 40 to 79 kg; 80 to 119 kg; 120 to 159 kg; 160 to 199 kg, 200 to 239 kg, 240 to 279 kg and 280 to 319 kg .

3.2.4.5 *<u>Average, maximum and minimum kill mass</u>*

At each site, the average, maximum and minimum kill masses were calculated for each represented cheetah social class, and means obtained across sites. There was high variability in both the average mass and distribution of masses of prey killed by each cheetah social class between sites (see results). Because I wished to specifically investigate the relative differences between prey masses killed by each cheetah social class, the average mass of prey killed by solitary male and male coalition cheetah was standardized relative to the average mass of prey killed by female cheetah at each site. This method therefore controlled for variation in kill sizes between sites. Mean standardized masses were then calculated across sites. No standardization was performed on maximum and minimum prey masses since the largest (adult male giraffe) and smallest (juvenile vervet monkey) listed prey were available at all sites (Appendix Table C).

3.2.4.6 *<u>Prey preference analyses</u>*

Jacobs' Index (J.I.) values (Jacobs 1974) were calculated at each site for each prey category outlined in sections 3.2.4.1, 3.2.4.2 and 3.2.4.3, following Hayward *et al.* (2006b).

$$J.I._i = \frac{(r_i - p_i)}{(r_i + p_i - 2r_i p_i)}$$

J.I. standardizes the relationship between prey relative abundance p_i (i.e. the proportion p that prey category i makes up of the total abundance of censused prey at a site) and the proportion of cheetah kills that prey category i comprises r_i, to a value between +1 and -1. This scaling means that +1 indicates maximum preference, -1 indicates maximum avoidance and 0 indicates a prey category is killed relative to its abundance. The mean J.I. value for each prey category was calculated across sites.

3.2.5 *<u>Statistical analysis</u>*

3.2.5.1 *<u>Prey demographics</u>*

The mean J.I. value of each prey category outlined in sections 3.2.4.1, 3.2.4.2 and 3.2.4.3 was tested for significant preference or avoidance across sites using a single sample t-test against a mean of zero if data conformed to the assumptions of normality, and a Wilcoxon signed-rank test if not (Zar 1984). A value significantly greater than zero indicated preference, a value not significantly different from zero indicated prey killed relative to its abundance and a value significantly less than zero indicated avoidance. In situations where significant avoidance or preference was found for:

a. both ages in a weight range
b. both sexes in a weight range and weaponry dimorphism category
c. both sexes in a weight range and herding category,

J.I. values from all sites were used to test for significant difference in J.I. between the age or sex classes in the category using a paired t-test if data met the assumptions of normality, and a Wilcoxon paired-sample test if not (Zar 1984). Paired tests were used to account for the influence of site on preference value. Because insufficient demographic data precluded a preference analysis of prey in the small weight range, paired t-tests were performed to compare the average proportions of kills in the small prey weight range that fall within each sex, age, weaponry and herding category.

The mean proportion that prey adults constitute of kills in each prey species (section 3.2.4.1) was regressed against prey species-mass using a segmented model (Davies 1987). This model was used because it detects any threshold values or 'break-points', at which the relationship between the predictor and response variables changes significantly.

3.2.5.2 <u>Cheetah social class - comparison of kill masses across sites</u>

Primer 6 (Primer-E Ltd 2006) was used to calculate Bray-Curtis similarity indices (Bray & Curtis 1957) of the proportions of cheetah kills within eight mass categories between sites (section 3.2.4.4). Kills by each cheetah social class were compared separately. Ordination by non-metric Multidimensional Scaling (MDS) plots were generated to display the position of each site in two-dimensional Euclidean space where the relative distances between sites reflects their approximate degree of similarity (Kruskal & Wish 1978).

3.2.5.3 <u>Cheetah social class - prey mass</u>

Differences between mean, standardized mean, maximum and minimum prey mass killed by each cheetah social class were analysed using a Kruskal-Wallace test and *post hoc* Mann-Whitney tests, which were Bonferroni corrected to control for multiple analyses (Zar 1984).

3.2.5.4 <u>Preferred prey weight range: a new approach</u>

By plotting the cumulative mean J.I. value of each prey item against its mass, cumulative from the lowest prey mass, and fitting a segmented model (Davies 1987), any threshold prey masses (break-points) at which the relationship between prey mass and degree of preference significantly changes can be detected. A value of one was added to each mean J.I. value because the importance lies in the relative degree of increase in cumulative J.I. with mass, as opposed to actual values, and to avoid negative J.I. values which would subtract from the cumulative J.I.

Prey were included if they had two or more J.I. values contributing to the calculated mean. While Hayward *et al.* (2006b) calculated preferred prey weight range of cheetah using prey which weighed less than 200 kg, this study aimed to calculate both preferred prey weight ranges, and those avoided. No upper prey mass cut-off was therefore used. The proportion of the total cheetah kills and prey population, in each weight range identified by the model break-points, was then calculated for each site, and corresponding J.I. values were calculated. A mean J.I. value for each weight range across sites was tested for significant difference from zero (section 3.2.5.1). Each prey weight range could thus be identified as preferred, killed relative to its abundance, or avoided. The mean proportions of kills, across sites, that fell within the weight ranges found to be preferred, killed relative to their abundance or avoided were then calculated.

The preferred weight ranges of different cheetah social classes were calculated separately as cheetah social class was found to influence diet (see results). Prey species-demographic-classes were included as prey demographics were found to influence diet (see results). The presence or absence of weaponry in each species-demographic-class was accounted for as weaponry influenced diet, while herding behaviour was not included as it did not influence diet (see results).

3.2.5.5 <u>Statistical packages used</u>

Segmented models were calculated in the statistical package R (R Development Core Team 2008). All other statistical tests were performed in Statistica 10 (StatSoft Inc 2011), at a significance level of 0.05. Adjusted r^2 values are reported in all cases.

3.3 Results

3.3.1 <u>Cheetah kill summary</u>

In total, the 12 datasets comprised 1290 cheetah kills (Table 3.2). All 12 datasets included female cheetah kills, while seven datasets included solitary male cheetah kills and seven datasets included male coalition cheetah kills. Solitary male cheetah kills from Kwandwe 03-04, and male coalition cheetah kills from Sabi and Shamwari, were omitted due to small sample sizes.

Table 3.2. The number of kills recorded for three cheetah social classes, at 12 sites in South Africa (* omitted from analyses).

Site	Total kills	Female cheetah	Solitary male cheetah	Male coalition cheetah
Amakhala 07-09	148	80	68	0*
Amakhala 10-11	144	101	43	0*
Camdeboo	36	24	12	0*
Mala Mala	139	108	0*	31
Phinda	276	216	26	34
Kwandwe 03-04	171	115	4*	52
Kwandwe 05-07	120	77	0*	43
KNP	66	33	0*	33
Sabi	36	17	14	5*
Samara 10-11	29	29	0*	0*
Samara 11-12	35	35	0*	0*
Shamwari	90	61	19	10*
Total	**1290**	**896**	**186**	**208**

3.3.2 The influence of prey demographics on cheetah diet

There were insufficient demographic data for small prey, therefore no preference analyses could be performed on this weight range. Cheetah diet in this weight range was therefore analysed using kill proportions instead of preference values.

3.3.2.1 Prey age

When considered relative to their abundance in the prey community, large prey adults are avoided (t = -14.01, d.f. = 11, $p < 0.001$; Fig. 3.2), while large prey juveniles are preferred (t = 18.40, d.f. = 11, $p < 0.001$; Fig. 3.2). Prey adults and juveniles in Hayward's preferred weight range are killed relative to their abundance (t = 0.45, d.f. = 11, p = 0.66 and t = 1.97, d.f. = 11, p = 0.08, respectively; Fig. 3.2). Within the small prey weight range adults comprise a significantly greater percentage of kills than do juveniles (87 ± 1.1% versus 13 ± 1.1%; t = 6.33, d.f. = 11, $p < 0.001$).

There is a strong segmented relationship between the species-mass of each prey species, and the average proportion that adults constitute of kills in that prey species (r^2 = 0.85, n = 21; Fig. 3.3). The model identifies a significant change in the relationship between prey species-mass and proportion of adults killed at a mass of 126 kg (Davies Test $p < 0.001$). For prey weighing less than 126 kg, as species-mass increases there is a significant decrease in the average proportion that adults constitute of kills (r^2 = 0.69, n = 16, F = 31.66, $p < 0.001$; Fig. 3.3). For prey weighing more than 126 kg, there is no significant influence of increasing prey mass on the proportion of adults versus juveniles killed (r^2 = -0.22, n = 5, *F* = 0.28, *p* = 0.64; Fig. 3.3).

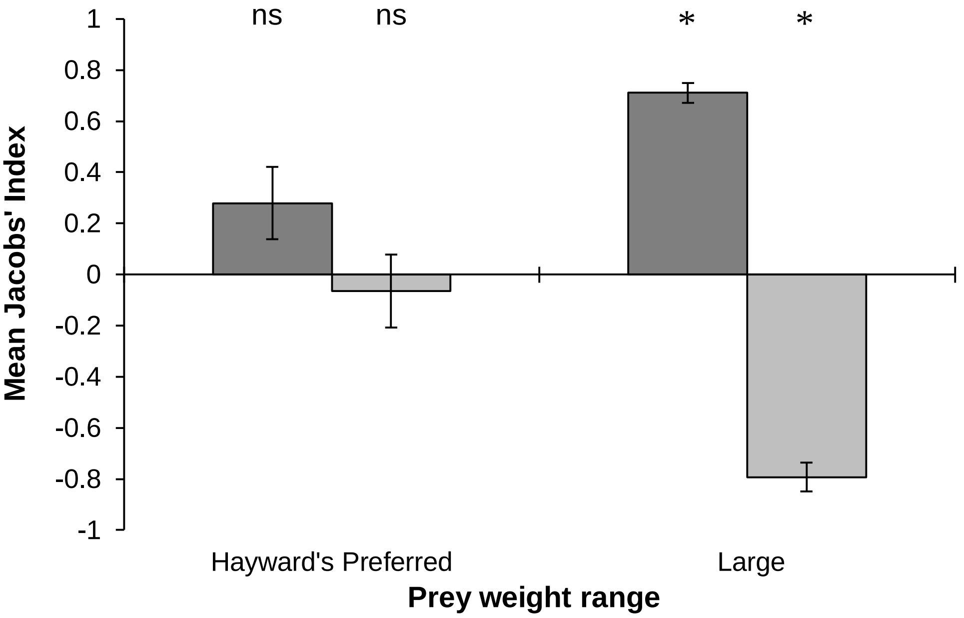


Figure 3.2. The mean Jacobs' Index values (± SE) for juvenile prey (dark grey) and adult prey (light grey) in each of two weight ranges. (Small prey weight range excluded due to insufficient demographic census data preventing preference analysis). * - significant preference or avoidance, ns - not significant (killed relative to its abundance).

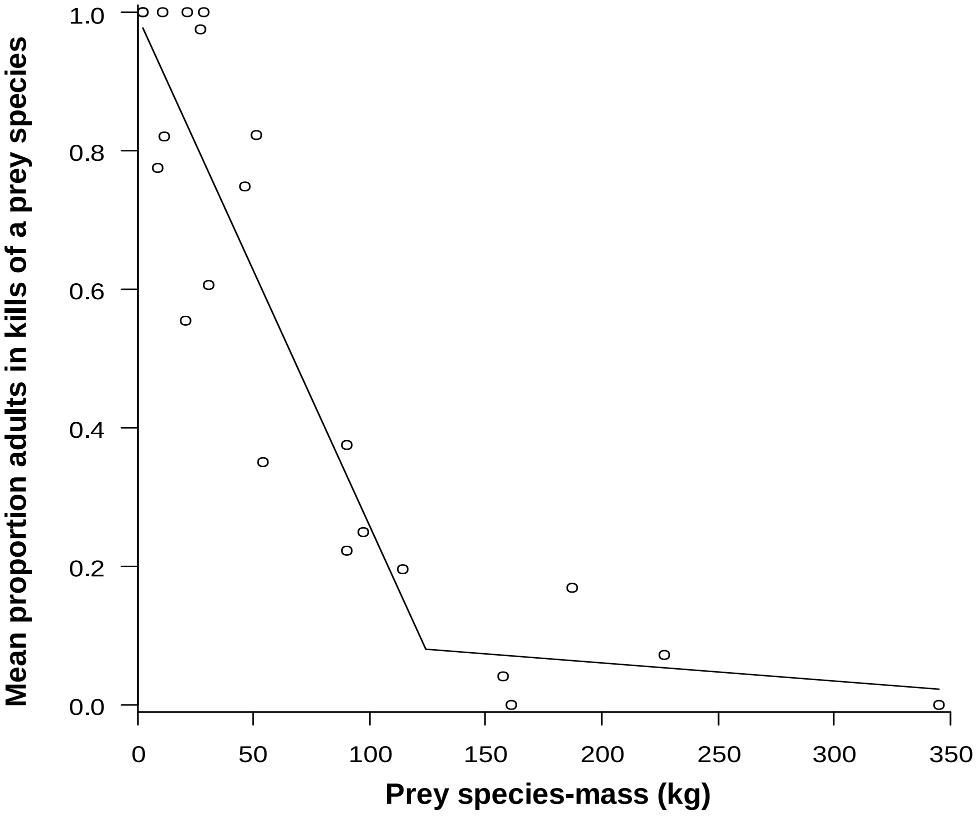


Figure 3.3. Segmented relationship between prey species-mass and the proportion that adults constitute of the kills in each species.

3.3.2.2 *Prey sex - prey sexual weaponry dimorphism*

Both males and females of large, sexually weaponry dimorphic prey are avoided (t = -6.70, d.f. = 12, p < 0.001 and t = -3.98, d.f. = 12, p < 0.005, respectively; Fig. 3.4a), as are both males and females of large sexually non-dimorphic prey (t = -9.19, d.f. = 12, p < 0.001 and t = -20.54, d.f. = 12, p < 0.001, respectively; Fig. 3.4b). However, females of large sexually dimorphic prey are significantly less avoided than males (t = -3.05, d.f. = 11, p = 0.01). This does not hold true for large non-dimorphic prey (t = 1.91, d.f. = 11, p = 0.08). Both the males and females of sexually weaponry dimorphic prey in Hayward's preferred weight range are killed relative to their abundance (t = 1.90, d.f. = 9, p = 0.09 and t = -0.61, d.f. = 9, p = 0.56, respectively; Fig. 3.4a), as are both males and females of prey in Hayward's preferred weight range that are not sexually dimorphic (t = -0.25, d.f. = 8, p = 0.81 and t = -0.51, d.f. = 8, p = 0.63, respectively; Fig. 3.4b). Within the small prey weight range, the relative contribution of males and females to the small prey adults killed does not differ significantly (52 ± 3% versus 48 ± 3%, t = 0.30, d.f. = 6, p = 0.77).

3.3.2.3 *Prey sex - prey herding behaviour*

Within Hayward's preferred weight range, both the males and females of prey which form large breeding herds are killed relative to their abundance (t = 0.62, d.f. = 11, p = 0.52 and t = -0.20, d.f. = 11, p = 0.25, respectively; Fig. 3.5). The males of prey which do not form large breeding herds are killed relative to their abundance (t = -1.76, d.f. =6, p = 0.13; Fig. 3.5). The females of prey which do not form large breeding herds are preferred (t = 4.23, d.f. = 6, p = 0.005; Fig. 3.5).

For non-herding prey in the small prey weight range, the proportion that males and females comprise of prey adults killed does not differ significantly (43 ± 2% versus 57 ± 2%, t = -0.86, d.f. = 10, p = 0.41). The only small herding prey species are baboons and vervet monkeys, and with only two baboons and no monkeys killed across all sites, no analyses could be performed on this category.

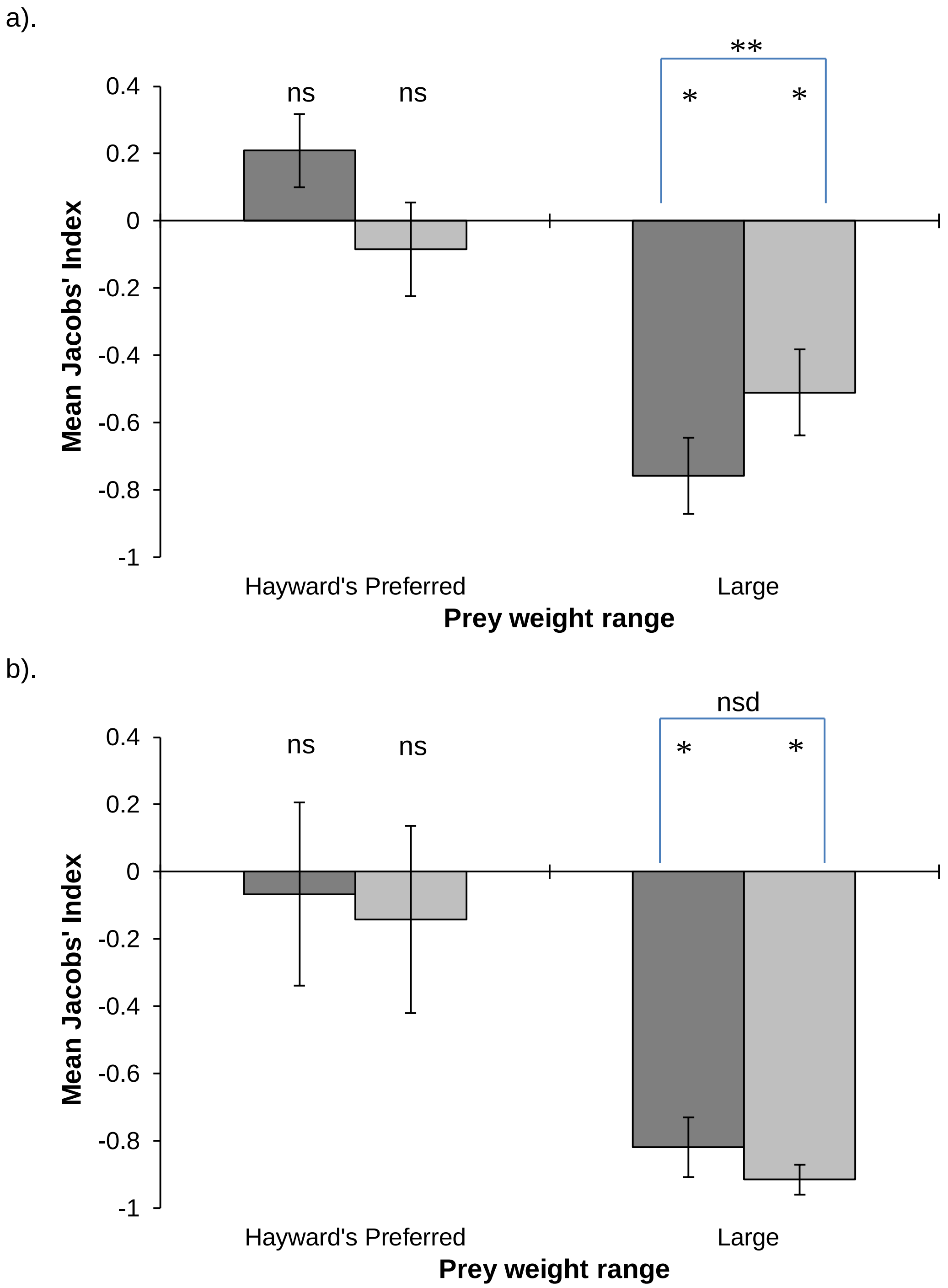


Figure 3.4. The mean Jacobs' Index values (± SE) for male prey (dark grey) and female prey (light grey) in each of two weight ranges, for prey displaying (a) sexual weaponry dimorphism, and (b) no dimorphism. (Small prey weight range excluded due to insufficient demographic census data preventing preference analysis). * - significant preference or avoidance, ns - not significant (killed relative to its abundance), ** - significant difference in preference/avoidance, nsd - no significant difference in preference/ avoidance

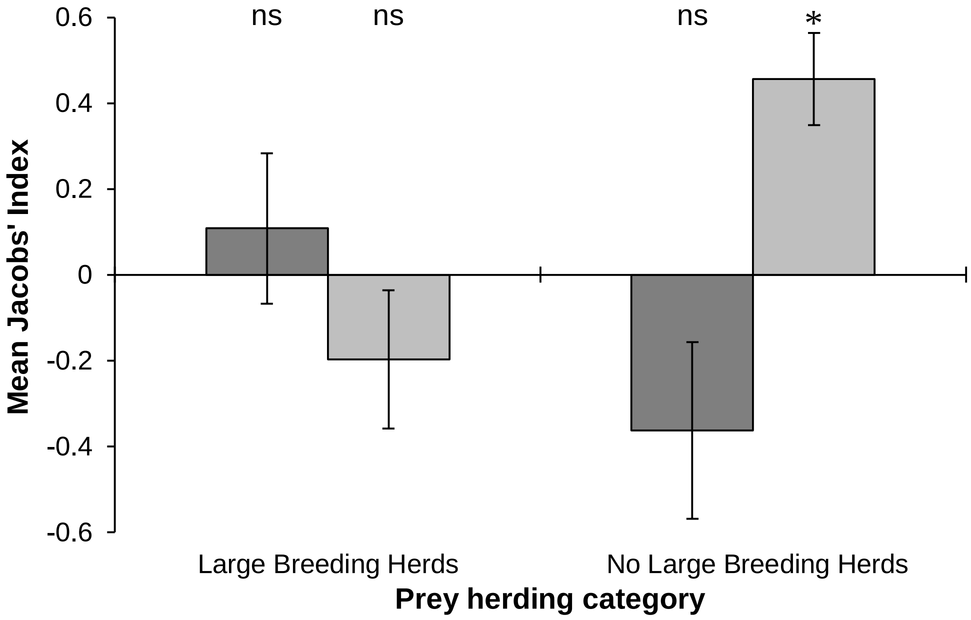


Figure 3.5. The mean Jacobs' Index values (± SE) for male prey (dark grey) and female prey (light grey) in Hayward's preferred weight range, for prey that do and do not form large breeding herds. (Small prey weight range excluded due to insufficient demographic census data preventing preference analysis). * - significant preference or avoidance, ns - killed relative to its abundance.

3.3.3 <u>The influence of cheetah social class on cheetah diet</u>

3.3.3.1 <u>Differences in average prey mass</u>

Male coalitions kill prey with an average mass of 71 kg (± 12 kg), solitary male cheetah kill prey with an average mass of 58 kg (± 8 kg) and female cheetah kill prey with an average mass of 44 kg (± 5 kg). These differences are not significant (H = 5.95, n = 23, p = 0.05), primarily as a result of the large variation in the data.

The range and frequency of masses of prey killed by female cheetah in the lowveld (KNP, Mala Mala and Sabi) are similar, the masses of prey killed by female cheetah in Phinda and the Eastern Cape, besides Kwandwe and Samara are similar, the masses of prey killed in the two Kwandwe datasets are very similar and Samara 10-11 and Samara 11-12 are outliers (Fig. 3.6a). The masses of prey killed by solitary male cheetah in the lowveld and Phinda are similar, as are the masses of prey killed in the coastal Eastern Cape, and Camdeboo is an outlier (Fig. 3.6b). The masses of prey killed by male coalition cheetah in the lowveld and Phinda are similar and the two Eastern Cape sites (Kwandwe 03-04 and Kwandwe 05-07) are outliers (Fig. 3.6c).The large variation in average prey mass therefore depicts the inter-site variability in kill sizes.

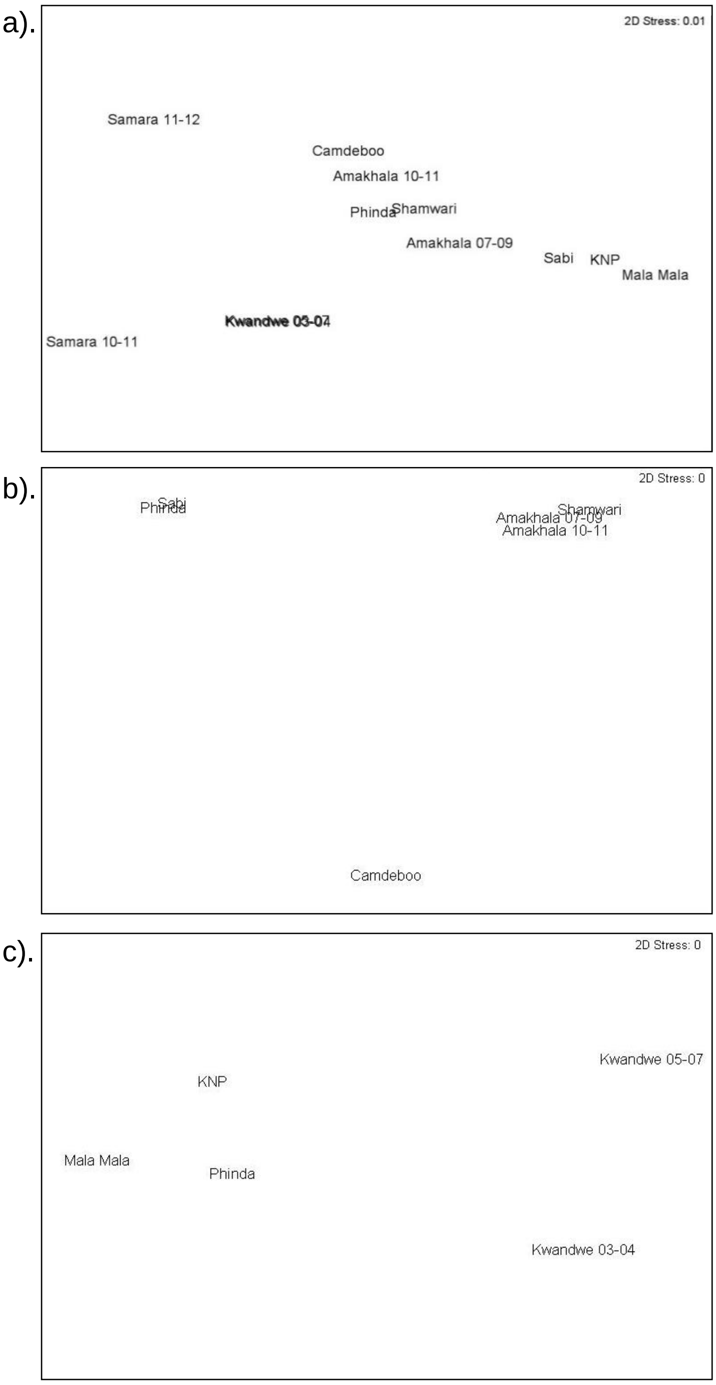


Figure 3.6. Multidimensional scaling (MDS) plot in 2 dimensions of Bray-Curtis similarities between sites, based on proportional kill data in eight prey mass categories, for (a) female cheetah, (b) solitary male cheetah and (c) male coalition cheetah.

To control for these inter-site differences, mean standardized prey masses were compared. The mean standardized prey mass killed by solitary male and male coalition cheetah differed from that killed by female cheetah ($H = 18.60$, n = 23, $p < 0.001$; Fig. 3.7). Relative to that of female cheetah, both solitary male and male coalition cheetah kill significantly larger prey ($U < 0.001$, $z = -3.20$, $p < 0.005$ and $U < 0.001$, $z = -3.00$, $p < 0.005$, respectively), with male coalitions taking larger prey than solitary males ($U = 2$, $z = -2.28$, $p = 0.02$).

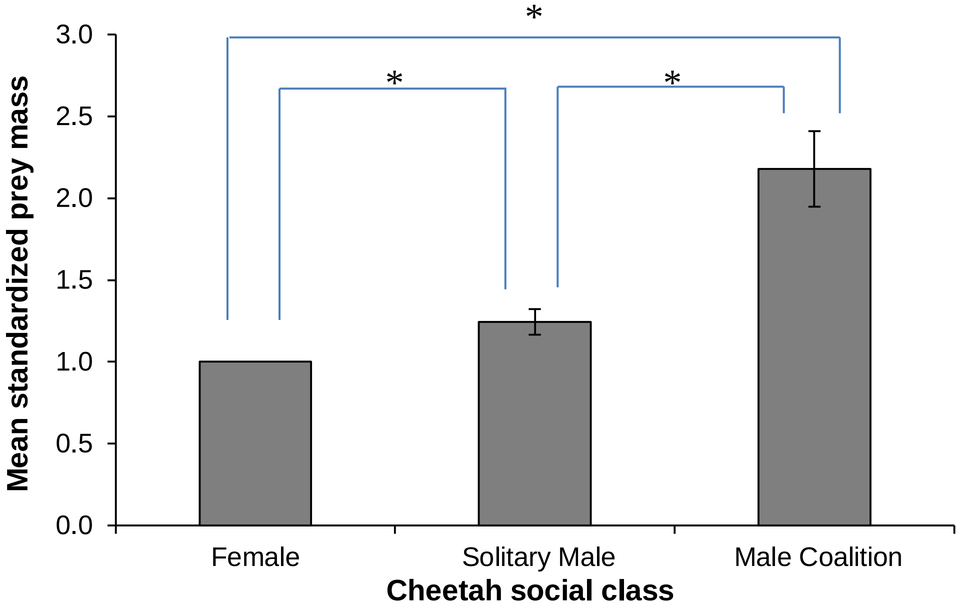


Figure 3.7. The mean standardized mass of prey killed by solitary male and male coalition cheetah, relative to that killed by female cheetah, at each site (± SE). * - significant difference.

3.3.3.2 Differences in maximum and minimum prey mass

The three cheetah social classes did not kill differently sized minimum prey (H = 4.14, n = 23, p = 0.13; Fig. 3.8a) but they did kill significantly different maximum sized prey (H = 7.96, n = 23, p = 0.02; Fig. 3.8b). This is as a result of male coalition cheetah killing a larger maximum prey mass than both female and solitary male cheetah (U = 83.5, z = -2.53, p = 0.005 and U = 23, z = -2.28, p = 0.01, respectively). There is no significant difference between the maximum mass of prey killed by female and solitary male cheetah (U = 34, z = 0.14, p = 0.44).

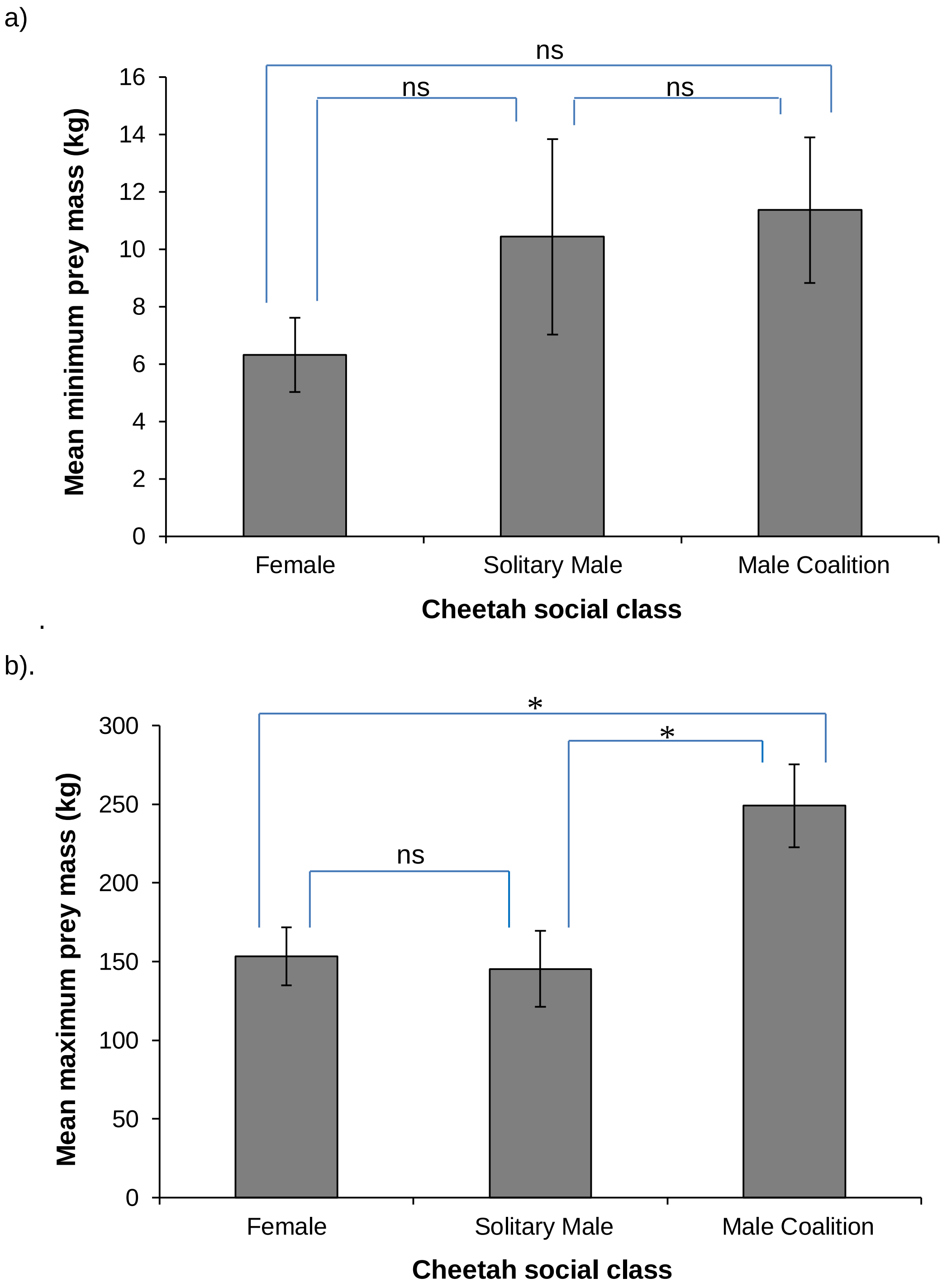


Figure 3.8. The mean (a) minimum and (b) maximum mass of prey killed by the three cheetah social classes (± SE). * - significant difference, ns - no significant difference.

3.3.4 <u>The preferred prey weight range of cheetah</u>

3.3.4.1 <u>Identifying changes in the relationship between prey mass and preference</u>

For female cheetah, the relationship between prey mass and cumulative J.I. in prey (species-demographic-classes) with horns changes at 71 kg ($r^2 = 0.91$, n = 30, Davies Test $p < 0.001$; Fig. 3.9). The relationship between prey mass and cumulative J.I. in prey without horns changes at 48 kg and 138 kg ($r^2 = 0.99$, n = 37, Davies Test $p < 0.001$; Fig 3.9). The higher total cumulative J.I. for non-horned prey than for horned prey is an artefact of the number of prey items that contributed a non-zero J.I. value to these totals (23 and 11, respectively; Fig. 3.9).

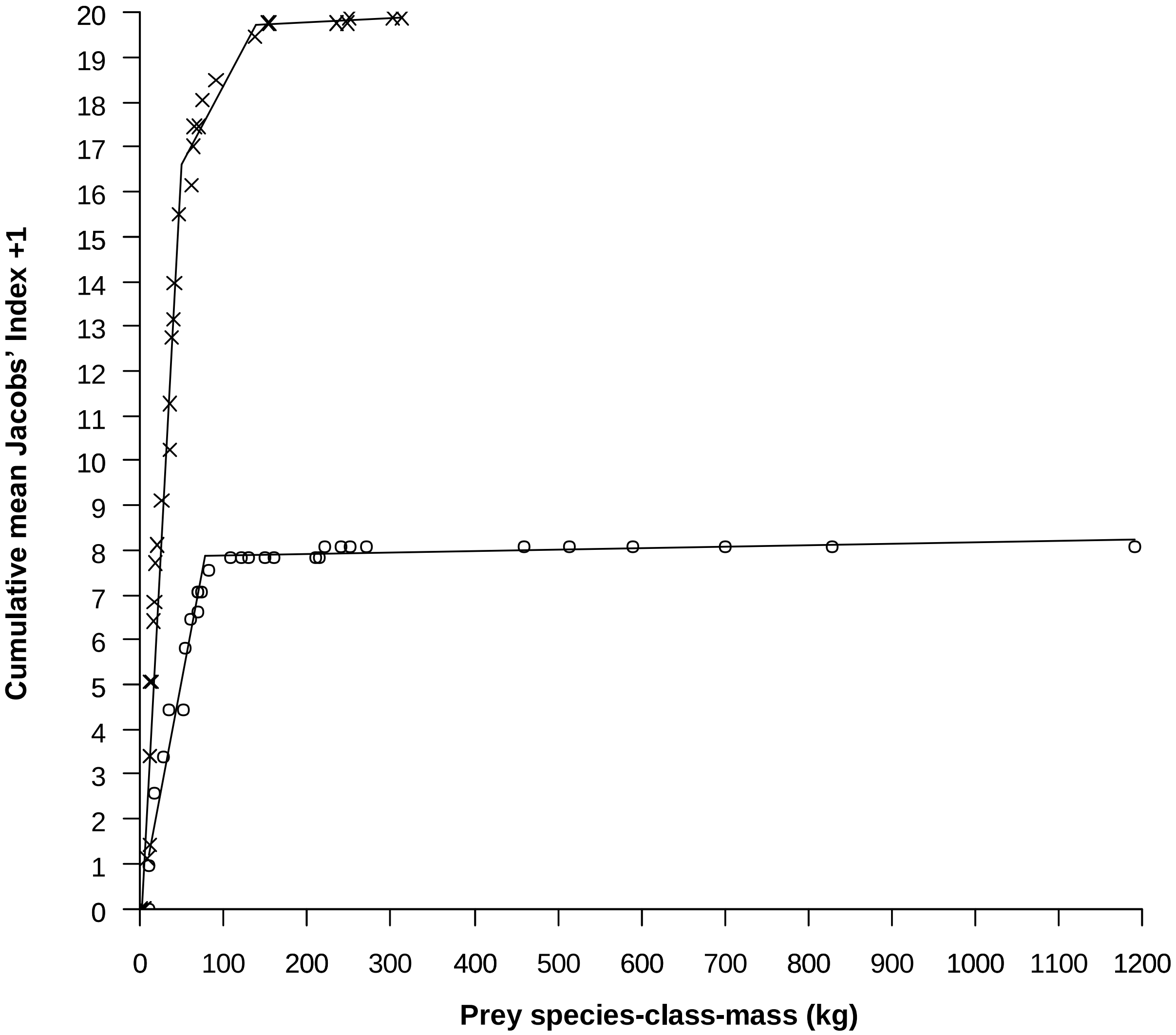


Figure 3.9. Segmented relationship between the mass of each prey species-demographic-class and the respective cumulative mean Jacobs' Index +1 for female cheetah, for horned (circles) and non-horned (crosses) prey.

For solitary male cheetah, the relationship between prey mass and cumulative J.I. in prey with horns changes at 81 kg and 152 kg ($r^2 = 0.97$, n = 26, Davies Test $p < 0.001$; Fig. 3.10). The relationship between prey mass and cumulative J.I. in prey without horns changes at 75 kg and 142 kg ($r^2 = 0.98$, n = 28, Davies Test $p < 0.001$; Fig. 3.10). The higher total cumulative J.I. for non-horned prey than for horned prey is an artefact of the number of prey items that contributed a non-zero J.I. value to these totals (17 and 10, respectively; Fig. 3.10).

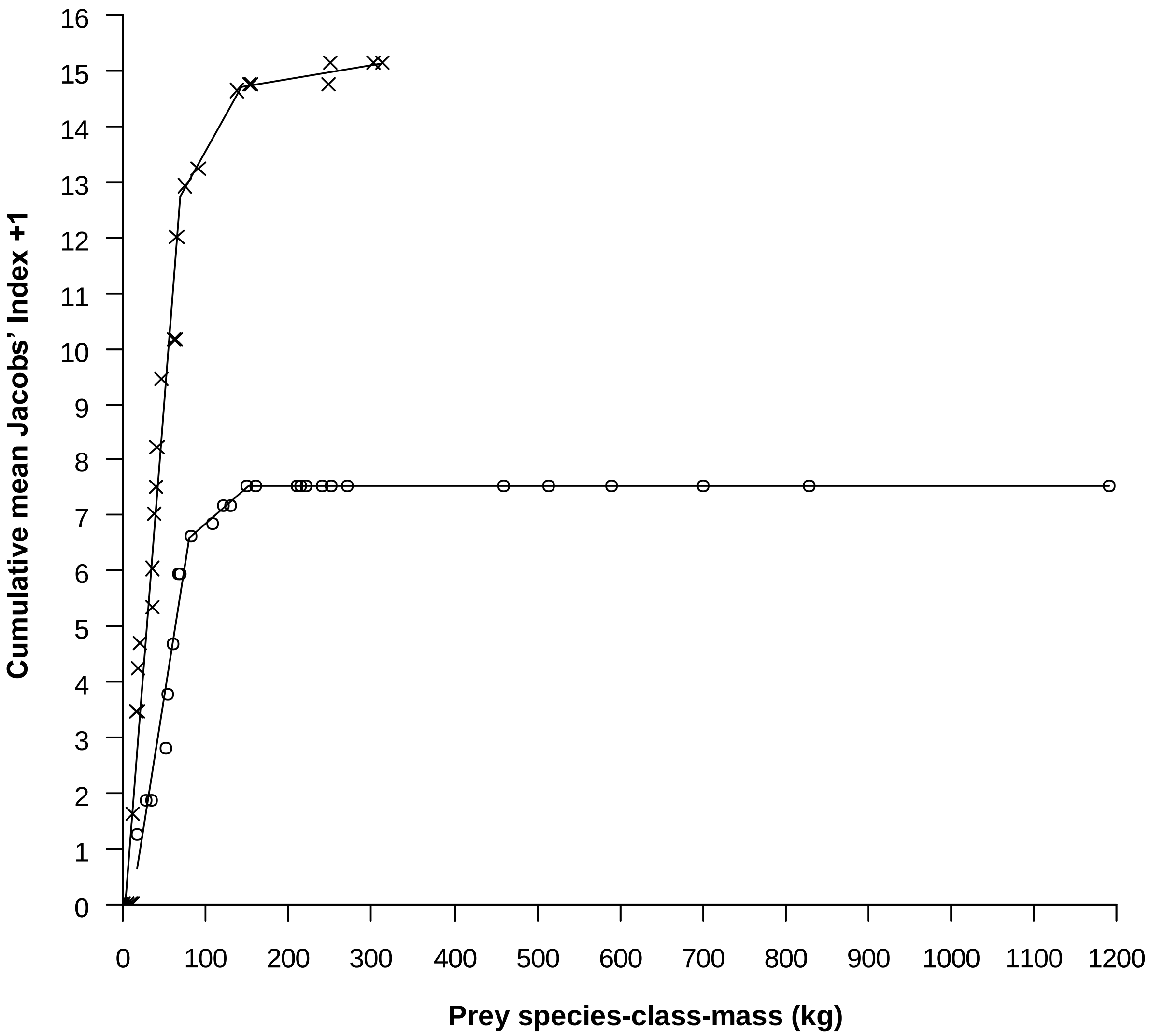


Figure 3.10. Segmented relationship between the mass of each prey species-demographic-class and the respective cumulative mean Jacobs' Index +1 for solitary male cheetah, for horned (circles) and non-horned (crosses) prey.

For male coalition cheetah, the relationship between prey mass and cumulative J.I. in prey with horns changes at 86 kg and 303 kg ($r^2 = 0.99$, n = 27, Davies Test $p < 0.001$; Fig. 3.11). The relationship between prey mass and cumulative J.I. in prey without horns changes at 96 kg ($r^2 = 0.99$, n = 27, break point $p < 0.001$; Fig. 3.11). The higher total cumulative J.I. for non-horned prey than for horned prey is an artefact of the number of prey items that contributed a non-zero J.I. value to these totals (17 and 12, respectively; Fig. 3.11).

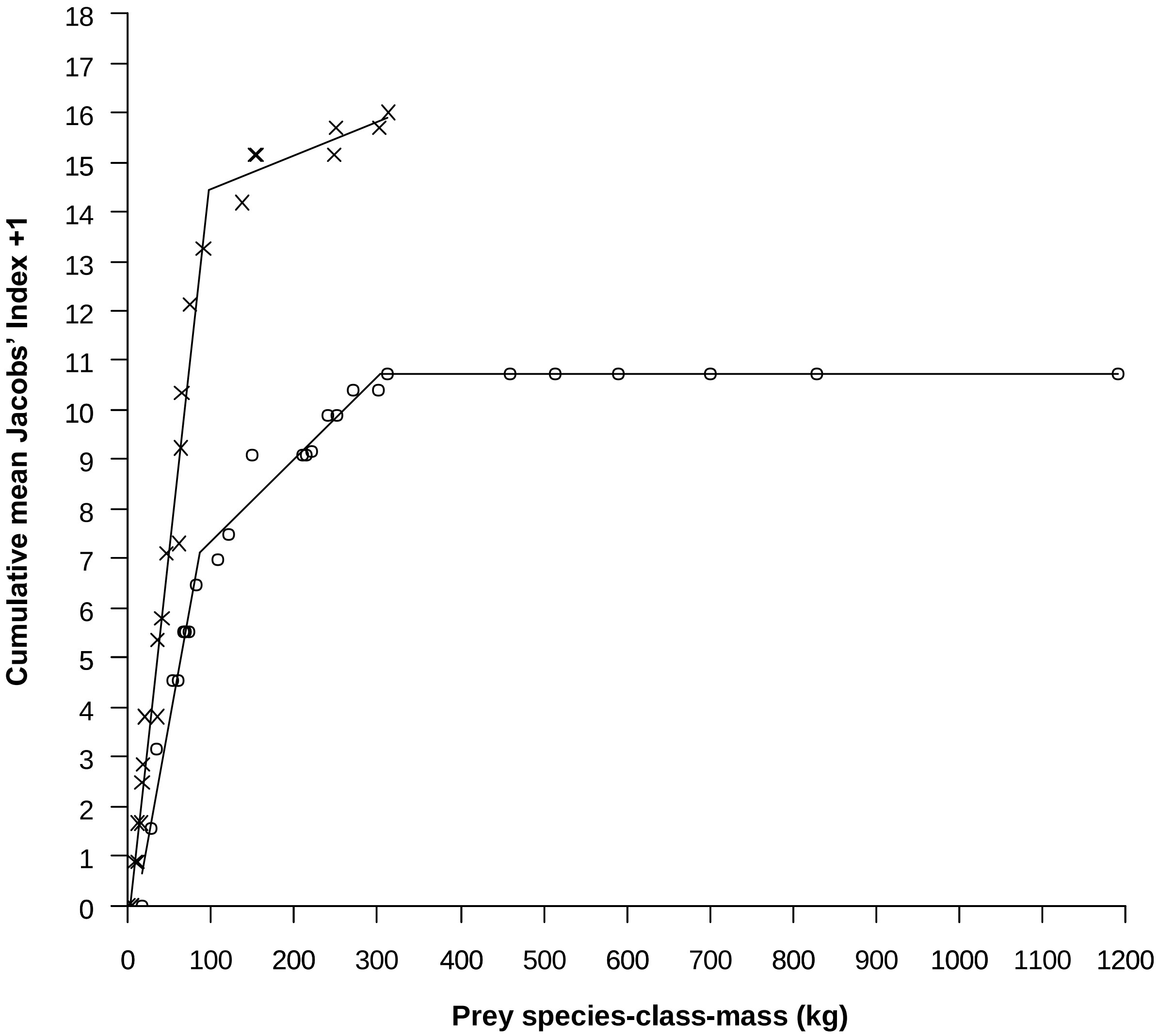


Figure 3.11. Segmented relationship between the mass of each prey species-demographic-class and the respective cumulative mean Jacobs' Index +1 for male coalition cheetah, for horned (circles) and non-horned (crosses) prey.

3.3.4.2 Calculating prey preference within identified weight ranges

Female cheetah do not display a preference for horned prey in any of the identified weight ranges. They take horned prey weighing less than 71 kg relative to its abundance (JI = 0.00 ± 0.53, t = -0.01, d.f. = 11, p = 0.99), and avoid horned prey larger than 71 kg (JI = -0.82 ± 0.30, t = -9.60, d.f. = 11, p < 0.001; Fig. 3.12). Female cheetah prefer non-horned prey with a mass of less than 48 kg (JI = 0.68 ± 0.26, t = 9.13, d.f. = 11, p < 0.001; Fig. 3.12), kill non-horned prey between 48 kg and 138 kg relative to its abundance (JI = 0.10 ± 0.45, t = 0.72, d.f. =11, p = 0.49; Fig. 3.12), and avoid non-horned prey with a mass larger than 138 kg (J.I. = -0.78 ± 0.31, t = -8.60, d.f. = 11, p < 0.001; Fig. 3.12).

Solitary male cheetah do not have a preference for horned prey in any of the identified weight ranges. They kill horned prey with a mass less than 81 kg relative to its abundance

(JI = 0.23 ± 0.42, $t = 1.32$, d.f. = 5, $p = 0.24$; Fig. 3.12), and avoid horned prey larger than 81 kg (81 to 152 kg: JI = -0.57 ± 0.52, $t = -2.61$, d.f. =5, $p = 0.048$; > 152 kg: J.I. = -1.00 ± 0, n = 6; Fig. 3.12). Solitary male cheetah display a preference for non-horned prey with a mass of less than 75 kg (J.I. = 0.57 ± 0.11, $t = 13.03$, d.f. = 5, $p < 0.001$; Fig. 3.12). Non-horned prey with a mass between 75 kg and 142 kg is killed relative to its abundance (J.I. = 0.49 ± 0.75, $t = 1.60$, d.f. = 5, $p = 0.17$; Fig. 3.12), and non-horned prey larger than 142 kg is avoided (J.I. = -0.82 ± 0.30, $t = 0.30$, d.f. = 5, $p < 0.005$; Fig. 3.12).

Male coalition cheetah do not have a preference for horned prey of any size. Horned prey with a mass of less than 303 kg is killed relative to its abundance (< 86 kg: J.I. = 0.11 ± 0.32, $t = 0.80$, d.f. = 4, $p = 0.47$; 86 to 303 kg: J.I. = -0.49 ± 0.48, $t = -2.27$, d.f. = 4, $p = 0.09$; Fig. 3.12) and horned prey larger than 303 kg is avoided (J.I. = -1.00 ± 0, n = 6; Fig. 3.12). Male coalition cheetah display a preference for non-horned prey with a mass less than 96 kg (J.I. = 0.38 ± 0.18, $t = 4.68$, d.f. = 4, $p = 0.009$; Fig. 3.12). Non-horned prey with a mass between 96 kg and 313 kg is killed relative to its abundance (J.I. = -0.14 ± 0.56, $t = -0.57$, d.f. = 4, $p = 0.60$; Fig. 3.12). The heaviest non-horned prey available to cheetah were male plains zebra, at 313 kg (Appendix Table C). There are no horned prey with a mass between 303 kg (above which horned prey are avoided) and 313 kg. Therefore, given the available prey, the mass at which prey become avoided by male coalitions is the same in horned and non-horned prey.

3.3.4.3 Summary of cheetah diet based on identified prey weight ranges

The mean percentages of kills made by female, solitary male and male coalition cheetah that fall within the weight ranges found to be preferred are 65 ± 2%, 59 ± 3% and 57 ± 3%, respectively (Fig 3.13). The mean percentages of kills made by female, solitary male and male coalition cheetah that fall within the weight ranges of prey killed relative to their abundance are 24 ± 1%, 33 ± 2% and 42 ± 4%, respectively (Fig. 3.13). Therefore, the mean percentages of kills made by female, solitary male and male coalition cheetah that fall within the weight ranges found to be either preferred or killed relative to their abundance (i.e. not avoided) are 89 ± 1%, 92 ± 1% and 99 ± 0.003%, respectively (Fig. 3.13). Prey within the weight ranges found to be preferred and killed relative to their abundance by each cheetah social class are hereafter referred to as “accessible prey”.

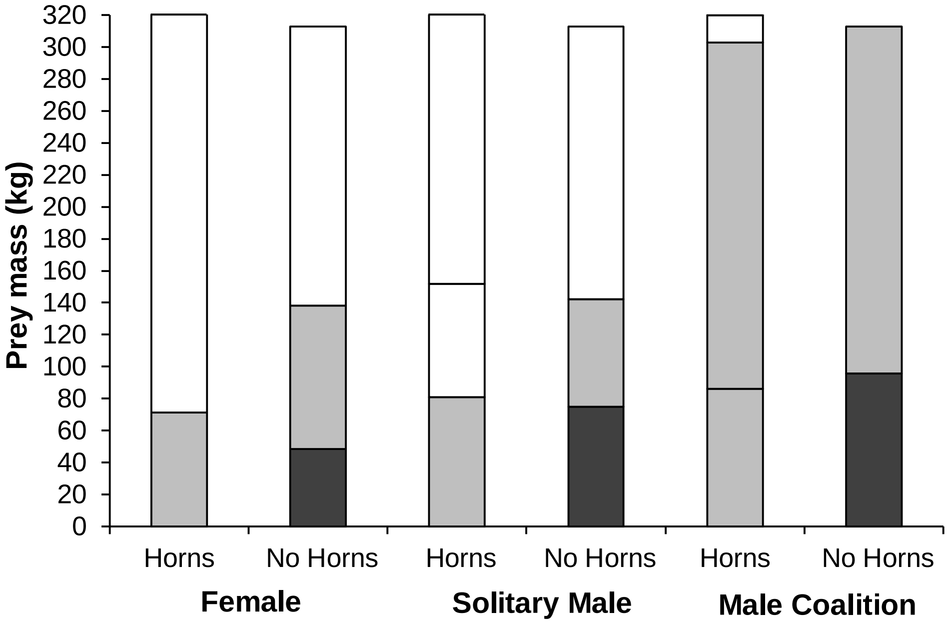


Figure 3.12. The weight ranges of horned and non-horned prey that are preferred (black), killed relative to their abundance (grey) and avoided (white) by the three cheetah social classes. Weight ranges are those identified by segmented relationships.

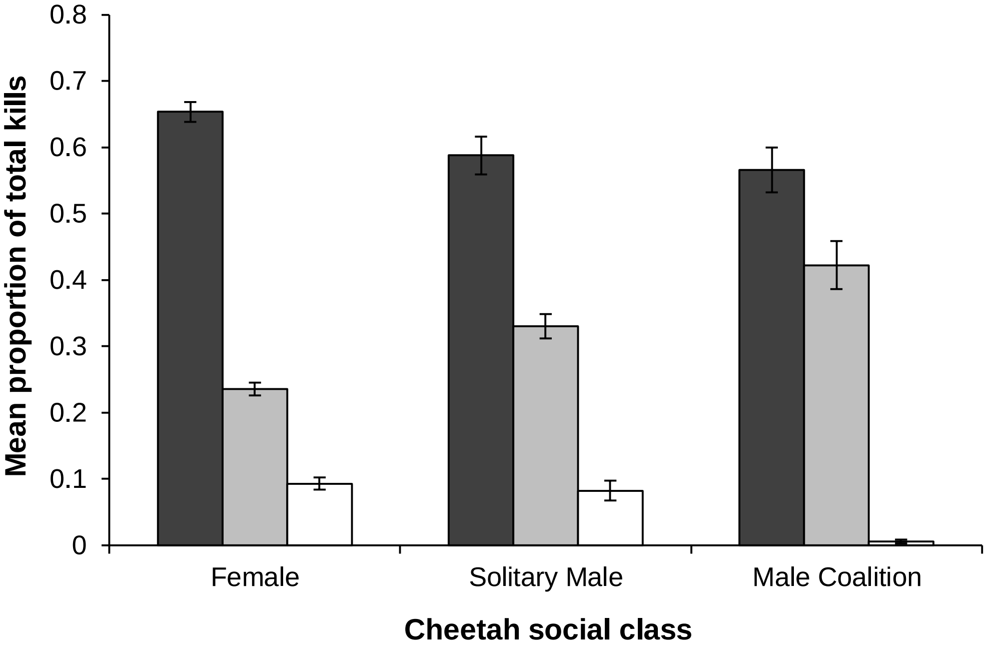


Figure 3.13 Mean proportion of kills (± SE) made by each cheetah social class that fall in the weight ranges found to be preferred (black), killed relative to its abundance (grey) and avoided (white).

3.4 Discussion

3.4.1 Summary of study objectives and limitations

This study met the objective of investigating the influence of prey demographics and cheetah social structure on cheetah prey preference. The value of investigating the prey preference of a predator using a multi-site analysis is that it is performed across different prey communities and varied prey abundances, thereby producing more robust preference results than single-site studies (Hayward *et al.* 2006b). However, the detail of kill data required for this study limited the amount of useable data available, and resulted in almost half the datasets used representing the coastal Eastern Cape. The field work section of this study was performed in the Eastern Cape, and acquaintance with other reserve managers in the province facilitated easier access to data from these reserves than others in the country. While autocorrelation should not exist since each dataset represents prey at different availabilities (Hayward *et al.* 2006b), the potential influence of an area bias on preference results could not be eliminated. This bias existed in Hayward *et al.*'s (2006b) cheetah prey preference study as well, with over half the datasets representing the lowveld and east Africa. The area biases between my study and Hayward *et al.* (2006b) were different because my study focused only on southern Africa. Furthermore, Hayward *et al.* (2006b) used species-level kill data and more published species-level cheetah feeding ecology studies exist for the lowveld than other areas in South Africa (Hayward *et al.* 2006b). This is perhaps due to the high number of reserves with cheetah in this area (Lindsey *et al.* 2011; van der Merwe 2012).

Limited data availability additionally prevented me from performing a multi-factorial analysis. Such an analysis would have allowed me to assess the relative influence of all investigated factors on prey preference, as well as their interaction with each other, instead of assessing their influence in isolation. An increase in reserves collecting detailed kill data would therefore allow for both a reduction in potential area-biases, as well an improvement in the rigour of the analyses.

An artefact of the way in which opportunistic kill data is collected is that there may be a greater chance of observing larger kills, which the predator will take longer to consume, resulting in an underestimation of small-bodied prey in the kill records (Owen-Smith & Mills 2008). While this risk was minimized in the majority of datasets used in this study by continuous and/or frequent cheetah location (Mills & Biggs 1993; Hunter 1998; Bissett 2004; E. Larson pers. comm.; S. Razzaq pers. comm.), it cannot be completely eliminated. Therefore, while a preference for small-bodied prey would be strengthened if the bias was eliminated, an absence of preference for small-bodied prey should be interpreted with caution. The interpretation of my results is therefore done with these limitations in mind.

3.4.2 Determining preferred prey weight ranges

The commonly used method for determining the preferred prey weight ranges of Africa's large carnivores is a distance-weighted-least squares curve fit to species-level preference data (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). This method provides no apparent quantitative means of detecting a prey weight range that is distinctly preferred over others, and is therefore a subjective approach. In contrast, the segmented model method proposed in this study identified significant changes in the relationship between prey mass and preference – which could then be classified into weight ranges of prey that were preferred, killed relative to their abundance, or avoided by cheetah. It therefore provides an objective approach to determining preferred prey weight ranges. While the previous method only identified a preferred prey weight range, the segmented model also identifies an accessible prey weight range, which accounted for over 90% of cheetah kills and is therefore a good predictor of cheetah diet. The segmented model additionally identifies the prey mass above which prey are avoided and thus contribute very little to the predator's diet. This objective approach is therefore a good predictor of cheetah diet.

3.4.3 *The influence of prey demographics on cheetah diet*

3.4.3.1 *Prey age*

To date, descriptions of prey preference in large African carnivores have been based on prey species-level analyses (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). By differentiating between adult and juvenile prey in this study, it became evident that a species-level analysis can mask age-biased prey preferences.

The upper size limit to the prey consumed by a predator is set by how successfully and safely larger animals can be captured and subdued (Owen-Smith & Mills 2008). The linear decline in the proportion that adults comprise of kills made on each prey species as a function of species-mass suggests that the probability of successful prey capture decreases as prey size and thus risk of injury to the predator increase. Hilborn *et al.* (2012) found prey size to be the most important factor in cheetah hunt success, with success being lower when hunting large-bodied prey. A prey species-mass of 126 kg highlights a threshold for cheetah, above which the high risk and energy required to successfully capture and subdue large adults results in no further change in the proportion of adults versus juveniles killed in these species (Fig 3.3). The relevant species in this study above the 126 kg threshold, which therefore appear to have escaped cheetah predation risk as adults, include eland, gemsbok, waterbuck, blue wildebeest *Connochaetes taurinus*, mountain zebra and plains zebra. It would be valuable to analyze cheetah kill data for other similar sized prey (e.g. roan *Hippotragus equinus* and sable *Hippotragus niger*) in order to test these findings.

At the other end of the prey size spectrum, age-dependent differences in cheetah diet operate in reverse, with the juveniles of prey weighing less than 23 kg contributing a mere

13% of small prey kills. Small prey juveniles are often hidden (Jarman 1974) and thus underrepresented in prey demographic surveys, which prevents preference calculations in this prey size range. Assuming that juveniles do not comprise more than 25% of a small prey population (according to Mason's 1990 prey demographic data for KNP), juveniles are found in the diet a maximum of half as often as would be expected from their proportional representation in the population. This suggests that adults are preferred over juveniles. Smaller ungulates are exposed to a greater array of predators than are larger ungulates (Sinclair *et al.* 2003; Radloff & du Toit 2004) and therefore experience stronger predation pressure (Kie 1999; Sinclair *et al.* 2003). Many small ungulate species, lacking the maternal defense offered by larger-bodied prey whose newborns stay with their mothers (Fisher *et al.* 2002), have evolved a life history strategy of hiding their newborn young (Jarman 1974; Lent 1974; Sinclair *et al.* 2000). The lower size limit to the prey consumed by a predator depends upon how frequently small prey can be found and eaten (Owen-Smith & Mills 2008). In accordance with optimal foraging theory, the low level of cheetah predation on smaller prey juveniles may be as a result of the energetic costs of seeking out hidden juveniles outweighing the energetic benefits of consuming these small-bodied individuals. The low level of predation on small-bodied juveniles suggests that, in the presence of cheetah, hiding young is a successful life-history strategy in these small-bodied species. Alternatively, the small size of juveniles means cheetah consume them rapidly and in their entirety, and predation on these small-bodied animals may be underestimated (Mills 1992, 1996), which would mean predation is more symmetrical across age classes in smaller-bodied prey. Given that the degree of prey size-bias in the data is unknown; this second prediction cannot be eliminated.

3.4.3.2 Prey sex – size and weaponry dimorphism

In the majority of antelope species, males possess horns, which are widely thought to have evolved for intra-sex combat over territories or mates (Geist 1966a; Clutton-Brock 1982; Janis 1982; Stankowich & Caro 2009). Despite sexual selection being the primary function of horns, it is believed that weaponry can also aid in deterring, repelling and surviving predatory attacks (Packer 1983; Caro 2005; Stankowich 2011). In contrast, the presence of horns in females is highly variable across antelope species (Stankowich & Caro 2009) and its evolution has been attributed to an anti-predatory mechanism (Packer 1983; Stankowich & Caro 2009), the defence of territories against other females (Stankowich & Caro 2009) and as a buffer against aggression towards male offspring by dominant males (Estes 1991). My findings are in support of horns serving as an anti-predatory defense mechanism in larger-bodied prey, where the level of cheetah prey-avoidance differs between the prey sexes only when sexual weaponry dimorphism exists. However in smaller-bodied prey it appears that sexual weaponry dimorphism does not induce female-biased predation. This therefore supports my prediction that smaller prey mass limits options for active predator defense (Packer 1983), independent of weaponry presence/absence.

For male coalition cheetah, which avoid prey above 303 kg, regardless of weaponry, prey accessibility appears limited purely by prey mass. For solitary cheetah, the influence of prey mass and the presence of horns appear to work together, lowering the mass threshold above which prey is avoided by between 61 and 67 kg. The greater weight range of non-horned prey than horned prey accessible to solitary cheetah may result in females of large-bodied prey being more vulnerable to predation than males in species which display sexual weaponry dimorphism. In a situation where predators are reintroduced onto an enclosed reserve at a density higher than that which an exploited prey population can sustainably support, a female-biased predation pressure could result in the reproductive potential of the population being reduced, leading to a prey population decline or even collapse (Festa-Bianchet *et al.* 2006).

Since weaponry dimorphism was not found to result in female-biased predation in small- and medium-bodied prey, it is surprising that horned prey do not have a prey weight range that is preferred by cheetah, while non-horned prey weighing up to 45 kg, 81 kg and 96 kg are preferred by female, solitary male and male coalition cheetah, respectively. This apparent contradiction may be explained by age-dependent prey preferences. Many of the large-bodied prey juveniles, shown to be highly preferred by cheetah, fall within the non-horned prey weight range that is preferred by cheetah. This weight range may therefore be preferred because it includes these large prey juveniles, rather than because it includes non-horned prey as opposed to horned prey. In some prey species, juveniles have almost fully-grown horns by the end of the first year (for example gemsbok – Dieckmann 1980 in Knight 1991). While categorizing all juveniles as non-horned may therefore be erroneous, avoiding this would require the kill and demographic data to include temporal detail which was unavailable in any of the datasets used. Incorporating this detail may influence the weight ranges of horned/non-horned prey found to be preferred or killed relative to their abundance. It will not, however, influence my finding that in small- and medium-sized prey, there was no difference in preference for adult males and females, regardless of the presence of weaponry, and thus no influence of weaponry on prey preference in small- and medium-sized prey.

3.4.3.3 Prey sex – size and herding behaviour

My findings do not support previous site-specific findings that male-biased predation occurs in medium-sized prey species which form large breeding herds (Fitzgibbon 1990; Mills 1990;

Mills *et al.* 2004). Allocating prey species into those that form large herds and those that do not is a fairly simplistic approach, given that males may be present in large herds only during the breeding season, otherwise forming bachelor herds or becoming solitary (Estes 1999). While the lack of male-biased predation therefore appears to reject my prediction that males are more vulnerable to predation than females in large breeding herds, this finding may also be influenced by variation in male behaviour and thus vulnerability during the non-breeding season (Estes 1999). Given the complexity of ungulate social systems (Estes 1999) and the scarcity of detailed kill data, such factors were not analyzed further in this study.

In prey which do not form large breeding herds, it was predicted that there would be no difference in vulnerability between the sexes. However the preference for females over males in prey which do not form large breeding herds suggests that females in non-herding prey are more vulnerable to predation. For prey which do not form large breeding herds, only three medium-sized species had sufficient prey demographic data to allow preference analyses. These were bushbuck *Tragelaphus scriptus*, common reedbuck *Redunca arundinum* and nyala, with nyala contributing the majority of kills. Nyala display large sexual size and weaponry dimorphism – with males weighing 1.8 times more than females (Skinner & Chimimba 2005). It is therefore likely that a preference for females in medium-sized prey which don’t form large breeding herds is an artefact of sexual weaponry and size dimorphism, and not due to herding behaviour. A multi-factorial analysis would assist in teasing out these various influencers and I predict that, once differences in size and weaponry are controlled for, there will be no difference in preference for males and females in prey which do not form large breeding herds.

3.4.4 The influence of cheetah social class on cheetah diet

Mean prey mass has been found to increase significantly with mean predator mass in large African carnivores (Radloff & du Toit 2004), primarily as a result of an increase in the maximum prey mass accessible to larger predators (Gittleman 1985; Cohen *et al*. 1993; Radloff & du Toit 2004). While this study supports this finding in terms of mean prey mass, it shows a lack of difference in maximum mass of prey killed between cheetah sexes. This suggests that solitary male cheetah merely capture more prey in the upper prey mass limits that are imposed on both the sexes, and that sexual dimorphism in cheetah is not sufficient to facilitate a hunting advantage to the slightly larger males.

The majority of male cheetah data collected at Mala Mala (Radloff & du Toit 2004) were from coalitions of two and occasionally three cheetah, not solitary males (F. Radloff pers. comm.). Therefore, while Radloff & du Toit (2004) only compared cheetah sexes and not group sizes, the discrepancy between their results and mine could have been because group hunting in males increased maximum prey mass of male cheetah relative to female cheetah in their data. This prediction is supported by my finding that male coalition cheetah are both capable of killing larger prey, and prefer a greater weight range of prey, than solitary cheetah. Paired/group hunting further appears to negate the size-dependent safety offered to horned-prey above 81 kg, which are avoided by solitary cheetah. Spotted hyaena forage alone for small items, as well as cooperate to bring down larger prey (Kruuk 1966, 1970), and African wild dog hunt more efficiently in packs than in pairs or alone (Fanshawe & Fitzgibbon 1993; Creel & Creel 1995). It therefore appears that, in large carnivores whose energy requirements necessitate foraging on prey with a mass greater than 45% of the predator's body mass (Carbone *et al.* 1999), hunting in groups facilitates an improved ability to hunt larger prey, and thus a broader range of prey.

This study was unable to investigate the influence of the presence of cubs on a female cheetah's diet. However, given that cubs do not assist with hunting (Caro 1994), I would predict that female cheetah hunting alone are morphologically unable to kill larger prey, despite increased energetic demands when rearing cubs. Hilborn *et al.* (2012) did not find female cheetah with cubs to have an increased hunting success when killing large prey than did solitary females. Unable to take larger prey, female cheetah may meet increased energetic demands associated with cubs by increasing their hunting effort, or hunting more prey in the upper prey mass limits imposed on solitary cheetah. At Kwandwe, female cheetah with cubs killed more medium-sized (30 to 65 kg) prey than solitary females, but not a greater maximum sized prey (Bissett 2004). This supports my prediction that female cheetah with cubs kill more prey in the upper size limits imposed on all solitary cheetah. At Phinda, females with cubs did have a larger maximum kill size than females without cubs (108 kg versus 62 kg, respectively), however prey in this larger size range unutilized by solitary females only constituted 5.7% of kills made by females with cubs (Hunter 1998). In the prey-scarce Kalahari, female leopard with cubs were found to increase their hunting success and reduce their energy expenditure by killing more smaller-bodied prey, and hunting more efficiently, than solitary leopard (Bothma & Coertze 2004). Similarly, pregnant puma and those with cubs increased their kill rate (Laundré 2008). This supports my prediction that the presence of cubs may influence hunting frequency, as opposed to the maximum size of prey killed.

A note must be made regarding the implications of intra-guild competition on cheetah diet. Cheetah are inferior predators to both spotted hyaena and lion, which chase them from their kills as well as prey upon adults and young (Caro 1994; Laurenson 1995; Laurenson *et al.*

1995). It is believed that intra-guild competition may promote cheetah preference for medium-sized prey, which is small enough to consume before kleptoparasites arrive (Radloff & du Toit 2004; Hayward *et al.* 2006b). Both cheetah and African wild dog have been predicted to increase their use of suboptimal prey in the presence of superior predators (Hayward & Kerley 2008). This may be as a result of cheetah seeking refuge in areas less utilized by lion and spotted hyaena, thereby reducing their access to medium-size ungulates that share habitat with prey that are preferred by these larger carnivores (Mills & Biggs 1993; Hunter 1998; Durant 1998, 2000). Where the risk of kleptoparasitism is reduced or absent, the cheetah's preferred prey weight range may expand, explaining the preference of cheetah for larger prey in Kwandwe and Namibia where kleptoparasitism events are rare (McVittie 1979; Bissett & Bernard 2007), though this may also be an artifact of the lower abundance of smaller prey in these areas. Dataset sample size prevented me from differentiating between reserves with and without other large carnivores. While Samara and Camdeboo were the only reserves supporting cheetah as the largest carnivore, the degree of kleptoparasitism may further vary across reserves that do support other large carnivores. For example kleptoparasitism is believed to be high in Sabi (Radloff & du Toit 2004) and low in Kwandwe (Bissett & Bernard 2007), despite both these reserves supporting lion. This is perhaps a result of Sabi supporting spotted hyaena while Kwandwe does not (Table 2.1), or as a result of the absence of vultures at Kwandwe reducing the ability of other large carnivores to locate cheetah kills. Given that some small reserves have introduced cheetah as their largest predator (Lindsey *et al.* 2011), the influence of competitive-release on cheetah prey preference may be an important consideration.

3.4.5 Conclusions and recommendations

This chapter highlights the importance of prey size and life history strategies, and predator social structure, in shaping cheetah prey preference. Species-level analyses can mask these determinants of prey preference. This chapter therefore provides preferred and accessible weight ranges, determined at the prey demographic- and predator social class-level, which can be used by reserve managers to establish which prey species and demographic classes will be preferred and accessible to cheetah on their reserves. This study further highlighted the method-limitations regarding the calculation of preferred prey weight ranges for the five large African carnivores. It is therefore recommended that these calculations are revisited using the segmented model method proposed in this study.

CHAPTER 4: INCORPORATING PREY DEMOGRAPHICS AND CHEETAH SOCIAL STRUCTURE INTO A CHEETAH CARRYING CAPACITY MODEL

4.1 Introduction

4.1.1 Carnivore carrying capacity regression models

The density of carnivores that a natural ecosystem can sustain is determined largely by the abundance of prey (East 1984; Fuller & Sievert 2001; Carbone & Gittleman 2002; Hayward *et al.* 2007d). Carnivore body size, sociality, intra-guild competition, dietary specialization and rainfall can further influence carnivore density (Grant *et al.* 1992; Laurenson 1995; Creel & Creel 1996; Stander *et al.* 1997; Carbone & Gittleman 2002; Hayward & Kerley 2008). Across the order Carnivora, 10 000 kg of prey supports about 90 kg of carnivores (Carbone & Gittleman 2002). In African savannas, where predator-prey relationships are related to rainfall and vegetation productivity (East 1984), the density of large carnivores has been successfully related to the biomass of all available prey species for lion (van Orsdol *et al*. 1985), and the biomass of prey weighing between 15 and 60 kg for cheetah and leopard (Laurenson 1995; Gros *et al.* 1996; Stander *et al*. 1997). Similar relationships have been found between tiger, Eurasian lynx and wolf and their respective prey (Breitenmoser & Haller 1993; Messier 1995; Karanth & Nicholas 1998; Herfindal *et al.* 2005).

The concept of preferred prey, defined as prey that are killed more frequently than would be expected from their relative abundance in the prey community, has allowed for a refinement of predator-prey abundance relationships for the large African carnivores (Hayward & Kerley 2005; Hayward 2006; Hayward *et al.* 2006a,b,c). Across ecosystems where carnivores were assumed to be at carrying capacity (i.e. predator numbers were a function of prey availability), significant linear relationships were found between carnivore density and the biomass of the preferred prey species of lion, leopard, spotted hyaena and African wild dog, and the biomass of prey species in the preferred weight range (23 to 56 kg) of cheetah (Hayward *et al.* 2007d).

Hayward *et al.* (2007d) applied their predator-prey abundance regression models to predict carnivore carrying capacities at nature reserves in South Africa where wildlife census data were available and where reintroductions either had occurred or were planned. Similarly, prey-predator abundance regression models have been used to predict the carrying capacity of a recolonizing wolf population in the United States (Mladenoff & Sickley 1998) and a reintroduced Eurasian lynx population in Scotland (Hetherington & Gorman 2007). While this is precisely the opportunity that such a model affords us, recent regression approaches to carrying capacity estimation make several assumptions. In this chapter the validity of these assumptions is tested using cheetah as a study species, with the aim of developing a refined regression model which eliminates tenuous assumptions. Under conditions where assumptions cannot be eliminated, an alternative model approach is proposed, with the objective of improving the predictive ability and thereby applicability of carnivore carrying capacity models.

4.1.2 Assumptions made by current carrying capacity regression models

Regression models can lead to relationships in which the cause-effect interactions may be via a third co-related factor. This study investigates three such factors which are unaccounted for in current carrying capacity regression models, and thus assumed not to influence the relationship between prey biomass and carnivore density.

Firstly, an artefact of the way in which prey preference is calculated is that a highly abundant prey item will not be found to be preferred by a predator, despite comprising a large proportion of the diet (Jacobs 1974; Strauss 1979; Lechowicz 1982; Hayward 2011). Regression models based on preferred prey as opposed to all available prey are believed to provide a better model fit (Hayward *et al.* 2007d). However, better fit does not necessarily mean a better explanation of the relationship between prey biomass and carnivore density, if there is variability in the relationship between preferred prey and what is actually eaten (accessible prey) across sites.

Secondly, because recent regression models are based on available or preferred prey biomass, calculated using species-level predictions of predator diet (Breitenmoser & Haller 1993; Karanth & Nicholas 1998; Carbone & Gittleman 2002; Herfindal *et al.* 2005; Hayward *et al.* 2007d), they assume that there is no influence of prey demographics and predator social structure on predator diet and thereby on carrying capacity. The current study (Chapter 3) has shown that, for cheetah, the body size and life-history strategies of the prey influence predator diet and prey preferences. Furthermore, cheetah social structure influences cheetah diet and prey preference, with group hunting allowing for predation on a much broader weight range of prey (Chapter 3). Additionally, juvenile cheetah have lower energetic requirements than adults (Owen-Smith & Mills 2008). However, they initially depend on their mothers for milk, with lactation being an inefficient means of energy transfer (Dall & Boyd 2004), and later depend on their mothers for meat (Caro 1994). Juvenile cheetah are therefore fed, indirectly and then directly, on the narrower weight range of prey accessible to solitary hunters. These findings therefore suggest that the current carrying capacity regression models, based on prey species-level dietary information and ignoring cheetah social structure, may be limited in their predictive ability.

Thirdly, a regression model of predator-prey abundance is derived from "natural ecosystems" which therefore support an intact large carnivore guild (e.g. Hayward *et al.* 2007d). Many new nature reserves in southern Africa are only reintroducing part of the large carnivore guild, for example introducing cheetah as the sole large carnivore (see Samara and Camdeboo; Chapter 2) or into ecosystems where kleptoparasitism is minimal (Bissett & Bernard 2007). Predicting carnivore carrying capacity on such a reserve, based on a model derived from reserves supporting an intact carnivore guild, therefore makes the assumption that the presence of other large carnivores does not influence the carrying capacity of individual carnivore species. However, African wild dog and cheetah densities are much lower in the presence of lion and spotted hyaena (Hofer & East 1995; Laurenson 1995), who compete with them for food – exploitation competition (Hayward & Kerley 2008), as well as kill them and displace them from optimal hunting areas - interference competition (Creel & Creel 1996; Mills & Gorman 1997; Durant 2000; Creel & Creel 2002; van Dyk & Slotow 2003). Such findings suggest that competition with other large carnivores can reduce carnivore carrying capacity through exploitation competition, as well as further reduce carnivore density through interference competition.

4.1.3 An alternative carrying capacity modelling approach

An alternative to the regression approach of carnivore carrying capacity modelling is a more mechanistic approach, which avoids the aforementioned assumptions by basing predictions on the specific parameters of the nature reserve in question. An example of such an approach is that of Maximum Sustainable Yield (MSY). This method requires an identification of available prey, an understanding of sustainable harvest (Caughley 1977) and the energy requirements of the carnivore (e.g. Owen-Smith & Mills 2008) to predict carnivore carrying capacity in terms of the maximum number of carnivores that can be sustained, or the minimum area required to sustain them (Purchase & du Toit 2000; Power 2002a; Lindsey *et al.* 2004, 2011). As with the regression approach, studies which have utilized the MSY approach to predict carnivore carrying capacity have done so based on predictions of predator diet or prey preference at a prey species-level, and omitting predator social structure (Purchase & du Toit 2000; Power 2002a; Lindsey *et al.* 2004, 2011). However, prey demographics and cheetah social structure influence which prey are accessible to cheetah (Chapter 3) and are therefore important determinants of the total biomass of prey available to cheetah at a site, on which the MSY model predictions are based.

4.1.4 The next step in carnivore carrying capacity modelling

Using cheetah as a study species, this study aims to investigate the influence of incorporating all accessible prey, prey demographic-level diet predictions and predator social class-level diet predictions into a carnivore carrying capacity model, by developing a refined regression model. This study further aims to develop a more mechanistic MSY model with which to test the validity of assumptions made by the regression model. By testing the below-listed predictions, the merits and disadvantages of both models will be assessed.

1. It is hypothesized that cheetah carrying capacity depends on the biomass of all accessible prey (preferred or killed relative to its abundance – Chapter 3), not just the biomass of preferred prey.
    - I therefore predict that the biomass of accessible prey will be a better predictor of cheetah density in a natural ecosystem than the biomass of preferred prey. The ability of preferred prey to predict cheetah density will be dependent on the variability in the relationship between preferred and accessible prey biomass.

2.1 It is hypothesized that the demographics of the prey and the social structure of the cheetah are important determinants of cheetah carrying capacity in a natural ecosystem.
    - Therefore, a model which accounts for prey demographics and cheetah social structure will have stronger predictive strength than one based on preferred prey species and pooled cheetah social classes (e.g. Hayward *et al.* 2007d).

2.2 It is hypothesized that because male coalition cheetah are capable of capturing a broader weight range of prey than solitary cheetah, the presence of prey accessible only to male coalitions will result in decreased resource competition between solitary and coalition cheetah and therefore a higher cheetah carrying capacity. Furthermore, as a result of reduced dietary requirements, a larger cheetah population can be supported on a given prey population when the cheetah population comprises a greater proportion of juveniles.
    - I therefore predict that because the species-level model does not account for the influence of cheetah social structure on diet, there will be a positive linear relationship between the biomass of prey accessible only to male coalition cheetah at a site, and the degree to which the species-level model underestimates carrying capacity relative to the model which accounts for cheetah social structure.
    - Applying the MSY model to simulated prey populations, there will be a positive relationship between the proportion of juveniles in the cheetah population and the estimated cheetah carrying capacity (when the ratio of solitary adult cheetah to coalition cheetah is kept constant). In a natural ecosystem, the proportion of juveniles in a population should be related to the proportion of females (Fuller & Sievert 2001; Durant *et al.* 2004). I predict that as the proportion of juveniles and females in the cheetah population increases (i.e. the proportion of male coalition cheetah decreases), the predicted carrying capacity will decrease. This will be as a result of a

greater proportion of the cheetah population being sustained on the narrower accessible weight range of prey (and hence lower total biomass), initially through the inefficient conversion of energy from meat to milk, and subsequently through mothers supplying their young with meat.

3 It is hypothesized that competing carnivores reduce cheetah carrying capacity through exploitation competition, and can also reduce cheetah density through interference competition.

   - Therefore, predicting cheetah carrying capacity utilizing a MSY model based on cheetah resource requirements alone will result in an overestimation of cheetah density at each of the nature reserves used to develop the regression model (since these reserves support intact large carnivore guilds). This overestimation will be positively related to the relative density of the other large carnivores on the reserve.

4 Finally, I hypothesize that on a reserve where cheetah are the only large carnivore, by incorporating prey demographics, cheetah social structure and the lack of intra-guild resource competition into a cheetah carrying capacity model, the MSY model should provide the most realistic predictions of cheetah carrying capacity. Departures in actual cheetah density from carrying capacity predictions should correspond to prey population decline/growth. Similarly, on a reserve where cheetah are not the only large carnivore, the refined regression model, by incorporating prey demographics, cheetah social structure and intra-guild resource competition should provide realistic predictions of cheetah carrying capacity. A MSY model, adjusted to account for dietary overlap between cheetah and other large carnivores, should also provide realistic cheetah carrying capacity predictions on such a reserve.

   - Therefore, the MSY model predictions of cheetah carrying capacity for MZNP (Table 2.3) will be below actual density, as this park experienced rapid cheetah population growth in the absence of competing carnivores, resulting in management relocating cheetah (Zimmerman *et al.* 2011). The refined regression model should underestimate cheetah carrying capacity since it does not account for the lack of competing carnivores. The refined regression and adjusted MSY models should predict cheetah carrying capacity to be above actual density at Phinda (Table 2.1), where prey population numbers are believed to be stable (T. Burke pers. comm.). The refined regression model will not underestimate cheetah carrying capacity at Phinda when compared to the adjusted MSY model, since Phinda supports lion and leopard populations.

4.2 Methods

4.2.1 Developing a refined carrying capacity regression model for cheetah

4.2.1.1 Dataset selection and manipulation

Seven datasets from nature reserves in southern Africa, for which cheetah and prey abundance data were available, were selected to develop a carrying capacity regression model, and are hereafter referred to as model development sites (Table 4.1; Table 2.2 for further details). Sites that were selected had been relatively unmanaged by humans (Hayward *et al.* 2007d), and cheetah could therefore be assumed to be at carrying capacity (as in Hayward *et al.* 2007d). Five of these datasets were used previously in the development of the carrying capacity regression model detailed in Hayward *et al.* (2007d). I excluded three datasets that were used by Hayward *et al.* (2007d), namely two from the Serengeti since the current study focussed on southern Africa, and one from Imfolozi since it was not apparent how these data were distinguished from the temporally corresponding Hluhluwe-Imfolozi data, or what the source of these data was. The Pilanesberg prey abundance data used by Hayward *et al.* (2007d) were obtained from van Dyk & Slotow (2003); however these data were incorrectly recorded in Hayward *et al.*'s (2007d) Appendix A for eight prey species. The original data from van Dyk & Slotow (2003) were therefore used. For the KNP in the 1980's, Hayward *et al.* (2007d) obtained prey abundance data from Mills & Biggs (1993), which lacked data for some species. Since the abundance of a greater number of prey species was available from the KNP annual census (SANParks unpubl. data), these data were used instead, with cheetah abundance still obtained from Mills & Biggs (1993) (Table 4.1). In addition to the five datasets obtained from Hayward *et al.* (2007d), a dataset from Sabi from 2006 to 2011 and from the KNP from 1998 to 2005 were also used (Table 4.1).

The temporal separation of data from a study site, such as the KNP, into separate datasets with different prey abundances has been used previously in studies of carnivore feeding ecology (Creel & Creel 2002, Hayward *et al.* 2006b; Hayward *et al.* 2007d). It is not believed that autocorrelation exists by using data from the same area at different prey abundances, since a major determinant of carnivore density is the abundance of available prey (Carbone & Gittleman 2002). For sites representing more than one dataset, each dataset is referred to by the name of the site followed by the last two digits of the decade from which the cheetah and prey abundance estimates were obtained (the second decade if the data span two decades; Table 4.1). Where data were available for more than one year, average cheetah and prey abundances for the period were used.

As the methods used to gather prey and cheetah abundance data varied among model development sites (Hayward *et al.* 2007d), no *post hoc* corrections on abundance data were performed by Hayward *et al.* (2007d), as it was considered to be too subjective. Therefore, no corrections were performed in the current study in order to allow for direct comparison with the regression model developed by Hayward *et al.* (2007d). While the majority of model development sites have been relatively unaffected by humans, they have all been fenced, population control (culling) has taken place in the KNP and population reintroductions have also occurred at Hluhluwe and Pilanesberg (Hayward *et al.* 2007d). Where reintroduced populations were included, a sufficient time was left to allow the populations to attain carrying capacity (Hayward *et al.* 2007d).

I reviewed the literature using electronic databases and reference lists of other papers to obtain prey demographic data for model development sites that corresponded temporally with prey abundance data (Table 4.1). Where no demographic data were available, standard proportions of 35% adult male, 50% adult female and 15% juvenile were applied (Table 4.1). These standard ratios were calculated by averaging ungulate demographic ratios across all species censused by Mason (1990) between 1983 and 1991, in the KNP. It was therefore assumed that, in the absence of substantial human management, all ungulate species at all sites would display consistent demographic ratios.

Based on site size (see Table 2.2), prey abundance data and prey demographic ratios, the biomass (kg.km^{-2}) of each prey species-demographic-class at each model development site was calculated. Refer to Appendix Table C for species-class-masses and Chapter 3 for details on how they were calculated. Cheetah abundance was converted into cheetah density (#.km^{-2}).

4.2.1.2 Calculating preferred and accessible prey biomass

Chapter 3 identified weight ranges of both horned and non-horned prey species-demographic-classes that are preferred, killed relative to their abundance or avoided by the three cheetah social classes. These weight ranges are summarized in Table 4.2. In Chapter 3, prey falling within the weight ranges found to be either preferred or killed relative to their abundance by each cheetah social class were classified as “accessible prey”. Refer to Appendix Table C for masses and horn categories of all prey species-demographic-classes, and to Chapter 3 for details on how these were calculated. The biomass of (a) preferred and (b) accessible prey (in kg.km^{-2}) was calculated for solitary female, solitary male and male coalition cheetah at each model development site.

Table 4.1. Sources and years of cheetah and prey abundance data, and sources of prey demographic data used from each model development site.
(NOTE: When data from a site were divided temporally into two datasets, the dataset is identified by the name of the site followed by the last two digits of the decade from which the data were obtained. Refer to Appendix Table C for scientific names of prey species).

Model development site	**Years**	**Cheetah abundance source**	**Prey abundance source**	**Prey demography source**	**Standard demographic ratios used**
Hluhluwe	1983 to 1992	Whateley & Brooks (1985)	Whateley & Brooks (1985)	Buffalo: Jolles (2007); Impala & Nyala: Kruger *et al.* (1999)	Bushbuck, Bushpig, Duiker Blue, Duiker Common, Duiker Red, Kudu, Reedbuck Common, Reedbuck Mountain, Steenbok, Warthog, Waterbuck, Wildebeest Blue, Zebra Plains
Kalahari	1980's	Mills (1990)	Mills (1990)	Gemsbok & Wildebeest: Knight (1991); Hartebeest & Springbok: Mills (1984)	Duiker Common, Eland, Kudu, Scrub Hare, Springhare, Steenbok
KNP60's	1954 to 1966	Bryden (1976); Pienaar (1969)	Bryden (1976); Pienaar (1969)	Mason (1990)	Duiker Common, Eland, Klipspringer, Reedbuck Mountain, Roan, Steenbok
KNP80's	1987 to 1990	Mills & Biggs (1993)	SANParks (unpubl. data)	Mason (1990)	Duiker Common, Eland, Klipspringer, Reedbuck Mountain, Roan, Steenbok
KNP00's	1998 – 2005	Marnewick *et al*. (submitted for review)	SANParks (unpubl. data)	Mason (1990)	Duiker Common, Eland, Klipspringer, Reedbuck Mountain, Roan, Steenbok
Pilanesberg	2000	van Dyk & Slotow (2003)	van Dyk & Slotow (2003)	North West Parks unpublished data	Bushbuck, Eland, Gemsbok, Impala, Klipspringer, Kudu, Reedbuck Common, Reedbuck Mountain, Sable, Springbok, Warthog, Zebra Plains
Sabi	2006 to 2011	Sabi Sand Wildtuin (unpubl. data)	Sabi Sand Wildtuin (unpubl. data)	Mason (1990)	Duiker Common, Klipspringer, Ostrich, Steenbok

Table 4.2. Weight ranges (kg) of horned and non-horned prey (species-demographic-classes) that are preferred, killed relative to their abundance (relative), accessible and avoided by the three cheetah social classes.

Prey preference category		Weaponry category	Cheetah class		
			Female	Solitary male	Male coalition
Preferred	Accessible	Horned	None	None	None
		Non-horned	< 48	< 75	< 96
Relative		Horned	< 71	< 81	< 303
		Non-horned	48 to 138	75 to 142	96 to 313
Avoided		Horned	≥ 71	≥ 81	≥ 303
		Non-horned	> 138	> 142	> 313

4.2.1.3 Assessing the influence of using preferred versus accessible prey biomass to predict cheetah density

In the absence of information on social class composition of the cheetah populations at any of the model development sites, the social structure of the adult cheetah population at each site was assumed to be consistent with that recorded for the cheetah population in the Serengeti, namely 62% female, 16% solitary male and 22% male coalition (Caro & Collins 1986; Durant 1994). For each cheetah social class, cheetah density was regressed against the biomass ($kg.km^{-2}$) of preferred and accessible prey (Zar 1984). Both prey biomass and cheetah density were log transformed to control for non-normality (Zar 1984).

To test the strength of the relationship between preferred and accessible prey biomass ($kg.km^{-2}$), a linear regression of preferred (x axis) versus accessible (y axis) prey biomass was performed for each cheetah social class (Zar 1984).

4.2.1.4 Developing a refined regression model

The biomass of accessible prey was found to be a better predictor of cheetah density than that of preferred prey for all cheetah social classes (see results). Because the weight ranges of prey accessible to female and solitary male cheetah are very similar, with only two listed prey items accessible to solitary male but not female cheetah (Table 4.2 and Appendix Table C), solitary male and female cheetah were pooled to represent solitary cheetah for diet and carrying capacity predictions based on accessible prey. The weight range of prey accessible to female cheetah was used to represent solitary cheetah, as the more conservative estimate. A multiple linear regression was then performed, using the model development sites, to relate total cheetah density to the biomass of prey accessible to both solitary cheetah and male coalition cheetah (Zar 1984). As there was a significant interaction between the two predictor variables (see results), this interaction term was also included in the model (Friedrich 1982). Both prey biomass and cheetah density were log transformed to control for non-normality (Zar 1984). This model is hereafter referred to as the refined regression model.

4.2.1.5 *Assessing the influence of incorporating prey demographics and cheetah social structure on the predictive strength of a regression model*

Hayward *et al.*'s (2007d) method for developing a regression model was applied to the seven model development sites used in the current study. Total cheetah density was therefore regressed against the biomass of prey species (kg.km^{-2}) with a species-mass falling within the 23 to 56 kg weight range (see Appendix Table C for species-masses). Both prey biomass and cheetah density were log transformed to control for non-normality (Zar 1984). This model is hereafter referred to as the recalculated Hayward regression model. The original Hayward *et al.* (2007d) regression model was not used for comparison since there were differences in the data used to develop the model. The coefficient of determination and significance of the recalculated Hayward regression model were then compared to those of the refined regression model.

4.2.1.6 *Using the regression models to predict cheetah carrying capacity at prediction sites*

Hayward *et al.* (2007d) used their regression model to predict cheetah carrying capacity at ten sites in South Africa where large carnivores had either been reintroduced, or where reintroductions were planned. Both the refined regression model and the recalculated Hayward regression model were used to predict cheetah carrying capacity at nine of these ten sites – hereafter referred to as prediction sites (Table 4.3; Table 2.3 for further details). The omitted site was Pilanesberg, since this site was used in the development of both regression models. Density data for all prey species at the nine prediction sites were obtained from Hayward *et al.* (2007d). The Greater Addo National Park project (GANP) is a proposed expansion of Addo, and a component of the conservation planning included estimating potential prey population numbers for the proposed expansion, based on each species' ecological requirements and available habitat (Boshoff *et al.* 2002). Prey population densities for this site are therefore model-derived estimates, as opposed to the other sites from which prey population densities are from actual census data. Because both the recalculated Hayward and refined regression models were developed based on uncorrected census data (see section 4.2.1.1), census data at prediction sites were also uncorrected. For five of the sites, prey density data were available for more than one year, and cheetah carrying capacity was predicted for each year (Table 4.3).

For sites where no prey demographic information was available, standard prey demographic proportions of 35% adult male, 50% adult female, and 15% juvenile (detailed in section

4.2.1.1) were used to apportion prey density data into the respective demographic classes in each listed prey species (Table 4.3). For Shamwari, prey demographic ratios were assumed to be the same as those recorded for neighbouring Amakhala (refer to section 3.2.2.3). Prey density data were converted into biomass (kg.km^{-2}) for each prey species (for the recalculated Hayward regression model) and each prey species-demographic-class (for the refined regression model), as detailed in section 4.2.1.1. The biomass of prey species that fall within the 23 to 56 kg weight range was calculated (for use in the recalculated Hayward regression model; see section 4.2.1.5). The biomass of prey species-demographic-classes accessible to solitary and coalition cheetah was calculated (for use in the refined regression model; see section 4.2.1.2).

4.2.1.7 Comparing predictions to investigate the influence of cheetah social class on cheetah carrying capacity

For each available year at each prediction site, the difference in biomass (kg.km^{-2}) of prey accessible to male coalition cheetah and to all cheetah (solitary and coalition) was calculated. The percentage difference in cheetah carrying capacity predictions between the recalculated Hayward and the refined regression models was then regressed against the biomass of prey accessible only to male coalition cheetah (Zar 1984). As a result of the biomass differences not being normally distributed, these data were log transformed (Zar 1984). Prediction site Madjuma for 1998 was excluded from the regression, as very low prey densities in the preferred species weight range resulted in the recalculated Hayward regression model predicting values over 700% lower than the refined regression model (in contrast to an average of 58% across the other 19 datasets – see results) and this outlier therefore skewed the results. Furthermore, modelled prey numbers for the GANP are based on the assumption that the energy-use of a population is independent of its mass (Damuth 1987; Boshoff *et al.* 2002). However, du Toit & Owen-Smith (1989) showed that for African savannah herbivores, population energy-use scales positively with mass, and as result of this the Boshoff *et al.* (2002) prey carrying capacity estimates overestimate the potential number of smaller prey species. This would explain why, according to the GANP modelled prey numbers, there is a much lower percentage of prey biomass available only to male coalitions than at the other sites (see results). The GANP cheetah carrying capacity estimate was therefore also omitted from the regression analysis.

Table 4.3. Model prediction sites and years from which prey density data were used, as well as sources of prey demographic data.

Model prediction site	Year	Prey demographic data source
Addo	2002	Standard ratios used
	2003	Standard ratios used
	2004	Standard ratios used
Darlington	2004	Standard ratios used
GANP	modelled	Standard ratios used
Karoo	2002	Standard ratios used
	2003	Standard ratios used
	2004	Standard ratios used
Madjuma	1997	Standard ratios used
	1998	Standard ratios used
MZNP	2002	Standard ratios used
	2003	Standard ratios used
	2004	Standard ratios used
Nyathi	2004	Standard ratios used
Phinda	1995	Phinda unpubl. data
Shamwari	2000	Amakhala unpubl. data
	2001	Amakhala unpubl. data
	2002	Amakhala unpubl. data
	2003	Amakhala unpubl. data
	2004	Amakhala unpubl. data

4.2.2 Developing a mechanistic cheetah carrying capacity model

Predation can be likened to the harvesting of animals from a population (Power 2002a), and therefore the concept of Maximum Sustainable Yield (MSY) (Caughley 1977) can be useful in determining how many individuals of a prey species can be sustainably killed by a predator in a year. Once the MSY for all prey species at a site has been calculated (*step 1*), this MSY can then be converted into the maximum sustainable biomass, accessible to solitary and coalition cheetah (*step 2*). The dietary requirements of adult and juvenile cheetah can then be used to determine how many cheetah the accessible biomass can sustain (*step 3*).

Step 1: The maximum number of a given species that can be sustainably killed per year (*MSY*) is a function of the intrinsic rate of increase of the prey species (r) and the size of the prey population at carrying capacity (K_p) (Caughley 1977):

$$MSY = \frac{rK_p}{4}$$

The intrinsic rate of increase of a prey species can be calculated from the weight of the species (W), where:

$$r = 1.5\mathrm{W}^{-0.36}$$

(Caughley & Krebs 1983). For each prey species, standard adult female body weight (Appendix Table C) was used to determine intrinsic rate of increase, as was done by Lindsey *et al.* (2004, 2011). At any site, the MSY of each prey species can be determined in this way. This MSY can then be apportioned into the three prey species-demographic-classes based on known or assumed demographic ratios of each prey species.

Step 2: Because this model approach is based on the energy requirements of the carnivore, not merely a regression between prey biomass and carnivore density, an estimate of edible prey biomass is required. Therefore, to convert MSY into maximum sustainable biomass (MSY_{kg}), the edible biomass of each prey species-demographic-class must be calculated. This can be done following Bissett & Bernard (2007), who suggest that 67% of prey items > 80 kg, 90% of prey items between 5 – 80 kg and 100% of prey items < 5 kg are consumed by cheetah. The weight range of prey accessible to solitary and male coalition cheetah (Table 4.2) can then be used to calculate the portion of total MSY_{kg} at a site that is accessible to each cheetah social class. Because male coalition cheetah can also access the weight range of prey accessible to solitary cheetah (Table 4.2), the MSY_{kg} that is accessible to solitary and coalition cheetah is hereafter referred to as MSY_{ALL}.

Step 3: In order to calculate, for a given prey population, the number of cheetah that can be supported in a given sex and age ratio, I needed to derive a variable, x, which divides the MSY_{ALL} between solitary cheetah and cubs ($xMSY_{ALL}$), and coalition cheetah ($MSY_{ALL} - xMSY_{ALL}$). This variable is needed in order to account for the lower dietary requirements of juveniles and the greater biomass of prey available to male coalitions when calculating carrying capacity. I assumed that a juvenile cheetah (defined as a cheetah still dependent on its mother for food) requires 0.75 of an adult cheetah's daily meat requirement (following Owen-Smith & Mills 2008; Lindsey *et al.* 2011), where an adult cheetah requires 2.1 kg per day (Owen-Smith & Mills 2008), or 766.5 kg per year (D). Therefore, for a cheetah population with a proportional population composition (p) of juveniles j; solitary adults SA; solitary adults and juveniles S; and male coalition cheetah c, the solitary and cub cheetah carrying capacity (K_s) can be calculated as:

$$K_S = \frac{xMSY_{ALL}}{D\frac{p_{SA}}{p_S} + 0.75D\frac{p_j}{p_S}}$$

I further assumed that male coalition cheetah consume prey within the weight range accessible to all cheetah (ALL) and accessible to only male coalition cheetah (c) relative to their proportional contribution (*pr*) to the sum of these edible biomasses. Therefore, the male coalition cheetah carrying capacity (K_C) can be calculated as:

$$K_C = \frac{MSY_{ALL} - xMSY_{ALL} + (MSY_{ALL} - xMSY_{ALL}) * \frac{pr_c}{pr_{ALL}}}{D}$$

Therefore, for a cheetah population with any given age and sex ratio, *x* can be derived as follows:

$$\frac{xMSY_{ALL}}{D\frac{p_{SA}}{p_S} + \ 0.75D\frac{p_j}{p_S}} * \frac{1}{p_s} = \frac{MSY_{ALL} - xMSY_{ALL} + (MSY_{ALL} - xMSY_{ALL}) * \frac{pr_c}{pr_{ALL}}}{D} * \frac{1}{p_c}$$

$$\frac{x}{(p_{SA} + \ 0.75p_j)} = \frac{pr_{ALL} - xpr_{ALL} + pr_c - xpr_c}{p_c pr_{ALL}}$$

Because $pr_{ALL} + pr_c = 1$ (proportional contribution of the biomass accessible to all cheetah and to male coalition cheetah only = 1), I can substitute pr_c with ($1-pr_{ALL}$):

$$\frac{x}{(p_{SA} + \ 0.75p_j)} = \frac{pr_{ALL} - xpr_{ALL} + (1 - pr_{ALL}) - x(1 - pr_{ALL})}{p_c pr_{ALL}}$$

$$\frac{x}{(p_{SA} + \ 0.75p_j)} = \frac{1 - x}{p_c pr_{ALL}}$$

$$xp_c pr_{ALL} = p_{SA} + 0.75p_j - xp_{SA} - 0.75xp_j$$

$$x \ \ p_c pr_{ALL} + \ p_{SA} + 0.75p_j \ \ = \ p_{SA} + 0.75p_j$$

$$x = \ \frac{p_{SA} + 0.75p_j}{p_c pr_{ALL} + \ p_{SA} + 0.75p_j}$$

Total cheetah carrying capacity K_{ALL}, can be calculated:

$$K_{ALL} = \ \frac{xMSY_{ALL}}{D\frac{p_{SA}}{p_S} + \ 0.75D\frac{p_j}{p_S}} + \frac{MSY_{ALL} - xMSY_{ALL} + (MSY_{ALL} - xMSY_{ALL}) * \frac{pr_c}{pr_{ALL}}}{D}$$

$$K_{ALL} =$$

$$\frac{xp_s MSY_{ALL}}{D(p_{SA} + \ 0.75p_j)} + \frac{MSY_{ALL}pr_{ALL} - xMSY_{ALL}pr_{ALL} + MSY_{ALL}(1 - pr_{ALL}) - \ xMSY_{ALL}(1 - pr_{ALL})}{Dpr_{ALL}}$$

Therefore:

$$K_{ALL} = \frac{xp_s MSY_{ALL}}{D(p_{SA} + 0.75p_j)} + \frac{MSY_{ALL} - xMSY_{ALL}}{Dpr_{ALL}}$$

where:

$$x = \frac{p_{SA} + 0.75p_j}{p_c pr_{ALL} + p_{SA} + 0.75p_j}$$

This model is hereafter referred to as the MSY model.

4.2.3 *Using the MSY model to test the assumptions of the regression model*

4.2.3.1 *Testing the assumption that cheetah social structure does not influence carrying capacity*

Two hypothetical reserves with differing prey population parameters are detailed in Table 4.4. The influence of (1) cheetah age composition and (2) cheetah social class composition on carrying capacity at the hypothetical reserves was investigated by calculating cheetah carrying capacity using the MSY model under the following conditions:

1. Varying the proportion of juvenile versus adult cheetah in the population, by varying the proportion of juvenile cheetah in the population from 0 to 0.75 in 0.05 increments, while keeping the ratio of solitary adult cheetah to adult coalition cheetah constant at 1 solitary adult cheetah : 0.3 coalition cheetah (as per ratios recorded in the Serengeti – Caro & Collins 1986).
2. Varying the proportion of juvenile and solitary cheetah versus male coalition cheetah in the population, by varying the proportion of juveniles in the population from 0 to 0.75 in 0.05 increments and keeping the ratio of juvenile cheetah to female constant at 2.77 juveniles: 1 female cheetah (as per ratios recorded in the Serengeti – Durant 1994).

The maximum proportion of juveniles in the population was set to 0.75 as it is unrealistic to have a population with only juveniles, since juveniles are dependent on their mothers.

Table 4.4. Prey population parameters for two hypothetical reserves.

	Hypothetical reserve 1	**Hypothetical reserve 2**
MSY (kg) accessible to all cheetah	50 000	50 000
MSY (kg) accessible only to coalition cheetah	200 000	66 667
Proportion of prey accessible only to coalition cheetah (*pr*$_c$)	0.75	0.25

4.2.3.2 Testing the assumption that competing carnivores do not influence cheetah carrying capacity

For the seven regression model development sites, cheetah carrying capacity was predicted using the MSY model. Cheetah social class composition in all "natural ecosystems" is assumed to mirror that observed in the Serengeti, namely 1 female : 0.63 males, 1 solitary male : 1.44 coalition males, and 1 female : 2.77 juveniles (Caro & Collins 1986; Durant 1994).

The percentage by which the cheetah carrying capacity predicted by the MSY model (hereafter referred to as predicted cheetah density) over- or under-estimated the actual cheetah density for each site was calculated. The percentage that the four other large carnivores (lion, leopard, spotted hyaena and African wild dog) (a) together comprise of total large carnivore density (percentage total density) and (b) each comprise of the density of just that carnivore and cheetah (percentage subtotal densities) at each site was calculated. The percentage difference between predicted cheetah density and actual cheetah density was then regressed against percentage total density and each percentage subtotal density (Zar 1984). Densities for the four other large carnivores, when present, were obtained from Hayward *et al.* (2007d), for the five original model development sites (see section 4.2.1.1; Table 4.5). Densities were obtained from annual aerial census data (Sabi Sand Wildtuin unpubl. data) for lion, leopard, spotted hyaena and African wild dog in Sabi between 2006 and 2011 (Table 4.5). For the KNP00's, density was obtained for lion from Ferreira & Funston (2010), for spotted hyaena from Funston & Ferreira (submitted for review), for African wild dog and cheetah from Marnewick *et al.* (submitted for review) and for leopard from SANParks (unpubl. data) (Table 4.5).

Table 4.5. Densities of the five large African carnivores at model development sites.

	Carnivore densities (#.km^{-2})				
Model development site	**Cheetah**	**Leopard**	**Lion**	**Spotted hyaena**	**African wild dog**
Hluhluwe-Imfolozi	0.10	0.08	0.11	0.36	0.04
Kalahari	0.01	0.01	0.01	0.01	0
KNP60's	0.01	0.03	0.06	0.08	0.02
KNP80's	0.02	0.03	0.07	0.05	0.02
KNP00's	0.02	0.08	0.08	0.16	0.01
Pilanesberg	0.04	0.1	0.05	0	0.02
Sabi	0.03	0.13	0.18	0.11	0.04

4.2.4 Comparing the MSY and regression models at test sites

MZNP in the Eastern Cape reintroduced cheetah as the only large carnivore in 2008 (Table 2.3). By 2010, cheetah numbered 32 and this rapid population growth led to managers translocating 19 cheetah off the reserve in 2010 (Zimmerman *et al.* 2011). The second selected test site, Phinda, in KwaZulu Natal, has supported a reintroduced cheetah population since 1992 (Table 2.1). While in 2008 two males were translocated off the reserve and another 2 translocated in 2011, these translocations were to supply cheetah to other KwaZulu Natal reserves and not for population control purposes (T. Burke pers. comm.). In 2010 three male cheetah were reintroduced at Phinda, in order to increase genetic variability (T. Burke pers. comm.).

The cheetah and ungulate census data available from each test site are detailed in Table 4.6. Prey demographic data were available for Phinda from Hunter (1998). At MZNP standard prey demographic ratios were applied. Census data were not corrected for visibility to predict cheetah carrying capacity using the two regression models, since uncorrected data were used to develop the models (see section 4.2.1.1). However the MSY model is dependent on an accurate prediction of available prey at each site, and since aerial censusing was used to obtain ungulate counts at both sites, standard visibility correction factors were applied to the ungulate census data used in the MSY model, as detailed in Owen-Smith & Mills (2008). Because prey population trends and predicted carrying capacities were compared between consecutive years, both corrected and uncorrected counts were further "smoothed" to account for variability in census accuracy between years (Owen-Smith & Ogutu 2003). This was done using a weighted census average (Owen-Smith & Ogutu 2003), where the corrected population count *N* in year *t* is calculated for each prey species by the equation:

$$N_t = 0.5N_t + 0.25N_{t-1} + 0.25N_{t+1}$$

Corrected smoothed and uncorrected smoothed prey census data were converted into edible biomass (kg; section 4.2.2) and biomass (kg.km^{-2}; section 4.2.1.1), respectively, for the respective purposes of the MSY and regression model carrying capacity calculations. The edible biomass and biomass of prey accessible to solitary and coalition cheetah was calculated (section 4.2.1.2). The biomass of prey species within the 23 to 56 kg weight range was also calculated (section 4.2.1.5).

In addition to cheetah census data, lion and leopard census data for Phinda were obtained (Table 4.6). Lion census data were available from ground counts and leopard census data from camera trap surveys (see Balme *et al.* 2009 for camera trapping methods). Leopard density is not available pre-2009, and density in 2010 was taken to be an average between 2009 and 2011 numbers. Cheetah census data for Phinda are also only available from 2009 (Table 4.6).

Table 4.6. Years and sources of census data for carnivores and ungulates at MZNP and Phinda.

	Census data							
	Cheetah		**Ungulates**		**Lion**		**Leopard**	
Test Site	**Years**	**Source**	**Years**	**Source**	**Years**	**Source**	**Years**	**Source**
MZNP	2008 to 2012	SANParks unpubl. data	2002 to 2006; 2008 to 2012	SANParks unpubl. data	n/a		n/a	
Phinda	2009 to 2012	Phinda unpubl. data	2001 to 2011	Phinda unpubl. data	2001 to 2012	Phinda unpubl. data	2009 and 2011	Panthera unpubl. data

For each site, cheetah carrying capacity was predicted using the recalculated Hayward regression, refined regression and MSY models for each year that prey census data were available. Cheetah social class composition was assumed to be that of a natural population (section 4.2.3.2). For Phinda the MSY model needed to control for additional “harvest” of prey by lion and leopard. Spotted hyaena were also present but in very low densities and African wild dog were transient through the area (T. Burke pers. comm.). It was therefore assumed that spotted hyaena and African wild dog were not present in sufficient densities to compete with cheetah for resources. The dietary requirements of lion and leopard were obtained from Owen-Smith & Mills (2008) and used to calculate the yearly biomass of prey (kg) required to sustain each of these carnivore populations. It was assumed that juveniles require 0.75 of the biomass required by an adult (Owen-Smith & Mills 2008) and comprise 46% and 41% of the lion and leopard population, respectively (Phinda unpubl. data; Balme *et al.* 2009). The percentage dietary overlaps between cheetah and lion, and cheetah and leopard were assumed to be 51% and 84%, respectively (Lindsey *et al.* 2011), and these percentages of the total biomass required by the lion and leopard populations were subtracted from the MSY_{kg} accessible to all cheetah (MSY_{ALL}) and to coalition cheetah (MSY_C). K_{ALL} was then calculated based on these adjusted MSY values. The MSY model which accounted for dietary overlap between carnivores is hereafter referred to as the adjusted MSY model. At MZNP cheetah are the only large carnivore, and therefore controlling for dietary overlap was not necessary. The yearly estimates of cheetah carrying capacity from the three models were compared with the actual number of cheetah at each site.

In order to investigate prey population trends, percentage annual change in smoothed, corrected population numbers for each prey species was calculated at each test site. For MZNP, prey off-takes occurred subsequent to the annual census in several years (A.

Gaylard pers. comm.). These off-takes were accounted for by adding them to the subsequent year's census data when calculating percentage annual change in population numbers. Annual declines of less than 5% (rounded off) were not considered to be notable since smoothing may not completely account for variability in sampling efficiency between years. Trends in preferred, accessible and avoided prey population numbers could not be analysed at a prey demographic class-level, since census data did not detail changes in demographic ratios within each prey species. Therefore, each prey demographic class in each available species was classified as preferred, killed relative to its abundance or avoided by each cheetah social class using Table 4.2 and Appendix Table C. Each prey species was then generalized as preferred, killed relative to its abundance or avoided based on which preference category had the highest occurrence across the three prey demographic classes and three cheetah social classes. Average annual percentage change in pooled population numbers of prey species in each of the three preference categories was calculated. Deviations in actual cheetah numbers from predicted carrying capacities were related to any prey population declines and recoveries.

4.2.5 <u>Statistical packages used</u>

All statistical tests (detailed throughout the methods) were performed in the statistical package R (R Development Core Team 2008), at a significance level of 0.05. Adjusted r^2 values are reported in all cases.

4.3 Results

4.3.1 <u>Carrying capacity regression models</u>

4.3.1.1 <u>Assessing the influence of using preferred versus accessible prey biomass to predict cheetah density</u>

For all three cheetah social classes, more of the variation in predicting cheetah density was explained by the biomass of accessible prey than by the biomass of preferred prey (Table 4.7).

The biomass of preferred prey was a significant predictor of the biomass of accessible prey at model development sites, for female, solitary male and male coalition cheetah (Table 4.8). The variability in the relationship between accessible prey biomass and preferred prey biomass for female and male coalition cheetah resulted in weaker linear regressions in comparison with solitary male cheetah (Table 4.8). The stronger regression for solitary male cheetah resulted in a reduced difference between the ability of preferred prey biomass and accessible prey biomass to predict cheetah density, when compared with the other two cheetah social classes (Table 4.7).

Table 4.7. Summary of the regression between cheetah density (log_{10}#.km^{-2}; y axis) and the biomass of either preferred or accessible prey (log_{10}kg.km^{-2}; x axis).

Cheetah social class	**Prey included**	r^2	***F***	**n**	***p***	**Equation**
Female	Preferred	0.28	3.32	7	0.13	y = 0.463x - 2.837
	Accessible	0.49	6.84	7	<0.05	y = 0.581x - 3.289
Solitary Male	Preferred	0.42	5.26	7	0.07	y = 0.524x - 3.608
	Accessible	0.50	7.02	7	<0.05	y = 0.585x - 3.895
Male Coalition	Preferred	0.46	6.08	7	0.06	y = 0.542x - 3.520
	Accessible	0.62	10.78	7	<0.05	y = 0.811x - 4.691

Table 4.8. Summary of the regression between the biomass of preferred and accessible prey at model development sites, for the three cheetah social classes.

Cheetah	r^2	***F***	**n**	***P***	**Equation**
Female	0.84	31.49	7	0.002	y = 2.28x - 17.97
Solitary Male	0.99	438.68	7	< 0.001	y = 1.56x + 37.85
Male Coalition	0.81	26.58	7	0.004	y = 2.70x + 398.67

4.3.1.2 Assessing the influence of prey demographics and cheetah social class on the predictive strength of a regression model

The biomass of prey accessible to solitary and to male coalition cheetah (at a prey demographic level) explains 75% of the variation in total cheetah density (C_{ALL}) at model development sites (r^2 = 0.75, F = 7.14, n = 7, p = 0.07). The equation for the refined regression model is

$$C_{ALL} = 10^{0.566-2.837*log_{10}(x_s)-0.389*log_{10}(x_c)+0.798*log_{10}(x_s)*log_{10}(x_c)}$$

where x is the prey biomass (kg.km^{-2}) accessible to solitary (s) and coalition (c) cheetah. This model explained more of the variation in the data than did the separate cheetah social class models (Table 4.7). The recalculated Hayward regression model (r^2 = 0.39, F = 4.84, n = 7, p = 0.08) explained less of the variation in the data than did the refined regression model.

4.3.1.3 Using the regression models to predict cheetah carrying capacity

The refined regression model predicts cheetah carrying capacity densities which are, on average, 92% (± 37%) higher than those predicted by the recalculated Hayward regression model (Table 4.9). The refined regression model predicts a notably lower (> 70% lower) cheetah carrying capacity for Darlington and the proposed GANP than does the recalculated Hayward regression model. At these sites only 56% and 33% more prey, respectively, was accessible to male coalitions than solitary cheetah, in comparison to an average of 70% (± 3%) across sites (Table 4.9).

Table 4.9. The predicted carrying capacity (#.km^{-2}) of cheetah at nine prediction sites using the recalculated Hayward and refined regression models (^{x} - refined regression model prediction lower than recalculated Hayward regression model prediction).

Prediction site	**Year**	**Recalculated Hayward regression model**	**Refined regression model**	**% prey biomass accessible to coalition cheetah only**
Addo	2002	0.019	0.028	0.79
	2003	0.020	0.056	0.83
	2004	0.010	0.036	0.77
Darlington	2004	0.021	0.008^{x}	0.56
GANP	Modelled	0.025	0.014^{x}	0.33
Karoo	2002	0.016	0.012^{x}	0.70
	2003	0.014	0.014	0.77
	2004	0.010	0.016	0.81
Madjuma	1997	0.021	0.042	0.84
	1998	0.015	0.124	0.91
MZNP	2002	0.025	0.034	0.73
	2003	0.023	0.031	0.74
	2004	0.028	0.037	0.69
Nyathi	2004	0.010	0.018	0.81
Phinda	1995	0.047	0.087	0.62
Shamwari	2000	0.034	0.056	0.64
	2001	0.035	0.050	0.61
	2002	0.036	0.065	0.62
	2003	0.038	0.073	0.63
	2004	0.035	0.050	0.58

4.3.1.4 Comparing predictions to investigate the influence of cheetah social class on cheetah carrying capacity

An increase in the (logged) biomass of prey accessible to male coalition cheetah only resulted in a significant percentage increase in cheetah carrying capacity predicted by the refined regression model compared to the recalculated Hayward regression model ($r^2 = 0.50$, $F = 17.64$, n = 18, $p < 0.001$; Fig. 4.1).

4.3.2 Using the MSY model to test the assumptions of the regression model

4.3.2.1 Testing the assumption that cheetah social structure does not influence cheetah carrying capacity

When the ratio of solitary adult to male coalition cheetah in the population remains constant, the predicted cheetah carrying capacity increases as the proportion of juveniles relative to adults in the population increases from 0 to 0.75 (Fig. 4.2a). Predicted carrying capacity is higher when there is 4 times more prey available to male coalition cheetah than when there is 1.33 times more prey available to male coalition cheetah. This difference in carrying capacity decreases as the proportion of juveniles in the population increases (Fig. 4.2a).

When the proportion of juveniles in the population is directly related to the proportion of females, with 1 female to every 2.77 juveniles, an increase in the proportion of juveniles and females in the population (and therefore a decrease in the proportion of male coalition cheetah) results in a decrease in the predicted carrying capacity (Fig 4.2b). This is far more notable when male coalition cheetah have more prey accessible to them than solitary cheetah: an increase in the proportion of juveniles in the population from 0 to 0.75 results in a carrying capacity decrease of 68% and 6% when male coalition have 4 times and 1.33 times more prey accessible to them than solitary cheetah, respectively (Fig 4.2b). Predicted carrying capacity is higher when there is 4 times more prey available to male coalition cheetah than when there is 1.33 times more prey available to male coalition cheetah and this difference in carrying capacity decreases as the proportion of juveniles and females in the population increases (Fig. 4.2b).

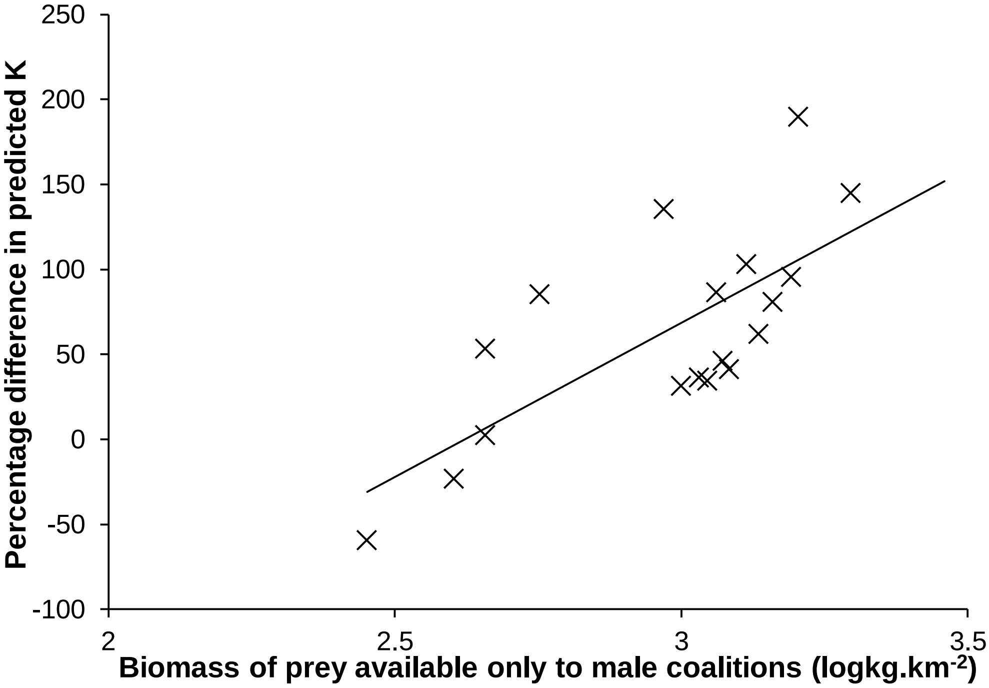
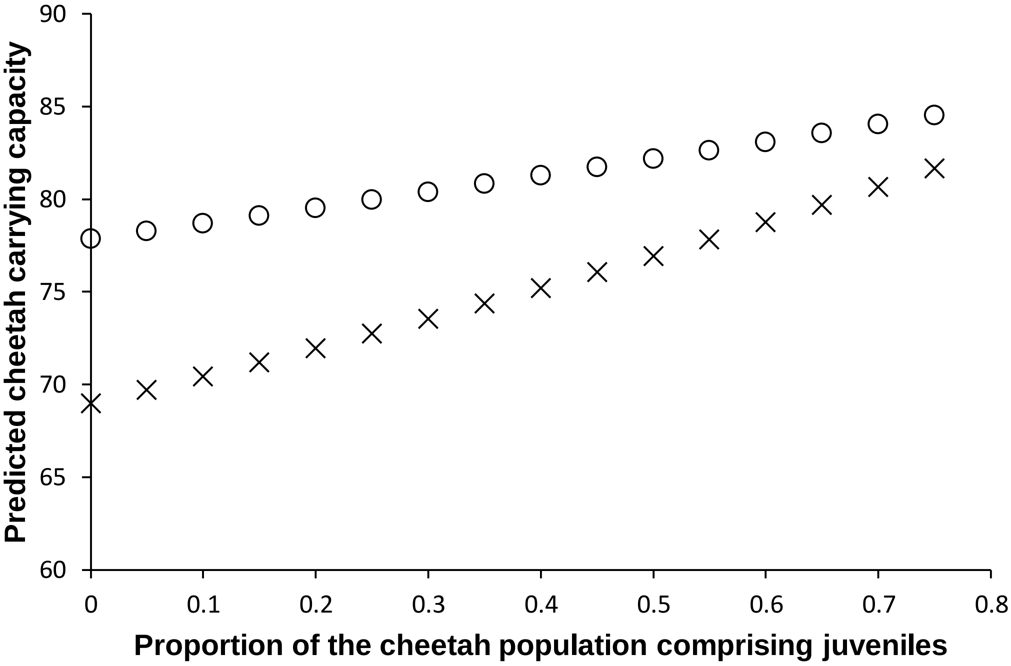


Figure 4.1. The percentage that the cheetah carrying capacity (K) predicted by the refined regression model differs from K predicted by the recalculated Hayward regression model, relative to the prey biomass accessible to male coalition cheetah only (r^2 = 0.50, F = 17.64, n = 18, p < 0.001; Madjuma from 1998 and GANP excluded – see section 4.2.1.7).

a.



b.

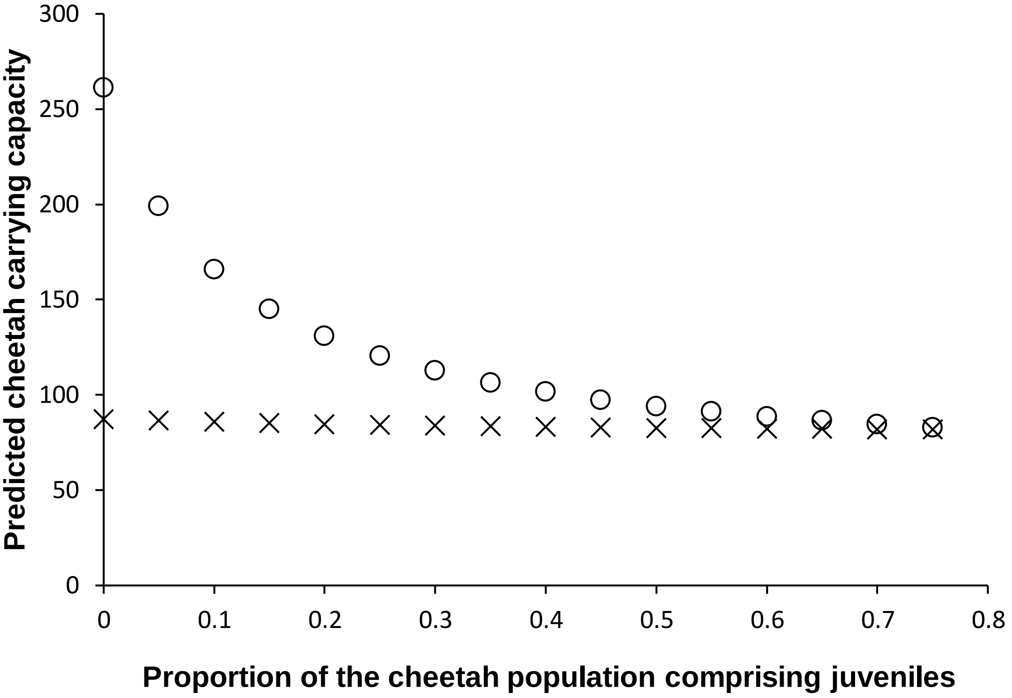


Figure 4.2. The predicted cheetah carrying capacity on two hypothetical nature reserves, dependent on the proportion of juveniles in the population, when male coalition cheetah have 4 times (circles) and 1.33 times (crosses) more prey accessible to them than solitary cheetah. (a) represents the ratio of solitary adult to male coalition cheetah in the population remaining constant and (b) represents the proportion of adult female cheetah in the population increasing relative to an increasing proportion of juveniles.

4.3.2.2 Testing the assumption that competing carnivores do not influence cheetah carrying capacity

An increase in lion density relative to cheetah density led to a significant increase in the predicted cheetah density compared to the actual cheetah density (Table 4.10). Similarly, an increase in African wild dog density relative to cheetah density led to a significant increase in the percentage difference between predicted and actual cheetah density (Table 4.10). An increase in relative lion density had a greater effect on the difference between predicted and actual cheetah density than did an increase in relative African wild dog density (β = 753.74 and β = 614.81, respectively; Table 4.10), but both had a greater effect than relative leopard and spotted hyaena density (Table 4.10).

Table 4.10. Summary of the regression between the percentage that each of the four large carnivores comprise of the density of that carnivore and cheetah at a site (x axis), and the percentage by which the predicted cheetah density differed from actual cheetah density (y axis).

Large Carnivore	**Slope (β)**	r^2	***F***	**n**	***P***
Lion	753.74	0.50	7.01	7	<0.05
Leopard	347.57	0.24	2.92	7	0.15
Spotted hyaena	295.36	0.19	2.41	7	0.18
African wild dog	614.81	0.70	15.16	7	<0.005
All	1332.80	0.36	4.31	7	0.09

4.3.3 Comparing the MSY and regression models at test sites

At MZNP cheetah were reintroduced in 2008, and according to the MSY model they were introduced below their carrying capacity, but according to the refined regression model they were introduced just above their carrying capacity (Fig. 4.3). By 2009, according to the MSY and refined regression models, cheetah were at carrying capacity and 7 individuals above carrying capacity, respectively (Fig. 4.3). In 2010 cheetah numbers reached 32, exceeding the carrying capacities predicted by the MSY and refined regression models by 16 and 19 cheetah, respectively (Fig. 4.3). In 2010, 19 cheetah were translocated out from the reserve, and in 2011 cheetah numbers were back at carrying capacity according to the MSY and refined regression models (Fig. 4.3).

Common duiker, grey rhebok, mountain reedbuck, springbok and steenbok populations declined from both 2009 to 2010 and from 2010 to 2011 at MZNP (Table 4.11). All five of these prey species are classified as preferred (Table 4.11). While common duiker, mountain reedbuck and steenbok declined pre-cheetah reintroduction, population declines were much higher post-cheetah reintroduction (Table 4.11). In contrast, no relatively killed or avoided prey species populations declined from 2009 to 2011 (Table 4.11).

In 2012 cheetah were below carrying capacity at MZNP according to both the MSY and refined regression models, and two of the five previously declining species displayed positive growth (common duiker and steenbok). Springbok was still declining but only by 5%, and mountain reedbuck declines had dampened from 42% in the previous year to 30% (Table 4.11). Grey rhebok was still declining and at a greater rate (Table 4.11). Klipspringer also declined from 2010 to 2012 (Table 4.11). Grey rhebok and klipspringer showed the highest annual declines from 2008 to 2009 and 2005 to 2006, respectively (Table 4.11).

The pooled prey population trends at MZNP show preferred prey to decline between 2009 and 2012, and most substantially between 2009 and 2011 (Fig. 4.3; Table 4.11). Prey killed relative to its abundance and avoided by cheetah show positive percentage annual changes over this period, with avoided prey increasing at over double the rate of prey killed relative to its abundance (Fig. 4.3; Table 4.11).

For MZNP the recalculated Hayward regression model consistently predicted the lowest cheetah carrying capacity numbers of the three models (Fig. 4.3). Actual cheetah numbers were above the carrying capacity predicted by the recalculated Hayward regression model from 2008 to 2012 (Fig. 4.3). With the exception of estimates for 2011 and 2012, the refined regression model predicted lower cheetah carrying capacities than the MSY model (Fig. 4.3). The difference between estimates made by these two models was less post-cheetah reintroduction than pre-reintroduction (2 ± 2 cheetah versus 11 ± 0.5 cheetah; Fig. 4.3).

At Phinda, according to the adjusted MSY and refined regression models, cheetah were above predicted carrying capacity in 2009 by 17 and 20 cheetah, respectively (Fig. 4.4). According to both models cheetah were below carrying capacity in 2010, and above carrying capacity in 2011 by 10 and 5 cheetah, respectively (Fig. 4.4). Kudu numbers declined annually from 2008 to 2011 and impala and nyala declined from 2009 to 2011 (Table 4.12). Additionally, common duiker, red duiker *Cephalophus natalensis,* common reedbuck and warthog declined from 2010 to 2011 (Table 4.12). All seven of these prey species are categorized as either preferred or killed relative to their abundance by cheetah (Table 4.12). No avoided prey species declined from 2009 to 2011 (Table 4.12). The pooled prey population trends indicate that preferred prey declined between 2009 and 2011, prey killed relative to its abundance declined between 2010 and 2011 and avoided prey increased marginally over the same period (Fig. 4.4).

For Phinda the recalculated Hayward regression model predicted lower carrying capacities than the adjusted MSY model in all years, and lower carrying capacities than the refined regression model in seven of the eleven years (Fig. 4.4). The refined regression model predicted lower cheetah carrying capacities than the adjusted MSY model in all years except 2012, though the difference in estimates was much greater from 2001 to 2008 (13 ± 1 cheetah) than from 2009 to 2011 (4 ± 1 cheetah; Fig. 4.4). Lion numbers increased dramatically from 2001 to 2009 (Fig. 4.4).

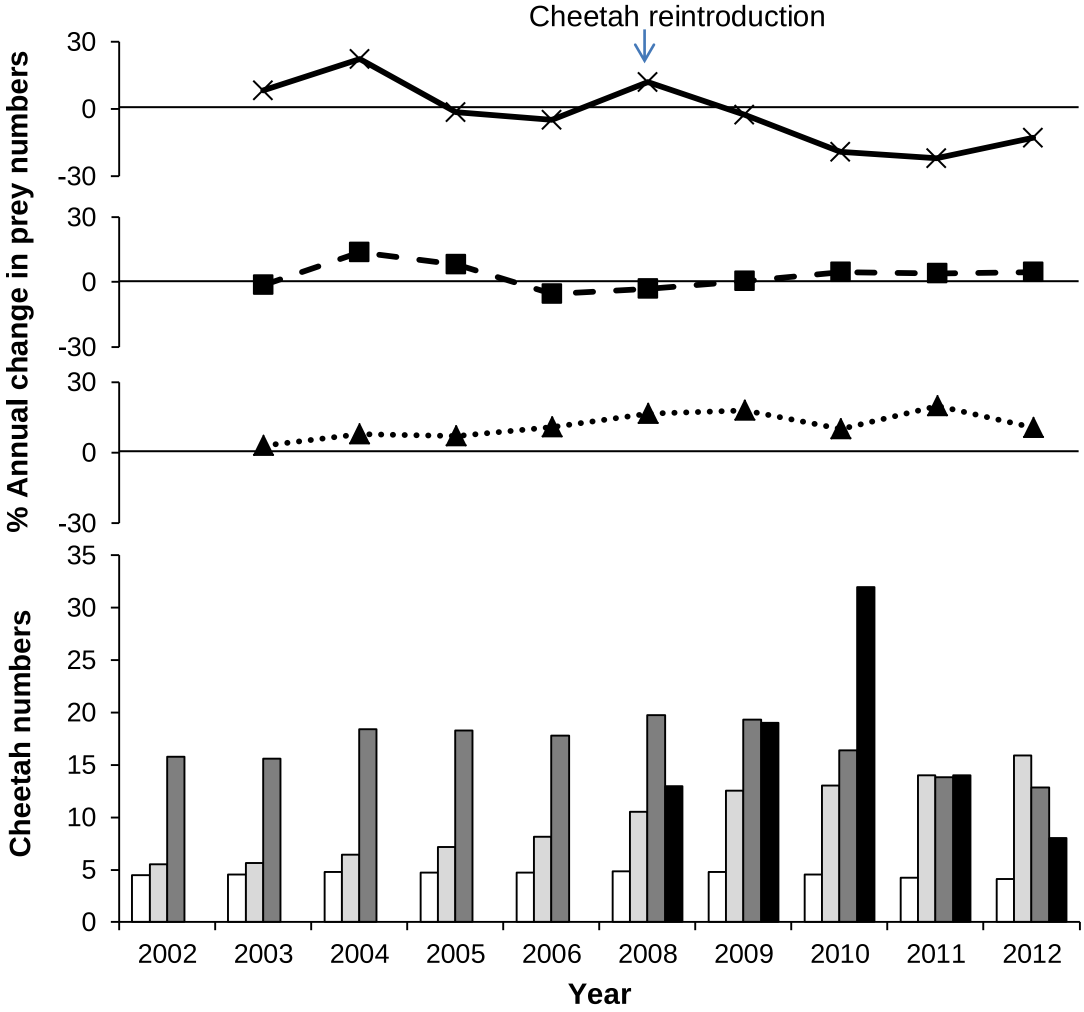


Figure 4.3. The actual cheetah population number (black bars) at MZNP, relative to the predicted cheetah carrying capacity according to the recalculated Hayward regression (white bars), refined regression (light grey bars) and MSY (dark grey bars) models. Lines indicate percentage annual change in prey population numbers of preferred prey (crosses and solid line), prey killed relative to its abundance (squares and dashed line) and avoided prey (triangles and dotted line).

Table 4.11. Annual percentage changes in prey population numbers, from 2005 to 2012, at MZNP (bold figures indicate population declines > 5%; refer to Appendix Table C for species scientific names).

Species	**Preference status**	**Percentage change in population number** **2005 to 2006**	**2008 to 2009**	**2009 to 2010**	**2010 to 2011**	**2011 to 2012**
Pooled Preferred		12.05	-2.52	**-19.28**	**-22.09**	**-12.82**
Duiker Common	Preferred	**-28.89**	**-18.42**	**-58.06**	**-30.77**	62.96
Grey Rhebok	Preferred	10.48	**-21.23**	**-6.38**	**-8.98**	**-17.01**
Klipspringer	Preferred	**-45.83**	4.76	77.27	**-15.38**	**-43.43**
Reedbuck Mountain	Preferred	**-24.68**	-1.83	**-32.19**	**-41.51**	**-29.59**
Springbok	Preferred	13.50	0.88	**-10.59**	**-11.98**	**-5.20**
Steenbok	Preferred	**-22.45**	**-45.83**	**-38.46**	**-12.50**	33.33
Pooled Killed Relative		-3.09	0.35	4.46	3.89	4.54
Blesbok	Killed Relative	**-18.70**	**-14.69**	14.68	5.80	-1.08
Kudu	Killed Relative	10.56	11.38	6.89	4.37	7.45
Ostrich	Killed Relative	20.00	**-14.86**	**-17.06**	-1.44	1.29
Pooled Avoided		16.68	17.88	10.19	19.77	10.52
Buffalo	Avoided	38.18	15.87	14.47	**-6.95**	12.04
Eland	Avoided	4.34	**-6.38**	-2.67	16.42	15.47
Gemsbok	Avoided	92.89	27.61	2.47	10.73	10.43
Red Hartebeest	Avoided	3.86	19.94	13.31	20.34	3.53
Wildebeest Black	Avoided	28.70	22.95	8.72	33.82	16.91
Zebra Mountain	Avoided	22.86	20.87	15.54	11.42	6.37
Zebra Plains	Avoided	2.70	17.31	20.22	37.42	15.32

Table 4.12. Annual percentage changes in prey population numbers, from 2007 to 2011, at Phinda Game Reserve (bold figures indicate population declines > 5%; refer to Appendix Table C for species scientific names).

Species	**Preference status**	**Percentage change in population number** **2007 to 2008**	**2008 to 2009**	**2009 to 2010**	**2010 to 2011**
Pooled Preferred		3.90	7.10	**-5.69**	**-17.98**
Duiker Common	Preferred	100.00	191.67	32.86	**-32.62**
Impala	Preferred	-0.66	-1.46	**-4.66**	**-5.62**
Nyala	Preferred	3.73	2.41	**-10.41**	**-21.96**
Reedbuck Common	Preferred	122.98	151.25	12.75	**-40.09**
Pooled Killed Relative		3.10	22.62	0.04	**-24.06**
Duiker Red	Killed Relative	40.00	42.86	9.5	**-38.51**
Kudu	Killed Relative	-2.16	**-5.90**	**-9.72**	**-22.92**
Warthog	Killed Relative	2.30	27.14	1.03	**-23.23**
Pooled Avoided		5.61	1.84	5.77	6.50
Buffalo	Avoided	28.39	20.57	12.23	8.51
Giraffe	Avoided	2.05	-1.84	5.12	7.36
Waterbuck	Avoided	5.71	**-10.81**	21.21	30.00
Wildebeest Blue	Avoided	-2.31	-3.23	6.21	5.32
Zebra Plains	Avoided	6.78	-0.77	0.49	5.06

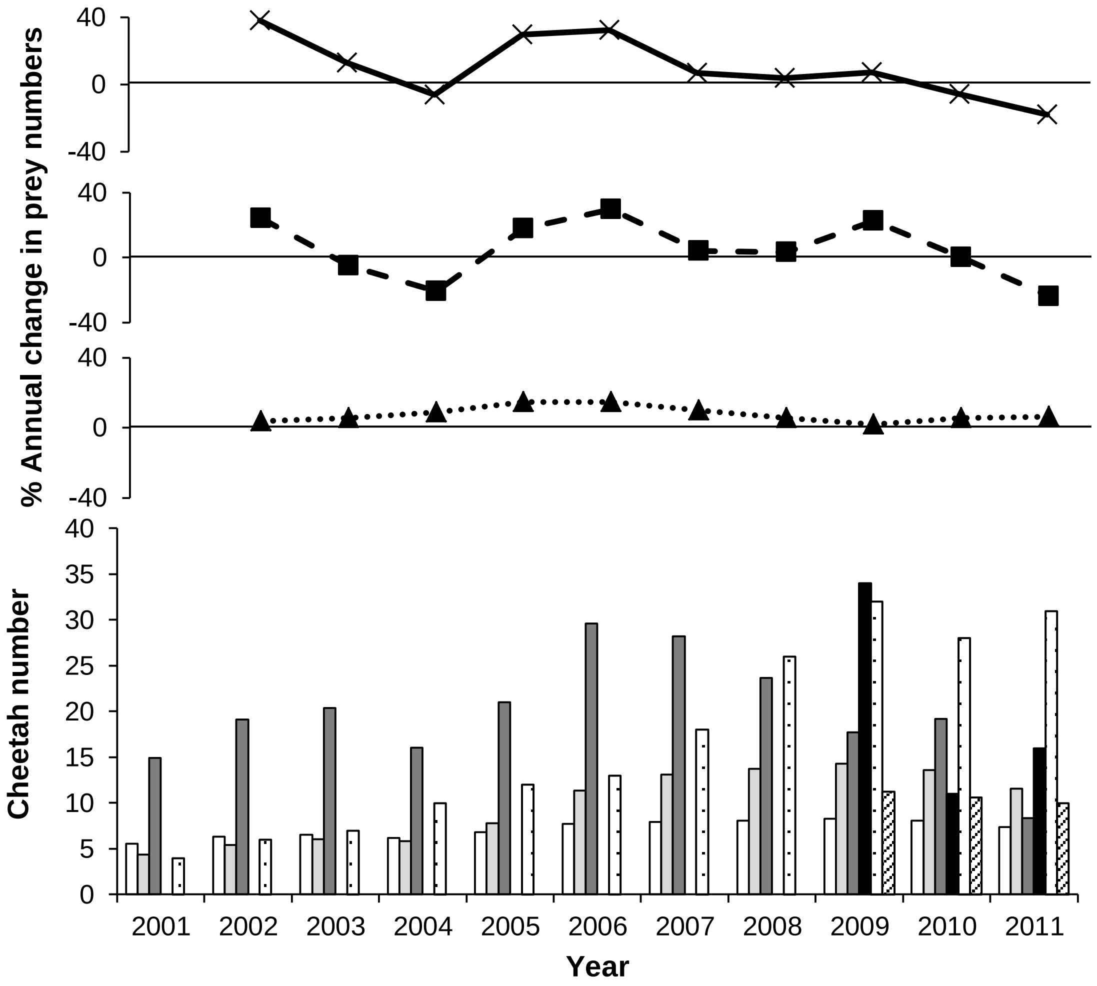


Figure 4.4. The actual cheetah, lion and leopard population number (black, spotted and striped bars, respectively) at Phinda, relative to the predicted cheetah carrying capacity according to the recalculated Hayward regression (white bars), refined regression (light grey bars) and adjusted MSY (dark grey bars) models. Lines indicate percentage annual change in prey population numbers of preferred prey (crosses and solid line), prey killed relative to its abundance (squares and dashed line) and avoided prey (triangles and dotted line). NOTE: cheetah and leopard counts unavailable from 2001 to 2008.

4.4 Discussion

4.4.1 Summary of study objectives and limitations

This study achieved its objective of investigating the influence of preferred versus accessible prey, prey demographic- versus prey species-level diet predictions and predator species- versus social class-level diet predictions on the predictive ability of a carrying capacity regression model for cheetah. By deriving a more mechanistic model, two assumptions made by carnivore carrying capacity regression models were tested. Deviations of model assumptions from reality provide insights into the value of regression versus mechanistic models, which will be further addressed in this discussion. While several assumptions made by carrying capacity models were specifically investigated in this study, additional factors, that may influence carrying capacity predictions, have not been investigated or controlled for in this study and must therefore be initially noted.

In order to relate predator density to the biomass of its prey in the development of a regression model, it was necessary to base the model on nature reserves in which both predator and prey density were not largely influenced by human intervention (such as hunting, culling, reintroduction or relocation), as done by Hayward *et al.* (2007d). There are a limited number of such reserves in South Africa and my regression model was therefore developed based on data from just seven sites. Even at these sites predator-prey abundance relationships can be influenced by the difficulty of accurately censusing carnivores (Wilson & Delahay 2001), variations in censusing methods (Gros *et al.* 1996), definitions of food availability at the appropriate scale (see Hayward *et al.* 2011) and disease (see Murray *et al.* 1999; Craft *et al.* 2009). Despite these confounding factors, the refined regression model developed in this study explained three quarters of the variation between predator density and prey biomass at model development sites. The model should, however, be applied bearing these limitations in mind.

In contrast, a more mechanistic carrying capacity model avoids the aforementioned limitations of a regression approach. It requires, instead, an estimate of the level of predation on each accessible prey species in a given ecosystem that is sustainable. The MSY concept (Caughley 1977) provides a means of obtaining such an estimate. However, as it is based on prey biomass alone, it makes the assumption that all prey falling within the weight range accessible to cheetah are actually vulnerable to predation. Based on available habitat and prey species behaviour however, some species may evade predation by using safer habitats (Hernández & Laundré 2005). The regression model inherently accounts for this as it is based on an observed predator-prey abundance relationship. Thus, as the MSY model is based on prey biomass alone it may overestimate actual available prey, which may therefore explain the higher carrying capacity predictions made by the MSY model compared with the regression models, which is further discussed in section 4.4.5.

4.4.2 Preferred versus accessible prey as predictors of carnivore density

Throughout South Africa, prey in the weight range preferred by cheetah constitute only 56 to 65% of the diet, with prey in the accessible weight range constituting at least 90% of the diet (Chapter 3). Determined by a carnivore's energy requirements, a carnivore's density should depend on the availability of all prey which it is capable of capturing. By attempting to predict carnivore density based on only a portion of this potential food source, namely that which is preferred, the importance of other prey to the diet is lost. This therefore explains why accessible prey was found to be a better predictor of cheetah density than preferred prey.

Preferred prey biomass is, however, a good predictor of accessible prey biomass. This suggests that preferred prey can still serve as a predictor of cheetah density as it consistently represents the entire diet. When the relationship between preferred and accessible prey biomass is strong, preferred and accessible prey biomass are similar in their ability to predict cheetah density. However, when greater variability in the relationship between the two biomasses exists, accessible prey biomass proves to have greater ability to predict cheetah density. This suggest that the strength of a carrying capacity model based on preferred prey biomass is dependent on the variability in the relationship between preferred and accessible prey biomass. The biomass of preferred prey relative to accessible prey may vary across sites. Preferred prey are likely to be those that a predator has evolved to optimally hunt (Hayward 2011). When preferred prey occur at densities insufficient to sustain a predator, the predator will also kill other prey, which it has not evolved to preferentially prey upon, but hunts during “prey switching” (Pech *et al.*1995; Harrington *et al.* 1999; Garrott *et al.* 2007; Hayward 2011; Grange *et al.* 2012). The degree of prey switching is therefore dependent on the relative abundances of preferred versus non-preferred prey, which can differ across sites. The accuracy of carrying capacity predictions using a model based on preferred prey will therefore be a function of the congruence in the relationship between preferred and accessible prey biomass at the prediction site and model development sites.

4.4.3 The influence of prey demographics and predator social structure on cheetah carrying capacity

Accounting for prey demographics and predator social structure when calculating available prey biomass improved the strength with which prey biomass predicted cheetah carrying capacity. This indicates that our ability to accurately predict cheetah diet, and thereby carrying capacity, is improved when predictions are made at a prey demographic-level, as well as accounting for variation in diet between cheetah social classes.

Resource-partitioning, or differences in how animals use resources, in a multi-carnivore guild occurs through the following mechanisms: selection for prey species (Karanth & Sunquist 2000; Hayward & Kerley 2008), selection for prey size (Gittleman 1985; Cohen *et al*. 1993), activity patterns (Fedriani *et al.* 1999; Karanth & Sunquist 2000), use of space (Palomares *et al.* 1996; Durant 1998, 2000) and evolution of different physiological adaptations for prey selection (Biknevicius & Van Valkenburgh 1996; Taber *et al.* 1997; Hayward *et al.* 2006b;

Christiansen & Wroe 2007). Mechanisms of resource-partitioning within species are less well studied, perhaps due to the difficulty of testing such hypotheses (Shine 1989). For the large African carnivores, larger carnivores did not specialize solely on larger prey, but rather killed a broader weight range of prey than smaller carnivores (Radloff & du Toit 2004), as was found for coalition versus solitary cheetah in this study (Chapter 3). It has therefore been proposed that resource-partitioning did not occur, either between the dimorphic sexes within a carnivore species, or between differently sized species within the guild (Radloff & du Toit 2004).

This study's findings however suggest that a degree of resource-partitioning between solitary and coalition cheetah may exist. A given prey population is capable of sustaining a larger number of cheetah when there is either a larger proportion of male coalition cheetah in the population, or a larger proportion of prey accessible to only male coalition cheetah. Therefore, despite coalitions still killing the same smaller prey as solitary cheetah (Chapter 3), their ability to take larger prey inaccessible to solitary cheetah may facilitate resource-partitioning, which thereby reduces resource-sharing and therefore increases cheetah carrying capacity. Given these findings, I would hypothesize that variation in hunting ability would also facilitate resource-partitioning in sexually dimorphic predators, such as lion and, perhaps more so, in the solitary hunting leopard (Funston *et al.* 1998; Salesa *et al.* 2006), and thereby result in the ecosystem being able to support a larger number of carnivores than if both sexes were limited to eating the same prey. While Radloff & du Toit (2004) disputed resource-partitioning in sexually dimorphic large carnivores, their analyses show that despite dietary overlap in the weight range of prey eaten, the average mass of prey killed by male lion, leopard and cheetah (in coalitions) was substantially greater than that killed by their female counterparts, suggesting that resource-partitioning does occur between males and females in each species. Reduced competition through niche-partitioning, including resource-partitioning, has been shown to be a valid alternative hypothesis to sexual selection in explaining the evolution of sexual dimorphism across a variety of taxa (Shine 1989).

A given prey population can support a larger cheetah population when that population comprises of a greater proportion of juveniles compared to adults. This is despite juveniles being dependent on the narrower weight range of prey accessible to their mothers and is a result of juveniles having reduced resource requirements (Owen-Smith & Mills 2008). This is obviously a short-term phenomenon, however, since once juveniles reach maturity their resource requirements will increase, thus reducing carrying capacity and bringing the population closer to this threshold. A simulated time-series model (e.g. Levi & Wilmers 2012) would provide a good opportunity to investigate the long term influence of recruitment rates and patterns on cheetah carrying capacity, but was beyond the scope of this study.

4.4.4 Evidence of intra-guild competition

The significant positive linear relationship, found in this study and others, between predator density and prey biomass (van Orsdol *et al.* 1985; Fuller 1989; Laurenson 1995; Stander *et al.* 1997; Hayward *et al.* 2007d), suggests that food availability is a limiting factor to population growth in large carnivores (Hayward & Kerley 2008). Therefore, in the absence of intra-guild competition, potential cheetah carrying capacity should be largely determined by available resources. In this study, the degree by which cheetah numbers in a natural ecosystem were below this potential carrying capacity was positively related to the relative density of lion, African wild dog, leopard and spotted hyaena, although this relationship was only significant for lion and African wild dog.

Other studies have similarly found cheetah density to be lower in the presence of lion (Hofer & East 1995; Laurenson 1995). Based on prey species-level diet analyses, cheetah and lion diets in southern Africa were found to overlap for roughly half of prey killed (Hayward & Kerley 2008; Lindsey *et al.* 2011), suggesting there is substantial exploitation competition between lion and cheetah. Furthermore, lion exert interference competition on cheetah (Caro 1994; Laurenson 1995; Laurenson *et al.* 1995; Durant 2000). Lion therefore suppress cheetah numbers below their potential carrying capacity through a combination of exploitation and interference competition. My findings show that competition increases as relative lion density increases, perhaps due to increased contact between cheetah and lion.

Cheetah and African wild dog in southern Africa display a very high dietary overlap (Hayward & Kerley 2008; Lindsey *et al.* 2011). Exploitation competition between the two carnivores may be intensified by the fact that both carnivores show similar temporal hunting patterns, being predominantly diurnal and hunting at night only when moonlight is sufficient (Hayward & Kerley 2008; Cozzi *et al.* in press). The finding that relative African wild dog density suppresses cheetah carrying capacity therefore suggests that strong exploitation competition alone can influence carnivore density, since African wild dog do not scavenge and therefore do not kleptoparasitize (Schaller 1972).

While cheetah and leopard diets in southern Africa have been found to overlap by between 69% and 84% (Hayward & Kerley 2008; Lindsey *et al.* 2011), relative leopard density does not significantly influence cheetah density, despite leopard being known to kill cheetah (Hayward *et al.* 2006a). Leopard have a high dietary niche breadth, which may result in high variability in dietary overlap with cheetah (Hayward & Kerley 2008). Leopard also use denser habitat than cheetah (Hayward & Kerley 2008) which may reduce exploitation and interference competition, though this remains to be properly tested. Additionally, predation risk from leopard could drive prey into more open areas, as observed with buffalo when lion were reintroduced into Addo (Tambling *et al.* 2012). This would actually facilitate cheetah predation by increasing cheetah access to prey in more open areas where cheetah have higher hunting success rates (Mills *et al.* 2004). Spotted hyaena kill cheetah and chase them from their kills (Caro 1994; Laurenson 1995; Laurenson *et al.* 1995; Durant 2000), however relative spotted hyaena density did not significantly influence cheetah density. Spotted hyaena do not display a preferred prey weight range (Hayward 2006) and have a flexible hunting strategy, cooperating to bring down larger prey or to steal carcasses from other predators, but foraging alone for smaller items (Kruuk 1966, 1970). The resultant variability in diet may mean that the degree of exploitation competition with cheetah is highly variable across ecosystems, and therefore the influence of spotted hyaena on cheetah density is variable across ecosystems.

In an analysis on 70 carnivore species in Africa, exploitation competition and inter-specific killing were found to be of widespread importance as an ecological factor (Caro & Stoner 2003). Intra-guild competition is likely to be less of an issue for more dominant members of a carnivore guild (e.g. spotted hyaena and lion), which have very rich and varied diets (Hayward & Kerley 2005; Hayward 2006) and whose numbers appear unaffected by competition (Hayward & Kerley 2008). However, most likely as a result of exploitation and interference competition, there is a negative relationship between African wild dog density and that of lion and spotted hyaena (Creel & Creel 1996; Mills & Gorman 1997; Creel & Creel 2002; van Dyk & Slotow 2003). A similar trend exists in other ecosystems, where tiger spatially exclude leopard (Seidensticker *et al.* 1990; Odden *et al.* 2010); wolf competition (and predation) limits coyote *Canis latrans* abundance (Murray Berger & Gese 2007); coyote-related mortality supresses kit fox *Vulpes macrotis* density (White & Garrott 1997; Cypher & Spencer 1998) and puma exert interference competition on bobcats *Lynx rufus* (Hass 2009). The degree of interference and exploitation competition should further be influenced by the habitat preferences of the competing carnivores, where competition is likely to be lower if the inferior carnivore is able to seek spatial refuges in areas less utilized by the dominant carnivore (Mills & Biggs 1993; Hunter 1998; Durant 1998, 2000). I therefore hypothesize that in a resource-limited system where one predator is superior to another in its ability to compete for shared resources, the superior predator will supress the carrying capacity of the inferior predator through exploitation competition, and in some cases additional interference competition. I further predict that competition will intensify with an increase in habitat preference overlap, a decrease in spatial refuges and an increase in the density of the superior predator relative to the inferior predator.

4.4.5 Regression versus mechanistic carrying capacity models

Regression models based on predictions of predator diet at the prey and predator species-level (e.g. East 1984; van Orsdol *et al*. 1985; Laurenson 1995; Gros *et al.* 1996; Stander *et al*. 1997; Fuller 1989; Carbone & Gittleman 2002; Hayward *et al.* 2007d) make tenuous assumptions. Specifically, preferred prey may not be consistently representative of accessible prey and hence cheetah diet resources; and prey demographics, cheetah population social structure and competing predators do influence cheetah carrying capacity. While a refined regression model accounts for prey demographics as well as the biomass of prey accessible to both solitary and coalition cheetah, it is still derived from systems with natural cheetah sex and age ratios and intact large carnivore guilds. The refined regression model is therefore unable to eliminate the assumptions that cheetah social structure and competing predators do not influence cheetah carrying capacity.

The application of the recalculated Hayward regression, refined regression and MSY models to predict cheetah carrying capacity at MZNP and Phinda provided insight into when each model was more or less suitable based on its assumptions. At both test sites, the recalculated Hayward regression model predicted cheetah carrying capacity to be generally lower than the other two models, always finding cheetah to be above carrying capacity. Deviations in actual cheetah density from predicted carrying capacity did not correlate with prey declines and subsequent recoveries. This model appears to consistently underestimate cheetah carrying capacity and therefore cannot be reliably used to predict prey responses to predation. At MZNP where cheetah were the only large carnivore, the refined regression model predicted lower cheetah carrying capacities pre-cheetah reintroduction compared to the MSY model. This was expected, since only the MSY model accounts for the lack of intra-guild competition, but may also be as a result of the MSY model including the biomass of prey species which are, as a result of their habitat use and/or behaviour, actually inaccessible to the cheetah, as discussed in section 4.4.1. Interestingly, for post-cheetah reintroduction at MZNP the discrepancies between the predictions made by the refined regression and MSY model were lower, most likely because high cheetah predation caused prey numbers to decline. The MSY model assumes prey to be at carrying capacity (Caughley 1977) and seems to predict a lower cheetah carrying capacity when this assumption is violated, as a result of prey being below carrying capacity. This trend also existed at Phinda where, as predation pressure increased due to lion numbers increasing and leopard numbers being accounted for after 2008, the discrepancies between the predictions made by the refined regression and MSY model were lower. This suggests that the MSY model is more sensitive to changes in prey numbers due to predation, or even other conditions such as drought or disease. By predicting lower cheetah carrying capacity in the presence of high predation pressure from other large carnivores, the MSY model controls for the relative impact of other large carnivores on these prey populations.

Both the MSY model and the refined regression model predicted cheetah numbers to be above carrying capacity at MZNP in 2010, the same year that management relocated 19 cheetah (Zimmerman *et al.* 2011). By 2012 both models found cheetah to be below predicted carrying capacity. While acknowledging that prey population trends are not only influenced by predation, but also largely by rainfall (East 1984; Owen-Smith 1990; Ogutu & Owen-Smith 2005), the declines and subsequent recoveries of prey in the preferred weight range of cheetah generally correspond with deviations in cheetah numbers from predicted carrying capacity, suggesting that both the MSY and refined regression model made realistic carrying capacity predictions at the test site. Despite cheetah numbers being below predicted carrying capacity at MZNP in 2012, grey rhebok, klipspringer and mountain reedbuck numbers were still declining. Klipspringer numbers declined most dramatically before cheetah reintroduction and grey rhebok numbers declined most dramatically prior to cheetah exceeding predicted carrying capacity, suggesting cheetah predation was not the primary cause of these declines. However, the mountain reedbuck declines correspond with cheetah predation pressure and this raises the potential limitation of the two proposed models. Because they are based on all prey accessible to a predator, they make the assumption that the predator will consume all prey within the accessible weight range in proportion to availability. If, however, certain prey items are targeted preferentially over others, they are likely to suffer declines despite there being sufficient prey to sustain the predator at a landscape level. A preference for certain species over others may arise as a result of a greater congruence in the habitat preferences of the predator and preferred prey (Hayward *et al.* 2006b) and be further influenced by the behavioural response of the prey to predation risk (Altendorf *et al.* 2001; Laundré *et al.* 2001; Tambling *et al.* 2012). The continued decline of mountain reedbuck may also be as a result of high sensitivity of this species to predation, perhaps resulting in an Allee effect (see Kramer *et al.* 2009), for example through reduced group vigilance in reduced populations (Mooring *et al.* 2004). Mountain reedbuck at MZNP showed further population declines after twelve years of culling during the 1970's and 1980's, despite the cessation of culling (Norton 1989), suggesting this species is susceptible to exploitation. Given the risk of prey declines when carnivores are below carrying capacity, an adaptive management approach is called for, whereby the carnivore is reintroduced below its carrying capacity, and prey in the preferred weight range monitored closely to detect signs of over-exploitation.

While cheetah numbers at Phinda are believed to be sustainable (T. Burke pers. comm.), predictions from the adjusted MSY and refined regression models find them to exceed carrying capacity in 2009 and again in 2011, with coinciding declines in preferred prey and relatively-taken prey species. Five species avoided by cheetah did not show declines, suggesting that prey declines were related to cheetah predation. A greater number of prey species showed declines corresponding to cheetah exceeding predicted carrying capacity in 2011 than in 2009, despite cheetah exceeding their carrying capacity by a lower margin in 2011. Nyala and impala constitute 80% of the cheetah diet at Phinda (Hunter 1998), and these are two of the three species to show declines from 2009 to 2010. This suggests that predation pressure was highest on these species and they therefore showed the earliest signs of carnivore overabundance. Cheetah predation is believed to have caused the common reedbuck declines at Phinda in the late 1990's (Hunter 1998), and common reedbuck showed the largest population decline of any prey species from 2010 to 2011, when cheetah exceeded their predicted carrying capacity. Lion numbers from 2009 to 2011 were almost double those of previous years. Over half of the diets of lion and cheetah comprise the same prey species (Lindsey *et al.* 2011) and warthog and nyala, both of which display declines from 2010 to 2011, constitute 50% of the lion diet at Phinda (Hunter 1998). It is possible therefore that this increased predation pressure from lion also contributed to prey declines. Refined diet predictions and thereby carrying capacity models for the rest of the large African carnivore guild would allow for a more holistic prediction of carnivore carrying capacity.

Based on this study's findings regarding the assumptions of the refined regression and MSY models, and when these assumptions are violated, Table 4.13 summarizes the conditions under which the regression and mechanistic models are suitable, and repercussions for using each model when assumptions are invalid.

4.4.6 Conclusion and recommendations

This study showed prey demographics and cheetah social class to be important determinants of cheetah diet and thus carrying capacity. This study used these findings to refine the current carrying capacity regression model for cheetah (Hayward *et al.* 2007d). This study also questioned the regression approach to carrying capacity modelling by showing that deviations in the conditions in which the model was derived (intact carnivore guild and normal cheetah social structure) can influence the relationship between predator and prey abundance (Table. 4.13). In contrast, the value of a mechanistic approach to carrying capacity modelling is that it is not derived from an observed relationship between predator and prey abundance, and is thus more realistic when the conditions differ from those under which the regression model was developed (Table 4.13). While the MSY model is still subject to the assumption that prey are at carrying capacity, the model's lower estimates of sustainable cheetah numbers when prey are below their carrying capacity suggests that the model is sensitive to changes in prey population numbers and therefore provides a conservative approach. However, the MSY model does not account for prey species-specific behaviour, or habitat availability, which may influence prey vulnerability to predation, and thereby predator carrying capacity. While the regression model accounts for this to an extent, by being based on observed prey-predator biomass relationships, it still makes the assumption that these influencers are uniform across sites, which may be invalid given habitat variability. Potentially as a result of this, neither model accurately predicted the observed population trends of all prey species at test sites. Further development of predator-prey models to account for these additional variables may thereby improve their accuracy. When predicting carnivore resource availability, and hence predator numbers using the models developed in this study, the most appropriate model should be selected in order to minimize assumption violations.

Table 4.13. Scenarios under which the assumptions made by the refined regression and MSY models are violated (x) and not violated (✓), as well as the consequences for using a model when its assumptions are violated (K = carrying capacity; * adjusted MSY model).

Scenario		Regression	MSY	Assumption violation
Prey	Below K	✓	x	K underestimation
	Above K	✓	x	K overestimation
	At K	✓	✓	
Cheetah social structure	"Natural"	✓	✓	
	High solitary : coalition ratios	x	✓	K overestimation
	Low solitary : coalition ratios	x	✓	K underestimation
	High juvenile : adult ratios	x	✓	K underestimation (short-term)
	Low juvenile : adult ratios	x	✓	K overestimation
Lion and African wild dog	Present	✓	✓*	
	Absent	x	✓*	K underestimation

CHAPTER 5: GENERAL DISCUSSION

This study achieved the research aims outlined in Chapter 1 of improving our understanding of the drivers of predator prey preference and carrying capacity, using cheetah as a study species. This was achieved by investigating the importance of prey demographics and cheetah social structure in shaping cheetah diet and prey preferences (Chapter 3). This more comprehensive prediction of cheetah diet was then used to refine the current cheetah carrying capacity regression model, and to develop an alternative mechanistic model (Chapter 4). This is the first study, that I am aware of, to calculate and then incorporate prey demographic- and predator social class-level diet predictions of a large African carnivore into a carrying capacity model. This chapter details this study's contribution to improving our understanding of predator-prey relationships, in an evolutionary context as well as in a conservation and management context. The findings of this study should, however, be interpreted in light of the chapter-specific limitations that have been detailed in Chapters 3 and 4, as well as the following overarching limits.

5.1 Study limits

While this study highlights the importance of prey size and weaponry and cheetah social structure in determining a prey individual's vulnerability to predation, it does not suggest that morphology is the only attribute likely to influence vulnerability. Risk of injury and ease of capture of a prey individual can be further influenced by its ecology (e.g. prey vegetation preferences and prey scarcity), behaviour (e.g. large herd size and increased vigilance) and how the prey individual responds to the landscape of fear, which can also be dependent on available habitats (Karanth & Sunquist 1995; Hayward *et al.* 2006a,b,c; Laundré *et al.* 2001; Hayward 2011). While incorporating these factors into a prey preference analysis would improve its accuracy, doing so would require site-specific habitat availability and use information unavailable in any of the datasets used. Because this study was based on a multi-site, multi-species analysis, for a prey weight range to be preferred it had to be so across multiple–sites and multiple-species. This study therefore presents trends in the relationship between prey size and weaponry, cheetah social structure and cheetah prey preference, which are robust across a multitude of species and ecosystems. However, since species- and site-specific attributes have not been considered, it is proposed that these cheetah diet and preference findings serve only as guideline, by which to identify prey species and demographic classes that are most likely to be vulnerable to predation on a given reserve. More specific habitat information for that reserve could then be used to gauge which prey will be specifically targeted within accessible/preferred weight ranges.

Similarly, this study refines the regression carrying capacity model, and develops an MSY model, to illustrate the importance of accessible prey biomass, influenced by prey demographics, predator social structure and intra-guild competition, in determining the number of predators that a reserve can sustain. However, the study was limited in its ability to (a) gain accurate and consistent prey census data and (b) accurately identify, within the weight ranges of prey accessible to cheetah, which prey are actually available. Gaining accurate and consistent prey census data was limited by the study's multi-site approach, which made the variability in census methods and accuracy (Gros *et al.* 1996; Wilson & Delahay 2001), for both predators and prey, difficult to account for. Accurately identifying actual available prey was limited because prey availability can be defined at several levels (Johnson 1980). The use of census data essentially defines prey availability as total prey abundance, assuming prey to be equally and evenly dispersed across the landscape. However, abundance and availability may not be the same if the predator and prey do not utilize the landscape uniformly or if prey behaviour influences detectability and vulnerability (Johnson 1980; Creel & Winnie 2005). Lion encounter preferred prey more than non-preferred prey, suggesting that prey preferences can determine how predators utilize the landscape, and thus influence prey availability (Hayward *et al.* 2011). Similarly, differences in prey availability at a reserve, home range, and habitat level resulted in discrepancies between calculated cheetah prey preferences, suggesting that prey availability is not homogenous across the landscape (Johnson 1980; Bissett 2004). This may be as a result of prey displaying habitat preferences, as well as responding to the landscape of fear (Laundré 2010; Laundré *et al.* 2010). Prey group size can influence the rate at which prey are encountered by a predator, with larger groups being relatively easier for the predator to detect (Hebblewhite & Pletscher 2002; Creel & Winnie 2005). This suggests that prey herding behaviour can additionally influence prey availability. It has been proposed that predator-prey interactions should be modelled around prey social groups and not individuals to account for the influence of prey sociality on predation (Fryxell *et al.* 2007).

Since the carrying capacity model development was dependent on quantifying available prey, the definition of available prey as all censused prey within accessible weight ranges will have influenced carrying capacity predictions. However, both the multi-site nature of this study and the lack of sufficiently detailed data prevented me from incorporating habitat- and behavioural-level information into diet predictions and thereby carrying capacity models. The models developed in this study served as a tool by which to investigate predator-prey density relationships, and should be a useful initial guideline to managers seeking to introduce and/or manage predators. However, the models' omission of the influence of prey behaviour and habitat on prey preference and carrying capacity means that (a) they should not be over interpreted as a means of understanding how these systems work and (b) an adaptive management approach is necessary when using the proposed carrying capacity models as a guideline, which is further detailed in section 5.3.1 and 5.4.

5.2 *The contribution of this study to understanding the evolution of life-history strategies in predators and their prey*

5.2.1 *The evolution of sexual dimorphism and sociality in carnivores*

Evidence that the males of several sexually dimorphic carnivores take larger, and a broader range of prey than females (Funston *et al.* 1998, 2001; Radloff & du Toit 2004; Sand *et al.* 2006; Knopff *et al.* 2010) and more effectively hunt available prey (MacNulty *et al.* 2009) suggests that predatory performance increases with predator size. Cheetah, however, appear to display a degree of sexual dimorphism insufficient to facilitate solitary males killing larger prey than solitary females (Chapter 3). Why evolution has not favoured more prominent sexual dimorphism in cheetah may be explained by the cheetah's morphological adaptation for rapid pursuit hunting (Eaton 1974; Russell & Bryant 2001). In both lion and wolf, larger males were found to be better hunters of larger, slower prey, but less effective pursuers of the smaller quicker prey favoured by females (Funston *et al.* 1998, 2001; MacNulty *et al.* 2009). This suggests that increased predator body size results in decreased pursuit ability, which thus reduced the evolutionary selection for larger body size in male cheetah.

While the evolution of cheetah sexual dimorphism may have been limited by hunting strategy, this study shows that sexual differences in predatory performance exist through a second mechanism: variation in sociality (Chapter 3). The primary reason for sociality within the order Carnivora has been debated, including the benefits of strength in numbers for defence of kills and territories, the ability to hunt and kill larger prey and to intimidate other predators (Macdonald 1983; Bekoff *et al.* 1984; Earle 1987). In the Serengeti, male coalition cheetah were more likely to hold a territory and survive longer than single males, with inferred reproductive benefits (Caro & Collins 1986). If improved intra-sex combat ability and territorial defense are the primary drivers of group-living, killing larger prey and a larger size range of prey may simply be a necessary adaptation to meet the increased (collective) energetic demands of group living (Caro 1994). Packer *et al.* (1990) also dispute group hunting as a reason for sociality in female lion, detailing defence of young and defence of territories as more promising drivers of sociality. My findings suggest that the benefits of group hunting may be a primary driver in group formation in male cheetah, or at least a secondary advantage. If solitary males, accessing the same prey weight range as female cheetah, have lower resource opportunities than male coalition cheetah who access a broader prey base (Chapter 3), coalition cheetah may increase their fitness relative to solitary males in a resource-limited environment, and thereby their chances of survival and reproduction. This fitness benefit will also be dependent on the extent to which hunting larger prey brings male coalition cheetah into competition with larger predators which also hunt this larger prey (Radloff & du Toit 2004).

Ultimately, the costs of forming groups, such as food- and mate-sharing (Schaller 1972; Kruuk 1975; Caro & Collins 1986; Packer *et al.* 1990), need to be outweighed by the benefits, be these improved mating chances, improved resource control and use or reduced energy expenditure during hunting (Caro & Collins 1984; Packer *et al.* 1990; Creel & Creel 1995). Costs and benefits will vary, depending for example on the availability and density of food and the risks of accessing, capturing and defending it (Macdonald 1983). While acknowledging that sociality in carnivores is therefore likely to be the result of several interacting variables, this study does suggest that increased resource opportunity and inferred fitness benefits is a direct benefit of sociality in male cheetah.

Trivers & Willard (1973) predicted that females, in any organism, should adjust the birth sex ratio of their offspring in relation to future reproductive benefits. In cheetah, male coalitions usually arise from brothers of the same litter (Caro 1994). Coalition males may have improved reproductive fitness compared with solitary males, through greater access to females (Caro 1994) and resources (Chapter 3). I therefore predict that it would be in a female cheetah’s advantage to produce litters with more than one male. This would result in males forming coalitions and having an increased chance of reproducing and passing on their mother’s genes. Analysing cheetah litter compositions would provide a way to test this hypothesis. I predict that the proportion of litters with only one male cub would be less than expected by chance.

5.2.2 The evolution of size and weaponry in prey species

The influence of prey size and weaponry on cheetah prey preference suggests that, in the face of predation by cheetah, it’s better for a prey item to be big and horned (Chapter 3). In multi-carnivore systems, size- and weaponry-derived protection from smaller carnivores such as cheetah, puma and leopard won’t necessarily protect the animal from predation from larger lion, jaguar and tiger who hunt larger prey (Karanth & Sunquist 1995; Taber *et al.* 1997; Radloff & du Toit 2004). Supporting this, in the Kruger National Park predation was responsible for almost all detected mortality in ungulate species up to the size of a giraffe (800–1200 kg), with predation a negligible cause of mortality only in megaherbivores substantially exceeding 1000 kg in adult body mass (Owen-Smith & Mills 2008). However, while an increased body size and the presence of weaponry may not eliminate predation for most prey species, it will determine the number of predators that the species is vulnerable to, with a bigger size and the presence of weaponry reducing predation pressure (Radloff & du Toit 2004). Therefore predation pressure, even in multi-carnivore ecosystems, could have contributed to the selection for large body size and the presence of weaponry in prey species.

In cervids, since only males possess antlers in most species, it is argued that antlers evolved primarily for intra-sex combat (Clutton-Brock 1982). Potential selective pressures for horns in antelope include sexual selection and intra-sex combat over territories or mates in male antelope (Geist 1966a; Clutton-Brock 1982; Janis 1982; Stankowich & Caro 2009), and the defence of territories against other females or as a buffer against aggression towards male offspring by dominant males in female antelope (Estes 1991; Stankowich & Caro 2009). Therefore, while a reduction in predation pressure may not have been the sole or primary selective pressure in the evolution of horns or antlers, the use of weaponry in defence against predators could have contributed to selection pressures favouring their retention (Clutton-Brock 1982).

5.2.3 The influence of human interference on these selective pressures

Many new reserves are introducing carnivores (a) in low population numbers (Hayward *et al.* 2007a; van der Merwe 2012) and (b) into systems which are stocked at artificially high prey abundances (Lindsey *et al.* 2011), resulting in reduced intra-species competition. In such systems, the costs of coalition-forming such as food and mate sharing (Caro & Collins 1986) may outweigh the benefits of acquiring and defending territories and improved resource access – since competition is low and food is no longer limiting. This trade-off between the costs and benefits of sociality would be further dependent on the size distribution of available prey, since coalition hunting should be more beneficial when a substantial proportion of the prey community are larger than that which can be captured by solitary cheetah (Chapter 3). While male coalitions are more likely to occupy territories and fare better in male-male conflict (Caro & Collins 1986), solitary males may be at an advantage in low-competition environments since they don’t have to share mating opportunities. It is possible that, as a result of human intervention, conditions can arise in which the costs of coalition-forming outweigh the benefits and solitary male cheetah are at an advantage. In such a situation, coalitions should break down, with male cheetah becoming solitary.

Large carnivores are not only exposed to intra-species competition, but intra-guild competition as well. For example, cheetah density is negatively influenced by competition from lion and African wild dog (Chapter 4). Therefore, while carnivores can reduce intra-species competition through a degree of resource-partitioning between sexes (Chapter 3; Knopff *et al.* 2010), they are also constrained in their ability to do so by other predators competing for these resources. There are size differences in the prey killed by tiger and leopard, and jaguar and puma, and between the five large African carnivores – suggesting that intra-guild competition influences prey use (Karanth & Sunquist 1995; Taber *et al.* 1997; Radloff & du Toit 2004). Therefore, while male coalition cheetah can reduce resource-sharing with solitary cheetah by hunting larger prey, in so doing they utilize a weight range of prey which is also utilized by the larger carnivore, lion, and may thus increase inter-specific competition (Hayward & Kerley 2005). The use, by coalition cheetah, of larger prey inaccessible to solitary cheetah will therefore be dependent on the strength of intra-species versus intra-guild competition. In many ecosystems throughout the world, the largest carnivores in the guild have been extirpated (Gittleman *et al* 2001). In southern Africa, cheetah have been introduced into nature reserves devoid of lion and spotted hyaena (Lindsey *et al.* 2011). Mesopredator release (Soulé *et al.* 1988) occurs when mammalian carnivores of intermediate body size are more prevalent in the absence of larger carnivores. In systems with reduced intra-guild competition (where the largest carnivore is absent), intra-species competition should predominate in the remaining carnivore. I therefore predict that, in systems devoid of lion, there will be a more pronounced size difference of prey killed by male coalition and solitary cheetah, due to the absence of intra-guild competition and the expression of mesopredator release.

While the reduction of intra-species or intra-guild competition can influence predator diet and behaviour, a third human-induced manipulation of natural ecosystems may have a notable impact on prey evolution. While some ecosystems support only partially intact large carnivore guilds, in other ecosystems large carnivores have been extirpated completely (Weber & Rabinowitz 1996; Hayward *et al*. 2007b) and prey populations are therefore no longer exposed to predation (Berger *et al.* 2001). Since weaponry is costly to grow, maintain and carry (Geist 1966b; Picard *et al.* 1996), in the absence of predation the selective pressure to grow horns may be reduced. Similarly, larger prey have higher absolute energy requirements (McCullough 1999) and, while capable of eating poorer quality food, require a lot of it (Demment & Van Soest 1985). Therefore, dependent on the nutritional quality of available food, a removal of predation from the system may dampen the selective pressures for large prey body size. It is therefore possible that, through the alteration of natural ecosystems, humans are influencing the selective pressures on prey body size and weaponry.

5.3 The implications of this study's findings for managing and conserving large carnivores

5.3.1 The value of identifying preferred prey as an indicator of predator-prey stability

The biomass of prey within the weight range accessible to cheetah is a better predictor of cheetah carrying capacity than that in the preferred weight range (Chapter 4). This finding therefore questions the value of identifying preferred prey. The value of preferred prey may lie in identifying prey that will be exposed to the strongest predation pressure. Regardless of whether preference calculations are biased towards rarer prey items (Jacobs 1974; Strauss 1979; Hayward 2011), or highlight prey for which a predator has evolved to optimally hunt (Hayward 2011), they identify prey that experience predation rates disproportionate to their relative abundance in the prey community (Jacobs 1974). These prey items should therefore be the first to show signs of overexploitation. Indicator species are those which reflect changes in ecosystem patterns or processes (Lindenmayer *et al.* 2001), and preferred prey could be used as indicators of predator-prey stability. At Phinda, Madjuma and Pilanesberg, high lion predation resulted in blue wildebeest declines (Hunter 1998, Power 2002b; Tambling & du Toit 2005), with blue wildebeest being a preferred prey species of lion (Hayward & Kerley 2005). Similarly, cheetah occurring above predicted carrying capacity at Phinda and MZNP resulted in common and mountain reedbuck declines, respectively (Chapter 4), and all three demographic classes of these species fall within the size class range preferred by all cheetah social classes (Chapter 3). While predation is not the only factor influencing population trends (East 1984; Owen-Smith 1990; Ogutu & Owen-Smith 2005), monitoring for population declines which are specific to indicator species should provide a means of detecting signs of excessive predation impact.

At Phinda, kudu and nyala populations declined subsequent to cheetah exceeding predicted carrying capacity (Chapter 4). Only juvenile kudu and juvenile and female nyala are preferred by cheetah (Chapter 3). Monitoring for changes in sex and age ratios within a prey species that mirror predictions of demographic-level preferences (Chapter 3), should therefore provide a valuable tool for detecting an overabundance of cheetah. In a system supporting a multi-carnivore guild, such as at Phinda, knowledge of demographic-level prey preferences and avoidances of all large carnivores present would further improve the ability to interpret shifts in prey demographic ratios. Monitoring based on prey species-level preference predictions would only permit a detection of carnivore overexploitation from preferred prey population declines, not changes in demographic ratios. Changes in demographic ratios can have recruitment implications (Festa-Bianchet *et al.* 2006) which may only be evident subsequent to the breeding season (when females are preferred) or once juveniles become reproductively active (when juveniles are preferred). Therefore, changes in demographic ratios should occur before dramatic changes in population numbers. For example, at Samara (Chapter 2), while kudu numbers still appear stable, there has been a demographic shift to an adult-biased population on the portion of the reserve where cheetah are present, compared to the portion of the reserve where cheetah are absent (Makin 2012). Management of carnivore numbers, based on subtle signs of prey response to carnivore overabundance (once the influence of weather on prey population trends is accounted for), should help avoid situations where prey numbers decline considerably before management action is taken (such as with mountain reedbuck at MZNP – Chapter 4), or where carnivores need to be removed from a reserve following prey population collapses (Pettifer 1981; Power 2002b). Detecting changes in prey population numbers also requires prey to be censused, in contrast to detecting changes in demographic ratios, which could be ascertained from random sampling of the population (as was done to obtain ungulate sex and age ratios in Chapter 3 and in Mason 1990). Therefore, demographic-level predictions of prey preference should allow for more focussed, economical monitoring and an earlier detection of carnivore overabundance.

5.3.2 The value of identifying accessible prey to inform reserve wildlife stocking

Many small game reserves in southern Africa purchase antelope, sometimes on a regular basis, in order to support predators for ecotourism purposes (Lindsey *et al.* 2011). Knowledge of which prey are likely to constitute the majority of a predator's diet would allow managers to achieve their objectives more effectively, by stocking the correct prey species to sustain the predator population. An accurate prediction of cheetah diet, using accessible prey weight ranges calculated in this study, would therefore be invaluable for management decision-making.

5.3.3 The manipulation of natural cheetah sex and age ratios

The availability of suitable habitat, devoid of threats and with sufficient prey, is a major limiting factor for carnivore conservation and reintroduction possibilities globally (Hersey *et al.* 2005; Davies-Mostert *et al.* 2009; Johnsingh & Madhusudan 2009; Kelly & Silver 2009). More coalition cheetah can be supported on a given prey community that solitary cheetah, since they are able to utilize a broader size range of prey (Chapter 3 and 4). Similar variation in the number of carnivores a system can sustain may also exist in other carnivores with fission/fusion social systems, such as lion and especially spotted hyaena who hunt alone for smaller items and cooperatively for larger items (Kruuk 1966, 1970; Funston *et al.* 1998). Therefore, manipulation of the social class composition of the reintroduced predator population by, for example, introducing male coalition cheetah instead of solitary male cheetah, could allow available habitats to be maximized in terms of their capacity to support carnivores. In South Africa, reserves favour male coalition cheetah over solitary cheetah, as it is believed the likelihood of sighting them for tourism purposes is increased (van der Merwe 2012). By South African reserves supporting coalition-biased cheetah populations, their capacity to support cheetah should therefore be greater than if they supported more solitary cheetah. However, supporting more cheetah may not necessarily meet conservation goals if only the dominant male in a coalition breeds, thereby reducing effective population size (Caughley 1994).

On some of these South African reserves, female cheetah have been contracepted, thus skewing normal age ratios (van der Merwe 2012). While this study did not investigate the long-term influence of cheetah recruitment rates and timing on carrying capacity, short-term results show that contraception reduces cheetah carrying capacity, since the resultant increase in the proportion of adult cheetah increases the energetic requirements of the population (Chapter 4). However, contraception also serves to reduce carnivore population growth rate and thus the time taken to reach this lower carrying capacity. Females who are not pregnant, lactating or feeding young are predicted to utilize available resources differently, by hunting less frequently or killing smaller prey within the prey weight range accessible to them (see Chapter 3; Hunter 1998; Bissett 2004; Bothma & Coertze 2004; Laundré 2008). This therefore suggests that carrying capacity estimates need to account for the influence of predator population age structure on predator diet. A better understanding of the implications of contraception for long-term carnivore carrying capacity could be gained through additional research, which will be detailed at the end of this chapter.

5.3.4 The manipulation of natural carnivore guild composition

In a natural system, the number of cheetah that can be sustained appears to be reduced by exploitation competition with lion and African wild dog, and cheetah numbers are further prevented from achieving this reduced carrying capacity through interference competition from lion (Chapter 4). Several small reserves in southern Africa have reintroduced cheetah as the sole large carnivore (e.g. Samara, Camdeboo, MZNP; Chapter 2). Such reserves can support a greater number of cheetah on a given prey population than reserves supporting competing predators (Chapter 4). The composition of carnivore species on a reserve is therefore an important consideration when predicting the carrying capacity of the inferior competitors. It should be of particular consideration when the reintroduction of several carnivore species is planned to occur in stages. The reintroduction of additional carnivore species could reduce the number of the initially introduced species that can be sustained and if this is not accounted for, excess carnivores could result in rapid prey population declines, especially of prey preferred/accessible to more than one carnivore species.

5.4 A conceptual framework of the drivers of predator diet and carrying capacity

Based on the insights of this study into what influences cheetah diet and thus carrying capacity, and the implications of this for management, a conceptual model has been developed (Fig. 5.1) which visually details the interaction between predator social class and size, prey weaponry and size, and competing predators, in shaping cheetah diet and carrying capacity. This framework can therefore serve as an initial guideline for managers introducing large carnivores, in terms of predicting cheetah diet and estimating cheetah carrying capacity.

While this framework has been developed based on cheetah and their prey in southern Africa, I predict that a similar framework can be used to predict predator diet and carrying capacity for other carnivores and in other ecosystems. For example, as detailed in Chapters 3 and 4, the upper size limit to the prey consumed by a predator is set by how successfully and safely larger animals can be captured and subdued, which is dependent on predator size and number of hunting individuals (Kruuk 1966, 1970; Fanshawe & Fitzgibbon 1993; Creel & Creel 1995; Radloff & du Toit 2004; Owen-Smith & Mills 2008). Therefore, predator size and sociality are important determinants of predator diet across an array of predators. Similarly, prey age- and sex-biases have been recorded in the diet of several Carnivora species (Ginsberg & Milner-Gulland 1994; Fuller *et al.* 1995; Karanth & Sunquist 1995; Power & Compion 2009; Tambling *et al.* 2012); meaning prey demographics is an important determinant of predator diet across an array of predators. Furthermore, predators who are superior competitors have been found to suppress inferior predator numbers in a variety of systems including those of Africa, Asia and North America (Seidensticker *et al.* 1990; Creel & Creel 1996; White & Garrott 1997; Cypher & Spencer 1998; Murray Berger & Gese 2007; Hass 2009), suggesting intra-guild competition influences the carrying capacity of many large carnivores. Therefore, as detailed in the conceptual framework, prey demographics, predator social structure and intra-guild competition are likely to be important drivers of predator diet and carrying capacity across a broad array of large carnivores.

An important process in this framework with respect to both managing large carnivores, and improving our understanding of predator-prey and predator-predator relationships, is that of focussed prey monitoring. As outlined in the section detailing this study’s limitations, site-specific factors such as habitat availability and prey behaviour are likely to further influence prey preferences and thereby predator carrying capacity (Laundré 2010; Laundré *et al.* 2010; Tambling *et al.* 2012). The value of focused prey monitoring for management is therefore to better understand the influencers of prey preference specific to the reserve in question, from which improved preference predictions and carrying capacity estimates can obtained and the predator numbers managed accordingly. The value of focused prey monitoring for improving our understanding of predator-prey relationships is addressed below in the section on priorities for future research.

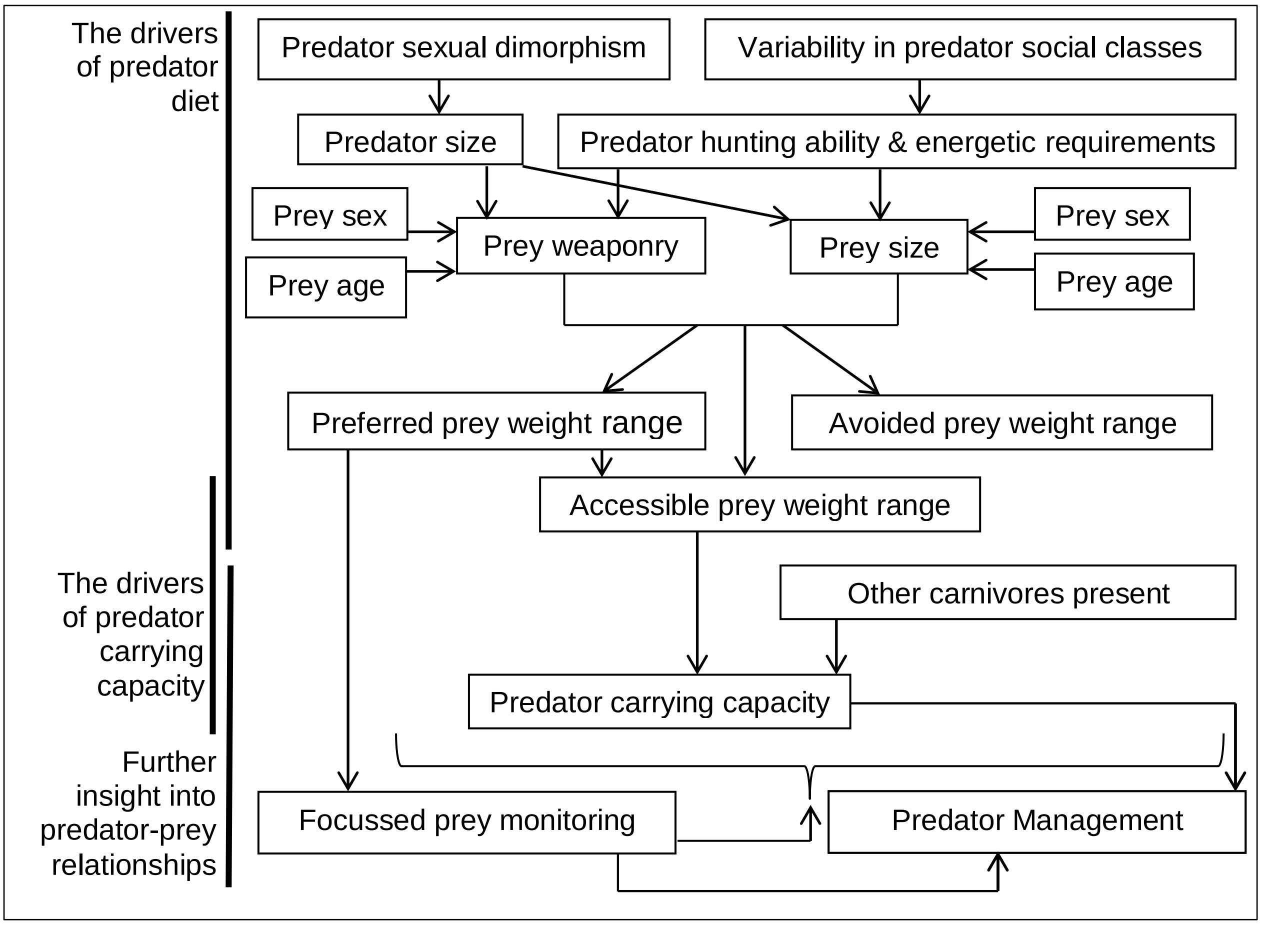


Figure 5.1. A conceptual framework for predator management detailing factors, and their linkages, which influence predator diet and carrying capacity, based on this study's findings for cheetah.

5.5 *Priorities for future research*

5.5.1 *Testing the robustness of carnivore carrying capacity models*

Both this study and Hayward *et al.* (2007d) tested the accuracy and applicability of the developed carrying capacity models by using them to predict carrying capacity at test sites, and relating observed prey population trends at a site to deviations of actual carnivore numbers from predicted carrying capacity. At both of this study's test sites, cheetah exceeded carrying capacity only within the last two years, and therefore my ability to draw conclusions regarding prey responses to potential carnivore overabundance is limited. A long-term study is therefore necessary, where cheetah are introduced into a reserve at their predicted carrying capacity and then maintained at this carrying capacity, with prey population trends monitored to detect any deviations from the predicted outcome (of prey population stability). Similarly, on reserves where a carnivore population has caused prey population declines and thereafter been reduced to predicted carrying capacity, prey populations should be monitored to detect if and how long it takes these populations to recover, and if there are differences in the recovery of different prey species. At MZNP mountain reedbuck are still declining despite cheetah now occurring below their predicted carrying capacity (Chapter 4). Long-term monitoring of the reedbuck population would allow an assessment of whether there is simply a delayed recovery, or if maintaining cheetah below or at the predicted carrying capacity does not protect all prey from overexploitation, thereby suggesting that the model needs revising. Investigating the relationship between predator density and prey population trends through long-term monitoring at many different nature reserves would enable us to better understand how accurate and robust carnivore carrying capacity predictions are. Evidence of inaccuracies could then be used to refine predator diet and carrying capacity predictions, as detailed in Figure 5.1. Such revision should incorporate prey behavioural traits, habitat availability and weather conditions that can influence predator-prey relationships (East 1984; Hernandez & Laundré 2005; Laundré 2010; Laundré *et al.* 2010; Tambling *et al.* 2012).

With 48 reserves in South Africa having reintroduced cheetah, 37 with lion and 14 with African wild dog (Lindsey *et al.* 2009, 2011; van der Merwe 2012) it is surprising that such little long term monitoring data of predator and prey populations exist. Situations where reintroductions failed, such as cheetah at Suikerbosrand or lion at Madjuma (Pettifer 1981; Power 2002b), where reintroductions succeeded (see Hayward *et al.* 2007b) or where carnivore numbers were manipulated (e.g. MZNP; Chapter 4) could provide valuable model test sites if prey and predator numbers were adequately monitored. Reserves which manipulate their predator communities by reintroducing a second large carnivore subsequent to a first could also provide an indication of the influence of the predator community on both prey population trends and the diets and behaviours of other predator species. If more reserves that have previously or are currently introducing carnivores could be encouraged to engage in long-term monitoring of their predator-prey abundance relationships, there would be huge scope for more vigorous testing of the accuracy and robustness of predator diet and carrying capacity predictions.

Many of the parameters used to develop the regression and MSY models (e.g. prey census data used to estimate prey biomass, cheetah energy requirements, breakpoints in the cheetah preference calculations, among others), have a degree of uncertainty around them. Variations in these parameters may therefore influence the outcomes of the modelled carrying capacities. Although it was beyond the scope of the current study, a sensitivity/uncertainty analysis can be conducted to assess how this variability influences the model outcomes (Doubilet *et al.* 1985). Parameters which have the greatest influence on model outcomes require the most accurate estimation, and identifying such parameters could therefore inform future research priorities, with the aim of further improving our ability to predict carnivore carrying capacity.

5.5.2 The prey preferences of cheetah in a different ecosystem

A useful way to test the robustness of the cheetah diet predictions developed in this study would be to use them to predict the diet of the same species in an entirely different ecosystem. Historically, the Asiatic cheetah *A. j. venaticus* occurred from the Indian subcontinent through Afghanistan, Turkmenistan and Iran to the Arabian Peninsula and Syria (Farhadinia *et al.* 2012). However, over the past three decades, Iran has been the last stronghold for a few dozen cheetah (Farhadinia 2004). Asiatic cheetah feed on medium-sized herbivores in north-eastern Iran (Farhadinia *et al.* 2012). In central Iran cheetah preferred Jebeer gazelle *Gazella bennettii*, though mountain ungulates in the form of wild sheep *Ovis orientalis* and Persian ibex *Capra aegagrus* comprised the majority of the diet (Farhadinia & Hemami 2010). Interestingly males of all three species were preferred over females, though juveniles were not included in the analysis (Farhadinia & Hemami 2010). A good research opportunity would be to predict the prey preferences of the Asiatic cheetah, based on the size ranges of prey demographic classes found to be preferred and accessible to the various cheetah social classes in this study. These predictions could then be compared with observed prey preferences of Asiatic cheetah. Since prey size and weaponry and cheetah social class have been shown to be drivers of cheetah prey preference in southern Africa, I predict that similar prey characteristics will drive prey selection of cheetah in Asia, and that their diet should therefore conform with the prey size and weaponry ranges predicted to be accessible to cheetah in southern Africa.

The extinct North American cheetah, *A. trumani,* is a close relative of the African cheetah (Byers 1997). Paleo-reconstruction of the North American cheetah's diet could be used to determine the correspondence of the North American cheetah's diet with the diet predictions made in this study (Bocherens *et al.* 1994; Schwarcz & Schoeninger 2011).

5.5.3 The prey preferences of other large carnivores

Estimates of the carrying capacities other large carnivores have been based on predictions of predator diet at the species-level of the predator and prey (Mladenoff & Sickley 1998; Hayward *et al.* 2007d; Hetherington & Gorman 2007). Furthermore, the carrying capacity models of the large African carnivores are based on the biomass of preferred prey (Hayward *et al.* 2007d), while accessible prey is a better predictor of cheetah carrying capacity (r2 improvement of 0.36; Chapter 4). It is therefore recommended that these predictions of predator diet are refined by calculating which prey will be preferred and accessible, at a prey demographic- and predator social class-level. Preferred and accessible prey weight ranges should also be calculated using the objective segmented model method developed in this study (Chapter 3). If sufficient kill data exist for any of these large carnivores to facilitate an investigation of the influence of prey demographics and predator social class on predator diet by means of a multi-factorial analysis, this would be an improvement on this study's analyses which investigated these influences in isolation. Such an analysis would improve our ability to understand the relative contribution of, and interaction between, these factors in determining predator diet.

In contrast to cheetah, the biomass of preferred prey species was found to be a better predictor of the density of the four other large African carnivores, than was the biomass of prey in a preferred weight range (Hayward *et al.* 2007d). Since predictions of preferred prey species and weight ranges are based on species-level calculations, and preferred weight ranges are calculated using the subjective distance-weighted-least-squares approach (Hayward *et al.* 2007d), these findings may differ once accessible prey and the segmented model approach are used. Based on refined predictions of preferred and accessible prey individuals and weight ranges, the current regression carrying capacity models for the other four large African carnivores (Hayward *et al.* 2007d) could be recalculated, as was done in this study for cheetah (Chapter 4). Similarly, the methods proposed in this study could be used to calculate prey preferences and carrying capacities of any large carnivore. Furthermore, this study used a mechanistic MSY model to highlight that accurately predicting carnivore carrying capacity using a regression model is dependent on replicating the conditions under-which the model was developed. Deciding which type of model is more suited to each specific large carnivore and ecosystem should be based on which model makes the least tenuous assumptions, as detailed in Table 4.13 for cheetah.

5.5.4 Carnivore dietary overlap and area requirements

Studies on the dietary overlaps of the large African carnivores have also been based on species-level predictions of predator diet (Hayward & Kerley 2008; Lindsey *et al.* 2004, 2011). It is recommended that these dietary overlap estimates are recalculated based on prey demographic-level diet predictions, and accounting for differences between predator social classes. This would improve our understanding of resource-partitioning, both intra- and inter-species. Such studies would also improve the accuracy of carrying capacity predictions based on a MSY model which accounts for dietary overlap between co-occurring carnivores (Chapter 4).

Similarly, current studies on the area requirements of cheetah and African wild dog are based on prey and predator species-level predictions of diet (Lindsey *et al.* 2004, 2011). Such analyses should be refined to incorporate prey demographic and predator social-level differences in predator diet. I predict that male coalition cheetahs' ability to capture a broader size range of prey will result in lower area requirements, in terms of food, for coalition cheetah than solitary cheetah. However, male cheetah are likely to be territory size maximizers in order to access more females, and male coalitions have the ability to maintain a larger territory than solitary males (Caro & Collins 1986). Therefore actual cheetah home range sizes are unlikely to correspond with those predicted based on resource-requirements and resource-accessibility alone.

5.5.5 Time series modelling

While Chapter 4 showed that the social composition of the cheetah population influenced carrying capacity, it did so in a snapshot of time, and thus did not account for juvenile cheetah reaching reproductive maturity. A simulated time-series model would allow the influence of recruitment rates on cheetah (or other carnivores) carrying capacity to be explored (Box & Jenkins 1976). The influence of breeding and weaning offspring on female diet and cheetah carrying capacity could thereby be better understood. Predator diet predictions, developed in this study (Chapter 3), and information regarding the dietary requirements of the carnivore (Owen-Smith & Mills 2008) could be incorporated into a simulated predator and prey population model. By manipulating the proportion of female carnivores that are contracepted in a modelled population, the implications of contraception on carnivore carrying capacity over time could be investigated. Similarly, the proportion of social versus solitary predators or males versus females could also be incorporated into this model, thus assessing the relative influence of changes in both sex and age composition of the carnivore population on the number of carnivores a system can sustain.

5.6 Summary

Prey demographics and predator social class influence cheetah diet when they influence the risk and ease of prey capture. Incorporating these factors into a cheetah carrying capacity regression model improved its predictive strength from a species-level model, and thus its ability to make accurate carrying capacity predictions, as demonstrated at test sites. The predictive strength of a regression model is dependent on replicating the conditions under which the model was developed. A more mechanistic approach is therefore a useful alternative, since it is based specifically on the parameters (prey size and abundance, predator social composition and carnivore guild composition) of the reserve for which a carrying capacity estimate is required. It is therefore a better approach for predicting carrying capacity in systems devoid of competing predators or with skewed predator social ratios. However, neither model fully explained observed population trends of all prey species. This therefore suggests that models accounting only for prey biomass and not accounting for prey behaviour (habitat preferences and responses to predation), as well as climatic conditions, may be limited in their ability to make accurate predictions regarding all species at all sites.

Cheetah prey preference is influenced by prey size and weaponry and this provided valuable insight into the selective pressures driving the evolution of these characteristics in prey species. Similarly, coalition cheetah hunt larger prey and a broader range of prey than solitary cheetah, which suggests sociality may have evolved due to the greater resource opportunity it provides. Human-induced ecosystem changes in the diversity or presence of large carnivores are predicted to alter these selective pressures.

Furthermore, this study provided useful considerations for the conservation and management of large carnivores. Firstly, refined predictions of which prey weight ranges will be targeted by the predator are helpful both in identifying which prey to monitor for signs of carnivore overpopulation, as well as which prey species (falling within these weight ranges) to stock a reserve with in order to increase the number of carnivores that can be sustained. Secondly, the influence of sociality on hunting ability allows insight into the implications of skewed carnivore sex and age ratios for carnivore carrying capacity. Finally, the influence of intra-guild competition on carnivore carrying capacity is an important consideration for reserves introducing only a portion of the large carnivore guild. These considerations are summarized in the conceptual framework outlined in Figure 5.1.

The two carrying capacity models developed in this study are put forward as the next step in an evolution of carnivore carrying capacity modelling, facilitated by a refinement of our understanding of the drivers of predator prey preference and diet. These models are not proposed exclusively for cheetah-prey interactions, but rather use cheetah as a tool to highlight the importance of beyond species-level factors in driving predator diet and carrying capacity. These drivers can be investigated for any carnivore species, guided by the conceptual framework in Figure 5.1. The accuracy and applicability of the models developed in this study across an array of ecosystems now needs to be more thoroughly tested, once adequate monitoring data become available. These models have evolved from the Hayward *et al.*'s (2007d) model and earlier species-level models. An improved understanding of the drivers of predator preference and carrying capacity, following recommended future research, will facilitate continued evolution of predator diet predictions and carrying capacity models.

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APPENDIX

Table A. Common and scientific names of mammalian species found on Samara Private Game Reserve (* extralimital or alien).

Order	Common name	Scientific name
Artiodactyla	Blesbok	*Damaliscus pygargus phillipsi*
	Buffalo	*Syncerus caffer*
	Bushpig	*Potamochoerus larvatus*
	Duiker, common	*Sylvicapra grimmia*
	Eland	*Tragelaphus oryx*
	Gemsbok	*Oryx gazelle*
	Giraffe*	*Giraffa camelopardalis*
	Hartebeest, red	*Alcelaphus buselaphus*
	Impala*	*Aepyceros melampus*
	Kudu, greater	*Tragelaphus strepsiceros*
	Klipspringer	*Oreotragus oreotragus*
	Nyala*	*Tragelaphus angasii*
	Reedbuck, mountain	*Redunca fulvorufula*
	Rhebok, grey	*Pelea capreolus*
	Springbok	*Antidorcas marsupialis*
	Steenbok	*Raphicerus campestris*
	Waterbuck*	*Kobus ellipsiprymnus*
	Warthog*	*Phacochoerus africanus*
	Wildebeest, black	*Connochaetes gnou*
Carnivora	Aardwolf	*Proteles cristatus*
	African wild cat	*Felis silvestris lybica*
	Bat-eared fox	*Otocyon megalotis*
	Black-backed jackal	*Canis mesomelas*
	Cape clawless otter	*Aonyx capensis*
	Cape fox	*Vulpes chama*
	Caracal	*Caracal caracal*
	Cheetah	*Acinonyx jubatus*
	Small grey mongoose	*Galerella pulverulenta*
	Small spotted cat	*Felis nigripes*
	Small spotted genet	*Genetta genetta*
	Striped polecat	*Ictonyx striatus*
	Suricate	*Suricata suricatta*
	Yellow mongoose	*Cynictis penicillata*
	Water mongoose	*Atilax paludinosus*
Hyracoidea	Rock hyrax	*Procavia capensis*

Order	Common name	Scientific name
Eulipotyphla	South African hedgehog	*Atelerix frontalis*
Lagomorpha	Scrub hare	*Lepus saxatilis*
	Smith’s red rock rabbit	*Pronolagus rupestris*
Primate	Chacma baboon	*Papio ursinus*
	Vervet monkey	*Cercopithecus pygerythrus*
Rodentia	Springhare	*Pedetes capensis*
	Greater canerat	*Thryonomys swinderianus*
	Cape porcupine	*Hystrix africaeaustralis*
	Cape ground squirrel	*Xerus inauris*
Tubulidentata	Aardvark	*Orycteropus afer*
Perissodactyla	Rhinoceros, white*	*Ceratotherium simum*
	Zebra, Cape mountain	*Equus zebra*
	Zebra, plains	*Equus quagga*

Table B. Prey abundance data for Samara Private Game Reserve, pre- and post-2011 off-take, accounting for recruitment between 2010 count and 2011 off-take.
* visibility correction factor applied (Owen-Smith & Mills 2008).

Species	2010 Aerial Count*	2011 Off-take	Percentage Recruitment	Post-Capture Count
Blesbok	53		0.177	62
Buffalo	2			2
Bushpig	4			4
Duiker, Common	5			5
Eland	341	106	0.22	286
Gemsbok	382	148		234
Giraffe	23			23
Hartebeest, Red	237	5	0.069	248
Impala	8			8
Kudu	562		0.08	607
Klipspringer	6			6
Nyala	0			0
Ostrich	13			13
Reedbuck, Mountain	99			99
Springbok	188		0.081	203
Steenbok	10			10
Waterbuck	28		0.084	31
Warthog	15			15
Wildebeest, Black	248	127	0.139	138
Zebra, Plains	167	87	0.085	87
Zebra, Mountain	26		0.106	29

Table C. Common and scientific names of all potential cheetah prey species present at study sites (Chapter 2), as well as weight, herding and weaponry categories; species- and species-class-masses; the presence (H) or absence (NH) of horns and the number of diet analysis datasets (Table 2.1) recording the species as present (n_p) and killed (n_a) by cheetah.
NOTE: breeding and herding categories only detailed for species with sufficient data to be included in these analyses. All juveniles categorized as non-horned. Y – yes; N – no.

				Species-demographic-class Mass in kg (horns /no horns)						
Prey weight category	**Common name**	**Scientific name**	**Species-mass (kg)**	**Male**	**Female**	**Juvenile**	**n_p**	**n_a**	**Breeding Herds**	**Weaponry Dimor-phism**
Small	Baboon	*Papio ursinus*	10.7	25.4 (NH)	14.3 (NH)	4.3	5	1	Y	N
	Duiker, Blue	*Philantomba monticola*	3.45	4.1 (H)	4.6 (H)	1.38	0	0		
	Duiker, Common	*Sylvicapra grimmia*	11.9	16.3 (H)	15.9 (NH)	4.8	12	12	N	Y
	Duiker, Red	*Cephalophus natalensis*	8.9	11.7 (H)	11.9 (H)	3.6	1	0		
	Klipspringer	*Oreotragus oreotragus*	9.9	10.6 (H)	13.2 (NH)	4.0	6	0		
	Monkey, Vervet	*Cercopithecus pygerythrus*	3.1	5.5 (NH)	4.1 (NH)	1.2	5	0		
	Rhebok, Grey	*Pelea capreolus*	15.0	20.0 (H)	20.0 (NH)	6.0	1	0		
	Scrub Hare	*Lepus saxatilis*	3.0	3.2 (NH)	4.0 (NH)	1.2	12	6	N	N
	Springhare	*Pedetes capensis*	2.3	3.1 (NH)	3.1 (NH)	0.9	7	1	N	N
	Steenbok	*Raphicerus campestris*	8.5	10.9 (H)	11.3 (NH)	3.4	10	8	N	Y
Hayward Preferred	Blesbok	*Damaliscus pygargus phillipsi*	50.3	81.0 (H)	67.0 (H)	20.1	8	5	Y	N
	Bushbuck	*Tragelaphus scriptus*	27.0	60.0 (H)	36.0 (NH)	10.8	9	5	N	Y
	Bushpig	*Potamochoerus larvatus*	51.7	72.3 (H)	68.9 (H)	20.7	5	0		
	Impala	*Aepyceros melampus*	30.7	54.5 (H)	40.9 (NH)	12.3	11	9	Y	Y
	Nyala	*Tragelaphus angasii*	46.4	107.5 (H)	61.8 (NH)	18.5	7	3	N	Y
	Reedbuck, Common	*Redunca arundinum*	28.7	51.8 (H)	38.2 (NH)	11.5	4	3	N	Y
	Reedbuck, Mountain	*Redunca fulvorufula*	23.0	32.2 (H)	30.6 (NH)	9.2	9	5	N	Y
	Springbok	*Antidorcas marsupialis*	23.8	33.7 (H)	31.7 (H)	9.5	11	8	Y	N

Table C. cont.

Prey weight category	Common name	Scientific name	Species-mass (kg)	Species-demographic-class Mass in kg (horns /no horns)			n_p	n_a	Breeding Herds	Weaponry Dimor-phism
				Male	Female	Juvenile				
	Warthog	*Phacochoerus africanus*	42.4	79.6 (H)	56.5 (H)	17.0	12	7	N	N
Large	Buffalo	*Syncerus caffer*	384.8	590.0 (H)	513.0 (H)	153.9	10	0		
	Eland	*Tragelaphus oryx*	345.0	700.0 (H)	460.0 (H)	138.0	8	7	Y	N
	Gemsbok	*Oryx gazelle*	157.5	240.0 (H)	210.0 (H)	63.0	8	5	Y	N
	Giraffe	*Giraffa camelopardalis*	621.3	1191.8 (H)	828.4 (H)	248.5	10	0		
	Hartebeest, Red	*Alcelaphus buselaphus*	90.0	148.8 (H)	120.0 (H)	36.0	8	6	Y	N
	Kudu	*Tragelaphus strepsiceros*	114.1	220.8 (H)	152.1 (NH)	45.6	12	12	N	Y
	Ostrich	*Struthio camelus*	90.0	120.0 (NH)	120.0 (NH)	36.0	11	4	N	N
	Roan	*Hippotragus equinus*	195.0	270 (H)	260 (H)	78.0	3	0		
	Sable	*Hippotragus niger*	172.5	230 (H)	230 (H)	69.0	3	0		
	Tsessebe	*Damaliscus lunatus*	90.0	120 (H)	120 (H)	36.0	3	0		
	Waterbuck	*Kobus ellipsiprymnus*	187.5	270.0 (H)	250.0 (NH)	75.0	11	8	N	Y
	Wildebeest, Black	*Connochaetes gnou*	97.5	161.1 (H)	130.0 (H)	39.0	8	3	Y	N
	Wildebeest, Blue	*Connochaetes taurinus*	161.1	251.7 (H)	214.8 (H)	64.4	6	4	Y	N
	Zebra, Plains	*Equus quagga*	226.7	313.0 (NH)	302.2 (NH)	90.7	12	7	Y	N
	Zebra, Cape Mountain	*Equus zebra*	175.7	234.3 (NH)	234.3 (NH)	70.3	3	0		