CHAPTER 1
General introduction

1. The African wild cat, *Felis silvestris* (Forster, 1780) and synonym *Felis silvestris cafra* (Desmarest, 1822): an overview

The African wild cat (*Felis silvestris*) has a wide distributional range (Fig. 1.1). However there is a paucity of information on all aspects of its biology. Since the wild cat is the ancestor of the domestic cat and they can interbreed and produce fertile offspring, hybridisation with the domestic form may be the biggest threat to the survival of wild cats today (Nowell & Jackson, 1996).

1.1 Phylogenetic relations and taxonomic classification

Felid classification has a long and complex history fluctuating between extremes of “splitting” and “lumping” of the species (see historical review by Werdelin in Nowell & Jackson, 1996). Even on the subspecies level there has been considerable debate between the traditional taxonomic approach and the more contemporary approach using knowledge from population biology and genetics (Nowell & Jackson, 1996).

The recent revolution in sequencing of genomes and new technologies to probe DNA has lead to the development of valuable new tools and methods for investigating phylogenetic relationships. Consequently, the first clearly resolved Feliday family tree has only recently been constructed (Johnson, Eizirik, Pecon-Slattery, Murphy, Antunes, Teeling & O’Brien, 2006, O’Brien & Johnson, 2007). The 37 felid species were grouped into eight lineages by molecular analysis, consistent with observations that lineages shared morphological, biological, physiological characteristics found only in their group. The recent findings suggest that all modern cats are descended from one of several *Pseudaelurus* species that lived in Asia around 11 million years ago (O’Brien & Johnson, 2007). The eight lineages that are recognised are:

(i) the ‘Panthera lineage’ that give rise to the medium and large cats such as lion, tiger, jaguar, leopard and snow leopards,
(ii) the ‘Bay cat lineage’ including the Bay cat, Asian golden cat and the Marbled cat,
(iii) the ‘Caracal lineage’ including the caracal, African golden cat and the serval,
(iv) the ‘Ocelot lineage’ including the ocelot, margay, Andean mountain cat, Pampas cat, Geoffroy’s cat, kodkod and the tigrina,
(v) the ‘Lynx lineage’ consisting of the Iberian, Eurasian and Canada lynx and bobcat,

(vi) the 'Puma lineage' including the puma, jaguarundi and African cheetah,

(vii) the 'Asian leopard cat lineage' consists of the small pallas cat, rusty spotted cat, Asian leopard cat, fishing cat and the flat headed cat,

(viii) the 'Domestic cat lineage' including the jungle cat, black-footed cat, desert cat, Chinese desert cat, African wild cat, European wild cat and the domestic cat.

The general classification for the wild cat (*Felis silvestris*) in this study follows Driscoll's publications where 1,000 wildcats and domestic cats were analysed in order to determine which subspecies of wild cat gave rise to the domestic cat. Five clusters were identified as follows: (i) the Middle Eastern wild cat, *Felis silvestris lybica* and the domestic cat*, F. s. catus*, (ii) the Central Asian wild cat, *F.s. ornata*, (iii) the Southern African wild cat, *F.s. cafra*, (iv) the European wild cat, *F.s. silvestris*, and (v) the Chinese mountain cat, *F.s. bieti* (Driscoll, Menotti-Raymond, Roca, Hupe, Johnson, Geffen, Harley, Delibes, Pontier, Kitchener, Yamaguchi, O'Brien, & Macdonald, 2007, Driscoll, Clutton-Brock, Kitchener & O'Brien, 2009).

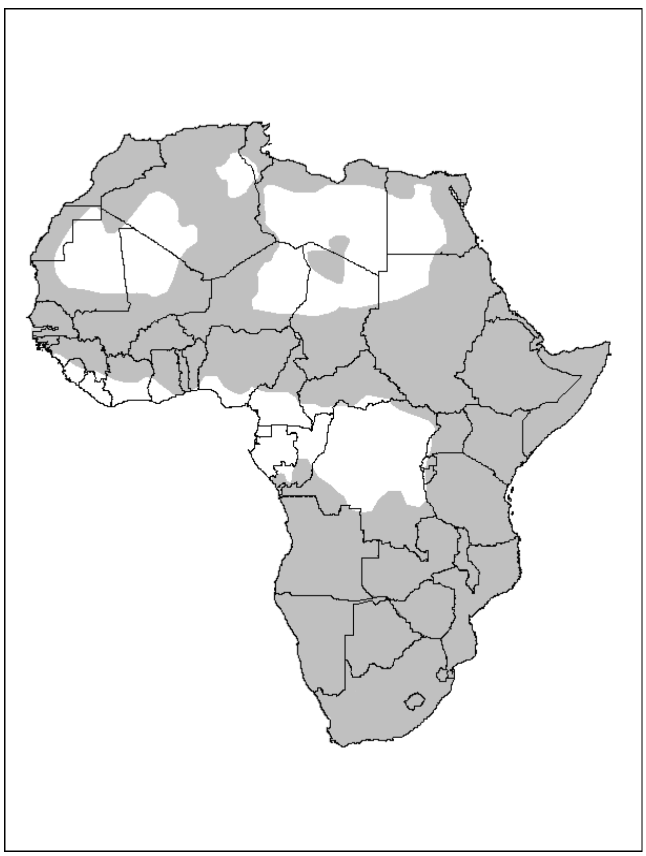

Figure 1.1 The geographical distribution of the African wild cat on the African continent (data from Stuart & Stuart as presented in Wilson & Reeder, 2005)

1.2 Geographical range

The African wild cat has a large geographic distribution throughout the African continent and is only absent in the tropical forests and true deserts (Nowell & Jackson, 1996) (Figure 1.1). It is described as the most common small felid in many parts of its range (Kingdon, 1977; Smithers, 1983; Stuart, 1981) and has a very wide habitat tolerance (Nowell & Jackson, 1996). Throughout its range it requires cover and protection such as rocky hillsides, bushes, dwarf shrubs and tall grasses in which to hide during the day (Smithers, 1983). In the semi desert and open areas such as the Kalahari they use isolated stands of *Acacia* scrub, *Galenia africana* and dense vegetation or the branches of camelthorn (*Acacia erioloba*) trees. If adequate cover is not available they will use holes in the ground (aardvark holes), roots of trees, piles of rocks, crevices and riverine under bush. Wild cat density is expected to vary widely with prey availability and home ranges may vary between individuals and regions (Nowell & Jackson, 1996).

1.3 Domestication of wild cats

The domestic cat is perhaps the best known and most numerous pet around the world (Kitchener, 1991; Clutton-Brock, 1999; Vigne, Guilaine, Debue, Haye & Gérard, 2004; O'Brien & Johnson, 2007; Driscoll *et al*. 2009). Scientists believed that domestication originated in Egypt around 3,600 years ago (Randi & Randi 1991; Nowell & Jackson, 1996; Clutton-Brock, 1999) and some researchers had even proposed that domestication occurred at a number of different locations (Driscoll *et al*. 2009). Genetic and archaeological discoveries over the last five years generated fresh insites into the ancestory of the domestic house cat and how their relationship with humans has evolved (Johnson *et al*. 2006; Driscoll *et al*. 2007; O'Brien & Johnson, 2007). Results revealed five clusters of wildcats and grouped the domestic cat with only one of these clusters which meant that domestic cats arose from a single location in the Middle East (Driscoll *et al*. 2007). The earliest evidence of cats associated with humans comes from deposits in Cyprus determined to be 9,500 years old (Vigne *et al*. 2004). It appears that cats were being tamed just as humankind was establishing the first settlements in part of the Middle East known as the Fertile Crescent.

Propbably the most interesting question is why cats became domesticated in the first place? Cats in general are unlikely candidates from domestication, since they are solitary hunters that defend their home ranges from other cats of the same sex and they are obligate carnivores. However the early settlements in the Fertile Crescent during the Neolithic period (9,000 – 10,000 years ago) created a completely new environment with the first grain stores from Israel. These new environments, as well as the increase in trash heaps around villages attracted rodents and consequently lured the cats closers to human settlements. Over time these cats became tolerant of living in a human dominated environment. However the competition among cats would also influence their evolution and limit how tame they become. Until today most domesticated cats remain excellent hunters and can fend for themselves.

Since these wildcats were small people certainly didn't fear them and they might even have encouraged cats to stay around and keep rodent pests low. Today there are more than 600 million cats around the world. The Cat Fancier's Assocciation and the International Cat Association recognise nearly 60 breeds of domestic cats. There are just a few genes that account for the differences in coat color, fur length and texture; therefore the genetic variation between the domestic cat breeds is very slight. Domestic cats can still interbreed with wildcats and this might prove the biggest threat to the wildcat today (Nowell & Jackson, 1996).

1.4 Conservation status of the African wild cat

According to IUCN classification wild cats are listed as Least Concern, with the exception of the Scottish wild cat, *F. s. grampia,* which is classified as vulnerable and restricted to Scotland. African wild cats (*F. silvestris*) are not protected over most of their range (CITES Appendix II). Indeed, they are the most abundant of the felid species; however, no density estimates are available. Threats such as habitat destruction, persecution and road kills are widespread for all felids (Nowell & Jackson, 1996), however, the major concern regarding wild cats is their ability to freely interbreed with domestic cats and produce fertile offspring. Hybridisation, especially in the north of their range where the domestication process of cats started, has been recorded for a long period (Nowell & Jackson, 1996) and the presence of feral domestic cats throughout their range is enhancing the risk of admixture events. Feral male cats may have a competitive advantage over male wild cats due to their larger size and higher densities (Mendelssohn, 1989). Smithers (1983) recorded that the distinctive characteristics of African wild cats, such as the long legs and reddish-backed ears, are lost in captive bred hybrids and that it is becoming more difficult to find pure-bred African wild cats near human settlements.

2. This study: *The African Wild Cat Project*

This study was initiated by the Carnivore Conservation Group of the Endangered Wildlife Trust and involved an intensive field-based research study focussed on the conservation genetics, behavioural ecology and ecological role of the African wild cat in the southern Kalahari. Three broad research topics were investigated:

1. The Behavioural Ecology of the African wild cat

Academici with focussed and spesialised research topics as well as the difficulty in studying the behaviour of small, nocturnal and elusive animals lead to a paucity of information on the natural history of many small felids (Nowell & Jackson, 1996). Knowledge of its natural history is imperative for the conservation of the species. First, should management initiatives be required (such as control of feral cats in or close to conservation areas), it is important to understand the basic ecological role and social system of the wild cat in a natural ecosystem (Caro & Durant, 1994; Komdeur & Deerenberg, 1997). As this study is the first field study on the species the results could, in the absence of more specific studies, be applied across its distribution range and be of considerable value to conservation of the species as a whole. Secondly, natural history is a subject that fascinates many people and therefore information on the life history patterns of the ancestor of the domestic cat has wide interest and appeal.

2. Social Evolution in the African wild cat

The evolution of social systems in carnivores is an interesting topic. With the exception of the lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*), the members of the cat family (Felidae) are solitary creatures (Poole, 1985; Packer, 1986; Sunquist & Sunquist, 2002). Feral domestic cats have been found to form colonies in the presence of clumped, rich food resources, while remaining solitary where prey is more evenly and thinly distributed (Dards, 1983; Fitzgerald & Karl, 1986; Weber & Dailly, 1998). In captivity female African wild cats have been observed to assist mothers in provisioning of young with food (Smithers, 1983), a behaviour also seen in feral domestic cat colonies, but not in any other cat species. The African wild cat is a solitary felid (Smithers, 1983; Sunquist & Sunquist, 2002), however, any social interactions would be fascinating to discover.

Solitary behaviour in carnivores indicates that factors are present that select against cooperative behaviour (i.e. when two or more animals cooperate to rear young, forage, achieve matings and defend against predators) and thus promote solitary living. The main factors are: prey characteristics and hunting mode (Sandell, 1989). Predators that take smaller prey than themselves (such as wildcats) can almost always subdue the prey alone and consume the whole prey quickly. Thus the presence of conspecifics in the immediate surroundings will almost always have a negative effect on foraging efficiency through disturbance or the depletion of the local food resource. However, domestic cats in environments where food and shelter are in abundance show strong evidence of sociality (Macdonald, 1983; Fitzgerald & Karl, 1986). It is suggested that domestication of cats increased selection for grouping and this characteristic has been retained in populations of feral cats (Liberg, 1980). Any social behaviour in wildcats would indicate that certain natural conditions, such as high prey abundances, may favour the development of cooperative behaviour in the wild.

Solitary species are reported to show signs of 'kin-clustering' in dispersion patterns (Clarke, 1978; Jones, 1984) and daughters may frequently demonstrate natal philopatry (Waser & Jones, 1983). In solitary carnivores male-biased dispersal has been demonstrated for example in black bears, *Ursus americanes* (Rogers, 1987; Schenk, 1994), tiger, *Panthera tigris* (Smith, McDougal & Sunquist, 1987), raccoons, *Procyon lotor* (Ratnayeke, Tuskan & Pelton, 2002) and female natal philopatry has been demonstrated in bobcats, *Lynx rufus* (Janečka, Blankenship, Hirth, Tewes, Kilpatrick & Grassman, 2004), swift fox, *Vulpes velox* (Kitchen, Gese, Waits, Karki & Schauster, 2005) and desert puma, *Puma concolor* (Logan & Sweanor, 2001). As the southern Kalahari has a high wild cat density and conditions are very favourable for the species, it presented an excellent opportunity to investigate this interesting and important topic of sociality and social evolution in the ancestor of the domestic cat.

3. *The Conservation Genetics of the African wild cat*

The southern Kalahari is one of the most isolated and undeveloped regions in southern Africa and African wild cats are known to be abundant in the area. The Kgalagadi Transfrontier Park (KTP) is also one of the largest conservation areas in the region and therefore the area was identified as important for the maintenance of a genetically pure wild cat population. However the genetic status of this population had to be established to determine the genetic purity, so that, if required, a management strategy can be drawn up and implemented to ensure the long-term integrity of this population. The identification of a genetically pure wild cat population is imperative for future assessments of the extent of hybridisation and introgression, especially for areas where African wild cats occur in close proximity to domestic and feral cats.

2.1 The study site

The study was conducted in the Kgalagadi Transfrontier Park (KTP), including the Kalahari Gemsbok National Park, South Africa and the Gemsbok National Park in Botswana. The main study area was along the dry Nossob Riverbed in the vicinity of the Leeudril waterhole (26º28'17.7 S, 20º36'45.2 E) (Figure 1.2).

The KTP is a 37,000 km^2 area in the semi arid southern Kalahari system, which forms part of the Kalahari dune veld Bioregion, Savanna Biome (Mucina & Rutherford, 2006). Rainfall is unpredictable and irregular with summer and autumn rainfall and dry winters. Large temperature fluctuations, both daily and seasonal, are characteristics of a semi-desert area.

Figure 1.2 Satellite image of the study site indicating the different habitats

Monthly minimum and maximum temperatures for the KTP (Twee Rivieren rest camp, 26°28'17.7"S, 20°36'45.2"E) for the study period (F ig. 1.3a) were obtained from the South African Weather Bureau as well as the estimates of hourly changes in temperature from the closest town, Upington (28º24'04"S, 21º15'35"E) (Fig. 1.3b). The mean maximum temperature for December is estimated at 37.3ºC and the mean minimum for July at 1.4ºC.

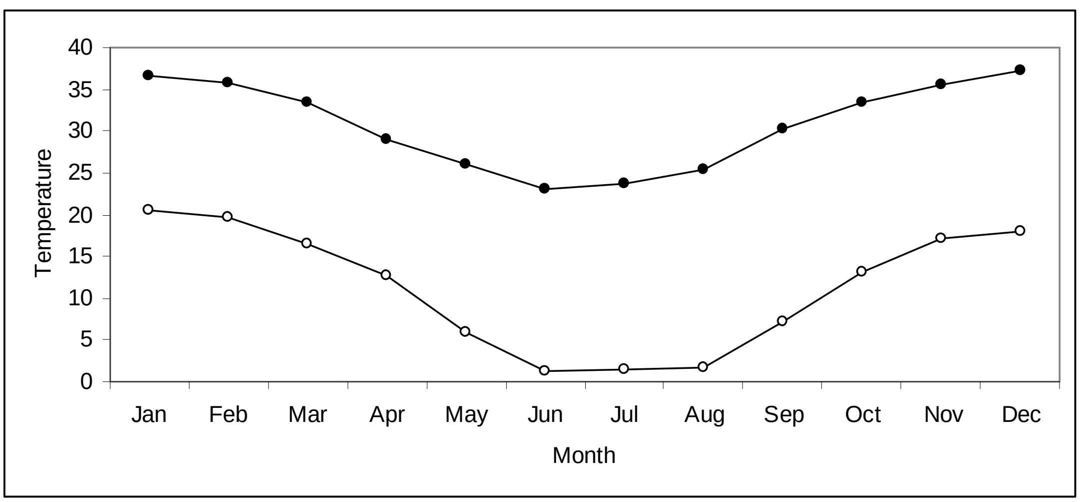

Figure 1.3a Monthly averages of the minimum (○) and maximum (●) temperatures (ºC) at the Twee Rivieren rest camp for the years 2003 to 2006

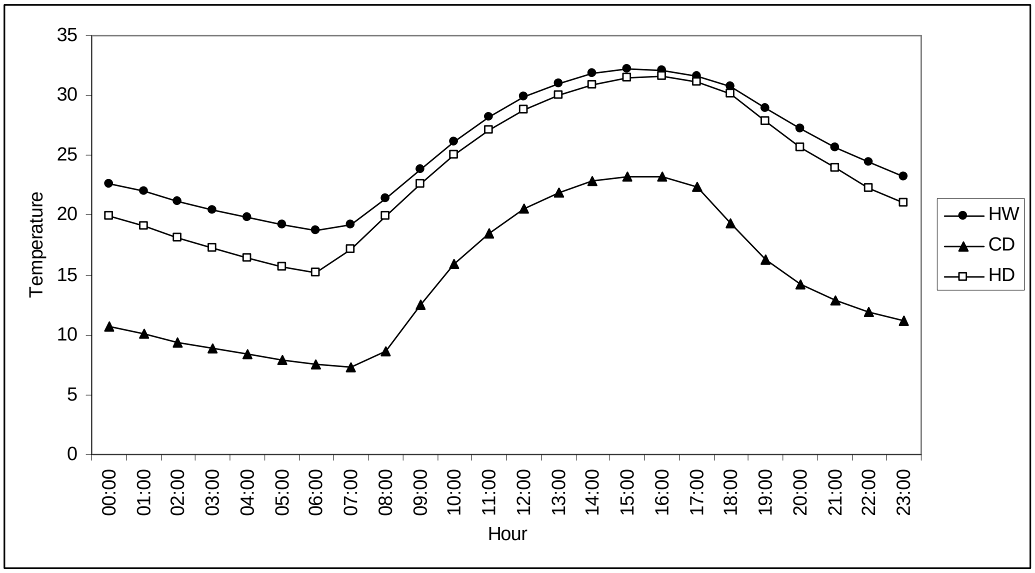

Figure 1.3b Average hourly changes in temperature in the hot-wet (HW), cold-dry (CD) and hot-dry (HD) seasons calculated from the nearest weather station in Upington

Monthly rainfall records for the KTP for the period of the study were obtained from the South African Weather Bureau. The closest weather station to the study site was at Twee Rivieren rest camp (26°28'17.7"S, 20°36'45.2"E), approximate ly 15km to the south-west, and these rainfall figures were used for the study. The first year of the study (2003) was a year with below average rainfall, with 122 mm recorded. All subsequent years (2004 – 2006) had average or above average rainfall (272 ± 41 mm per annum) (Table 1.1).

In the southern Kalahari sand dunes are arranged in a series of long, parallel dunes with fixed vegetation. The vegetation of the Kalahari is described by Mucina & Rutherford (2006) as Gordonia Bushveld and Auob Duneveld (an open scrubland with a low scrub layer and a well developed tree layer). For the purpose of this study four main habitats are described, (i) the dry riverbeds, (ii) *Rhigozym trichotomum* scrub veld (iii) the adjacent dune areas, and (iv) the calcrete sides and limestone plains (see Fig. 1.2).

The dry fossil riverbeds are characterised by large *Acacia erioloba*, smaller *A. haematoxylon*, bushy *A. mellifera*, the scrub *Galenia africana* and perennial grasses. Two rivers run through the Park, the Nossob and Auob. Although the rivers usually contain no surface water and only cover a small percentage of the area, they are important in the ecosystem (van Rooyen, 2001).

Table 1.1 Monthly rainfall (mm), mean minimum and maximum temperatures (ºC) at the Twee Rivieren weather station, KTP summarized into seasonal totals for January 2003 to December 2006 (Seasons: HW = hot-wet; CD = cold-dry; HD = hot-dry)

Year	2003				2004				2005				2006			
Season	HW	CD	HD	Total	HW	CD	HD	Total	HW	CD	HD	Total	HW	CD	HD	Total
Mean max temperature (ºC)	36	24	34		33	24	33		33	26	35		33	24	35	
Mean min temperature (ºC)	18	2	14		17	1	14		17	5	14		18	2	14	
Rainfall (mm)	82	1	39	122	183	0	53	236	214	2	49	265	212	4	100	316

Adjacent to the riverbeds, large limestone plains compacted with pink to white sands are found. This is a scrub savanna, characterised by scattered camel thorn (*A. erioloba*) trees and dominated by dense dwarf shrubs of *Rhigozum trichotomum* (driedoring), *Monechma incanum* (blouganna), *Aptosimum albomarginatum* and dominant grass species such as the perennial short bushman grass (*Stipagrostis obtusa*), Kalahari sour grass (*Schmidtia kalahariensis*), tall bushman grass (*Stipagrostis ciliata*) and silky bushman grass (*Stipagrostis uniplumis*). The calcrete ridges are sloping sides next to the riverbed.

The dune habitat consists of loose sand and is dominated by tall perennial grasses such as *Stipagrostis amabilis, Eragrostis trichophora,* and *E. lehmanniana.* Scrub species such as the dune bush (*Crotalaria spartioides*), lucern bush (*Hermannia tomentosa*) and the gemsbok cucumber (*Acanthosicyos naudinianus*) dominate the dune areas. Occasional smaller camelthorn and grey camelthorn trees, as well as shepherd's trees (*Boscia albitrunca*) are present. For more detailed descriptions of the vegetation see Mucina & Rutherford (2006).

2.2 Rationale

In spite of its wide range and popular profile no field study on the African wild cat has been published and there is at paucity of knowledge on the ecology and behaviour of the species. There is a need to understand its basic biology and ecology, both from the conservation and scientific viewpoints. Although not endangered, the African wild cat is generally recognized as the ancestor of the domestic cat and hybridisation is thought to be sufficiently extensive between these two forms as to severely threaten its status (Nowell & Jackson, 1996). A recent study in southern Africa found that the African wild cat and the domestic cat are indeed genetically distinct, although the level of genetic introgression appears lower than previously thought (samples were collected from cats in captivity and road kills, however, possible hybrids were excluded) (Wiseman, O'Ryan & Harley, 2000). This enhances the conservation status of the African wild cat and emphasises the need to minimise potential contact with feral and domestic cats. The Kalahari population was not included in the Wiseman *et al*. (2000) study, yet in the early 1980's in an area more than 75 km from the nearest domestic cat population, a black and white specimen believed to be a hybrid was seen (G. Mills, pers. obs.). Therefore, a study combining both field and behavioural observations with molecular genetics presented the ideal research opportunity to increase our knowledge and conservation attempts on the African wild cat in the southern Kalahari.

2.3 Objective

Broadly speaking, the study focused on the conservation genetics, behavioural ecology and ecological role of the African wild cat in the southern Kalahari.

2.4 Key questions

Behavioural ecology

a) What is the diet of the African wild cat and does the foraging behaviour and food availability change throughout the seasons?
b) Are there any differences between the sexes in their foraging behaviours?
c) What are the factors that determine the spatial organisation of the African wild cat with special reference to food availability, potential mating partners, territorial behaviour and social systems?
d) What are the home range size and movement patterns of the African wild cat and are there differences and overlap between sexes?

Social organisation

a) Are there any social interactions between cats (between different sexes and same sexes) other than mating?
b) What is the genetic structure of the observed population of African wild cats, i.e. does natal philopatry occur?
c) Will female African wild cats in the wild provide lactating females with food? (as previously observed in captive African wild cats (Smithers, 1983)).

Population genetics

a) What is the mating system of the African wild cat?
b) What is the genetic structure of the population of wild cats in the KTP?
c) What is the level of genetic variation between African wild cats and domestic cats in the Kalahari?
d) How extensive is hybridisation between the African wild cat and the domestic cat in the KTP?

2.5 The broader scientific framework of this study

Recent assessments on the conservation status of mammals present a decline in populations among terrestrial mammals with carnivores the most threatened (Ceballos *et al*. 2005; Schipper *et al*. 2008). This emphasis the need for informed conservation and management actions (Karanth & Chellam, 2009). However due to the difficulty in studying carnivores, especially small carnivores the majority remain poorly studied and the resulting paucity of reliable knowledge is impending species recovery efforts (Karanth & Chellam 2009). For many carnivores beyond anatomical descriptions and unrefined range maps we still lack the basic knowledge of diet, social organisation, community ecology, population biology and genetics (Karanth & Chellam 2009).

The African wild cat study was the first field study on the behavioural ecology of wildcats in southern Africa. The study aimed to address the areas of behavioural ecology where data were previously lacking. The results could in the absence of other studies be applied across distributional ranges and in different scales. Firstly, a thorough description of natural wild cat feeding habits, foraging behaviour, spatial organisation and reproduction are important for wild cat conservation in general. The understanding of African wild cat behaviour can assist in conservation actions for the species across distributional ranges.

Secondly, the ecological role of small or mesopredators in communities has received considerable attention in recent years (Estes, Crooks & Holt, 2001; Roemer, Gompper & Van Valkenburgh, 2009; Prugh, Stoner, Epps, Bean, Ripple, Laliberte & Brashares, 2009). Studies of more complex communities show that mesocarnivores have strong effects on their prey species, however their impact on other aspects of the community is less obvious, and bottom-up control of prey abundance may limit the potential for strong top-down indirect effects (Roemer *et al*. 2009). The results from this study in terms of predator-prey interactions, the effect of seasonal changes on foraging and reproductive behaviour can aid in the understanding of the role of the African wild cat as a small mesopredator in ecosystems.

Thirdly, the majority of natural history studies have been done in protected areas (including this study) and results can be compared with a large body of data on all aspects of the ecosystem. However it is important to recognise that many areas of cat distribution are in disturbed and unprotected habitats. Therefore studies outside protected areas are also important and needed. In the Kalahari several larger predators (lions, leopards, cheetahs and hyenas) are present however the role of wild cats can change in the absence of an apex predator. In many cases mesopredators increase in abundance in the absence of larger predators and often leads to a negative cascading effect on prey species (Berger, Gese & Berger, 2008). The ways in which wild cats adjust to different forms of habitat modification and disturbances are important to understand wild cat behaviour outside conservation areas. This could be very important in the African wild cat where they are perceived as “problem animals” to farmers with small stock. Information and results from this study could serve as benchmark data and assist in understanding general wild cat behaviour outside protected areas. In these areas behaviour such as activity patterns and predation, are likely to differ substantially from inside protected areas and understanding these differences is the key to appreciating the scope of species adaptability and evaluates probability of future survival of wildcats.

Wild cat genetic analyses has recently enhanced our understanding of wild cat phylogeny and the ancestry of the domestic cat (Johnson *et al*. 2006; Driscoll *et al*. 2007; Driscoll *et al*. 2009a; Driscoll *et al*. 2009b; O'Brien & Johnson 2009). The domestic cat is probably the biggest threat to wild cats through hybridisation (Nowell & Johnson, 1996). In our study we determined the genetic status of the Kalahari wild cat population and we concluded that the population are genetically pure and admixture with neighbouring feral domestic cats is low. Results from our study can be used as a reference collection to test samples from other southern African wild cat populations.

The role of small carnivores in ecosystems may be far more important than previously considered (Roemer *et al*. 2009). Available theoretical and empirical data suggest that in many cases, mesocarnivores may be fundamentally important drivers of ecosystem functions, structure or dynamics. Results from our study do not only describe the behaviour of a small and elusive carnivore and therefore increase our knowledge and improve our management actions for the conservation of a species, but also aid in the understanding of the interactions and role they may play in ecosystems.

2.6 Overview of thesis

This thesis has been written in the form of separate papers for publication, following the format of a publication in the *Journal of Zoology (London)*. Therefore each chapter forms an independent section with the study area and material and methods that might repeat and overlap in consecutive chapters. The four data chapters are presented in the same chronological order to answer the key questions as presented above. Appendix 1 is a detailed description of the mark and capturing techniques and is also presented in a paper format for publication (Herbst & Mills submitted). Appendix 5 is a copy of a comparative book chapter that is currently in press.

This study can be divided into two parts: (i) The behavioural ecology of the African wild cat (Chapters 2, 3 and 4) and (ii) the conservation genetics of the African wild cat (Chapter 5). The collection of wild cat samples to extract DNA for the molecular analysis was an ongoing process from the onset of the study until the end. Chapter 2 investigates the feeding ecology of wild cats from the view of optimal foraging theory (Perry & Pianka, 1997). The diet was determined through direct visual observations on eight habituated cats (three female and five male) and the biomass and frequency of prey items were calculated. Seasonal variability as well as sexual differences was recorded. The importance of food and prey availability was investigated through seasonal surveys of prey abundances and scat analyses and compared to our visual observations on the diet of the wild cats.

The foraging behaviour and activity patterns in male and female cats during the three seasons (hot-wet, cold-dry and hot-dry) are described in detail in Chapter 3. What entails a successful hunt, the hunting technique and the differences between sexes and their ability to catch different prey sizes are discussed. African wild cat activity patterns, the distances travelled, their time budgets and consumption rates are assessed. Differences in habitat utilisation between male and female wild cats are investigated.

Chapter 4 assemble the ranging behaviour and social organisation between male and female cats. Home range sizes and overlap are discussed in view of spacing patterns between male and female cats to increase their fitness and reproductive output (Sandell, 1989). The importance of prey abundances on the reproductive success and inter- and intraspecific interactions are also discussed. Observations on reproductive behaviour and scent marking activities are described.

In Chapter 5 we determined the genetic structure of our study population and compare that with domestic cats close to our study site as well as a reference collection from the Veterinary Genetics Laboratory at the University of Pretoria (Onderstepoort). We also address the question of hybridisation and the conservation status of African wild cats in the southern Kalahari. We combine behavioural observation of reproduction in Chapter 4 with genetic data on relatedness and briefly discuss mating strategies in the African wild cat.

Finally Chapter 6 is included to give an overall synthesis of all the results and a general conclusion of the study on the African wild cat in the southern Kalahari.

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CHAPTER 2

The feeding habits of the African wild cat (*Felis silvestris*), a facultative trophic specialist, in the southern Kalahari (Kgalagadi Transfrontier Park, South Africa/Botswana)

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1. Abstract

The seasonal feeding habits of the African wild cat *Felis silvestris* in the riverbed ecotone of the Kgalagadi Transfrontier Park were investigated over a period of 46 months. The diet was analysed through visual observations on eight habituated (three females and five males) radio-collared wild cats, supplemented with scat analysis. Murids formed the bulk of the biomass in the diet (73%), followed by birds (10%) and large mammals (4500 g) (9%). Although reptiles (6%) and invertebrates (2%) were frequently caught, they contributed less to the overall biomass of the diet. There were significant seasonal differences in the consumption of five food categories that related to changes in availability. Fluctuations in prey abundances could be the result of seasonal rainfall and temperature fluctuations or long-term variability in rainfall resulting in wet and dry cycles. As predicted, the lean season (hot-dry) was characterized by a high food-niche breadth and a high species richness. Despite sexual dimorphism in size in the African wild cat, both sexes predominantly fed on smaller rodents, although there were differences in the diet composition, with males taking more large mammals and females favouring birds and reptiles. These results indicate that African wild cats are adaptable predators that prefer to hunt small rodents, but can change their diet according to seasonal and longer-term prey abundances and availability.

Keywords: African wild cats, *Felis silvestris*, feeding habits, diet, prey abundances, southern Kalahari

2. Introduction

In Africa, the wild cat *Felis silvestris* Schreber, 1777, is represented by two subspecies, *Felis silvestris lybica* Forster, 1780, in northern Africa and *Felis silvestris cafra* Desmarest, 1822, in southern Africa (Driscoll *et al*., 2007), both of which have substantial geographical ranges, stretching throughout the African continent, excluding tropical forests and true deserts (Nowell & Jackson, 1996). In many parts of its range, it is a common small predator (Stuart, 1981) with a very broad habitat tolerance (Skinner, Chimimba & Smithers, 2005). Despite their wide distribution, African wild cats, like most small felid species (Nowell & Jackson, 1996), have not been well studied. Understanding the natural history of a species in its natural environment is important when formulating conservation and management strategies. This study provides a detailed description of the seasonal food habits of the African wild cat, based on direct observations in the southern Kalahari.

Discussions on whether to classify predators as generalists or specialists are widespread in the ecological literature (Futuyama & Moreno, 1988). Predators tend to be generalist hunters when the abundance of profitable prey is low, becoming more specialized when prey abundance increases (Pyke, Pulliam & Charnov, 1977). An obligatory trophic specialist, for example the aardwolf (Richardson, 1987), almost exclusively feeds on one species, regardless of abundance or whether other alternative prey is available, whereas a facultative specialist may be more opportunistic and changes its primary prey item when other profitable prey is available (Glasser, 1982). The prey composition in the diet of a generalist hunter would be expected to show a seasonal variation, depending on the abundance and availability of the prey species (Pyke *et al*., 1977).

Classical optimum foraging theory predicts that the diet of a facultative specialist will be more diverse during lean seasons than during abundant seasons, in response to the decreased availability of preferred food types (Perry & Pianka, 1997). This may lead to seasonal modifications in activity and foraging behaviour to satisfy their nutritional needs (Gittleman & Thompson, 1988; Gedir & Hudson, 2000). In addition, several predatory animals show sex-specific preferences for prey size. This is particularly apparent in felids, such as bobcat *Lynx rufus* (Fritts & Sealander, 1978; Litvaitis, Clark & Hunt, 1986), Eurasian lynx *Lynx lynx* (Molinari-Jobin *et al*., 2002) and cheetah *Acinonyx jubatus* (Mills, du Toit & Broomhall, 2004).

Numerous studies have investigated the feeding habits of the European wild cat *F. silvestris*. These include populations occurring in Scotland (Hewson, 1983), France (Condé *et al*., 1972), the Apennines (Ragni, 1978), the Iberian Peninsula in Portugal (Sarmento, 1996; Carvalho & Gomes, 2004), Spain (Gil-Sánchez, Valenzuela & Sánchez, 1999; Moleón & Gil-Sánchez, 2003; Malo *et al*., 2004), Hungary (Biró *et al*., 2005) and in the Carpathians (Kozena, 1990; Tryjanowski *et al*., 2002). Most of these studies concluded that the preferred prey for wild cats are murids and that they may be classified as facultative specialists on different prey items depending on prey availability (Malo *et al*., 2004; Lozano, Moleón & Virgós, 2006). In contrast, limited information is available on the feeding habits of the African wild cat, although it is reported that murids resemble the major component of their diet (Smithers, 1971; Stuart, 1977; Smithers & Wilson, 1979; Palmer & Fairall, 1988).

The feeding habits of the African wild cat are analysed by examining (1) the prey composition and overall diet; (2) the seasonal and/or annual variation in the overall prey composition and potential increase in diet variety in response to seasonal changes in food availability; (3) sexual size dimorphism and differences in relation to prey type, foraging strategies and consequently niche partitioning between wildcat sexes. Finally, a general comparison is drawn between feeding habits of the African wild cat and the European wild cat.

3. Materials and methods

Study area

The study was conducted from March 2003 to December 2006 (46 months) in the Kgalagadi Transfrontier Park (KTP). The main study area (53 km^2) was along the southern part of the Nossob riverbed and surrounding dune areas (Fig. 2.1). The KTP, shared between South Africa and Botswana, is a 37 000km^2 area in the semi arid southern Kalahari system, although our study area only included cats in the riverbed ecotone.

The vegetation of the Kalahari is described as the western form of the Kalahari Duneveld comprising an extremely open scrub savanna (Mucina & Rutherford, 2006). For the purpose of this study, four main habitat types were identified: (1) the dry riverbed; (2) the calcrete ridges; (3) the adjacent *Rhigozum* veld; (4) the sandy dune areas. For more detailed descriptions of the vegetation, see Bothma & De Graaff (1973) and Van Rooyen *et al*. (1984).

Climate and rainfall

The study site is characterized by low, irregular annual rainfall (Mills & Retief, 1984) and receives between 200 and 250mm annually. The irregularity of the rainfall plays a major role in the vegetation of the KTP (Leistner, 1967), and these cycles influence the availability of food and animal movement patterns (Van Rooyen, 1984). According to Nel *et al*. (1984), rodent numbers in the Kalahari fluctuate between seasons, with a slow buildup as rainfall increases, followed by sudden decreases. Variations in seasonal temperatures and factors such as rainfall, seed production and vegetation cover are involved in the fluctuations of rodent species and numbers.

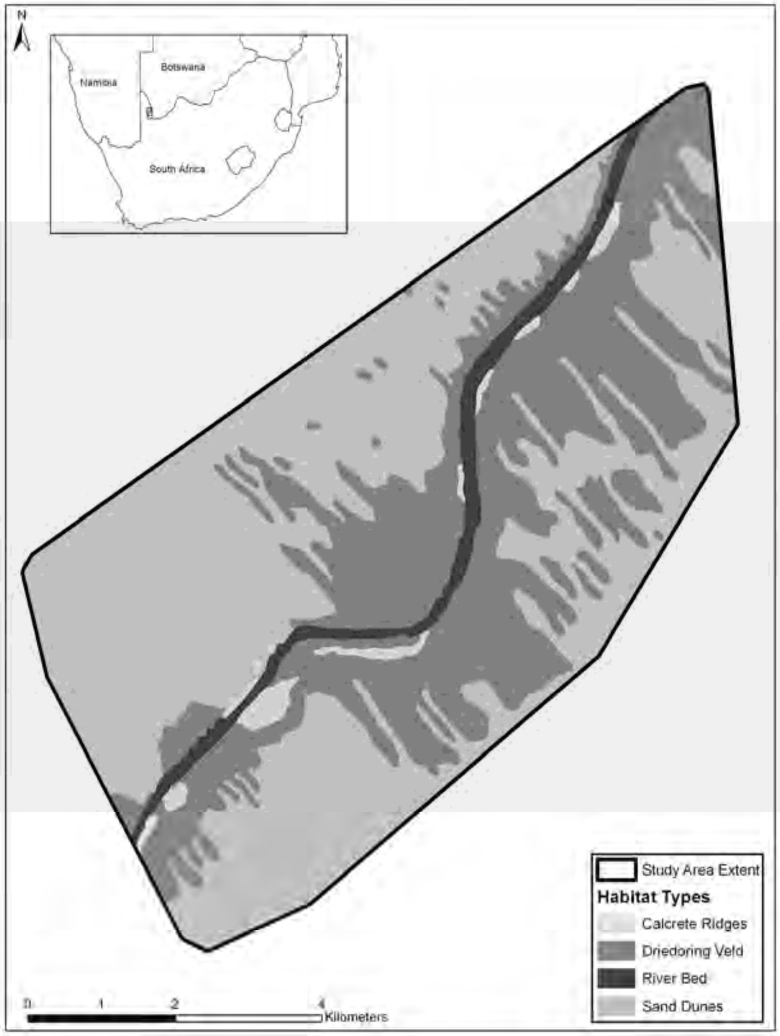

Figure 2.1 Map of the study area in the Kgalagadi Transfrontier Park indicating the different habitat types

Three seasons are recognized in the KTP: (1) A hot-wet season (HW) from January to April, characterized by mean monthly temperatures equal to or greater than 20℃, with 70% of the annual rainfall falling; (2) a cold-dry season (CD) from May to August, with mean monthly temperatures below 20℃ and little rai nfall; (3) a hot-dry season (HD) from September to December, with monthly temperatures approximately 20℃ and generally not more than 20% of the annual rainfall (Mills & Retief, 1984).

Monthly rainfall records for the weather station at Twee Rivieren rest camp (26°28'17.7"S, 20°36'45.2"E), approximately 15km to the south-west of the study site, were used (South African Weather Bureau). The first year of the study (2003) was a year with below average rainfall with 122 mm recorded. All subsequent years (2004 – 2006) had average or above-average rainfall (272 ± 41 mm per annum).

Data collection

Behavioural observations

African wild cats were either caught in cage traps or by the use of a dart gun (Appendix 1). After a radio collar was fitted, the cats were followed from a vehicle at a distance of 50 to 100 meters using the radio signal while they were being habituated to the vehicle. Visual contact was re-established until the cats could be followed from 10 to 30 meters without any obvious influence on their behaviour. During the course of the study 1,538 hours were spent observing habituated cats (Table 2.1). Cats were selected on a rotational system and followed for an average of 6.0 ± 3.2 hours of observation periods (range 1 - 14 hours). Thick vegetation and long grass sometimes precluded direct visual contact with the cats for short periods.

All hunting and feeding activities were recorded and timed to the nearest minute. The term hunting attempt is subjectively defined as any interaction between an African wild cat and a potential prey animal, where the cat moved towards the prey with considerable interest, caution and/or increased speed. A 1,000,000 candle power spotlight was occasionally used during night observations, although the vehicle's lights were usually sufficient to allow observations and record prey type. The beam of the spotlight was aimed slightly behind the cat to avoid illuminating the cat or prey item.

An observational study on a predominantly nocturnal animal, like the African wild cat, unavoidably has certain limitations (Sliwa, 2006). The disturbance caused by vehicle noise and light may have influenced the outcome of some hunts, particularly where larger prey species for example hare (*Lepus* sp.), springhare (*Pedetes capensis*) and spotted thick-knee (*Burhinus capensis*) were involved. Hunts could have been affected both positively for the cats where prey were blinded by lights and caught more easily, or negatively where prey were startled into fleeing, disrupting a stalking approach by a cat. Such effects are difficult to quantify, but we believe that our results show a slight bias against larger prey and that smaller prey such as mice was unaffected since cats often waited at a hole for a mouse to emerge without the spotlight being used.

Table 2.1 Time periods and total hours of direct observation of individual habituated cats for the duration of the study (Seasons and year indicated: CD = cold-dry, HD = hot-dry, HW = hot-wet and *n* = observation periods)

Cat ID	CD 2003	HD 2003	HW 2004	CD 2004	HD 2004	HW 2005	CD 2005	HD 2005	HW 2006	CD 2006	HD 2006	Hours
♀ VL01654												578
♀ VL01656												245
♀ VL01658												70
♂ VL01662												281
♂ VL01665												157
♂ VL01667												60
♂ VL01672												55
♂ VL01673												92
Hours	59	168	152	128	185	109	75	56	109	263	234	1538
	n = 11	*n* = 26	*n* = 18	*n* = 29	*n* = 33	*n* = 8	*n* = 22	*n* = 5	*n* = 23	*n* = 31	*n* = 33	

Rodent trapping

Rodent trapping was conducted to assess seasonal changes in relative abundance (R_a). On four consecutive nights, once during every season, two grids were set in each of the four habitats. Each grid consisted of 49 Sherman traps (7 x 7 traps) set ten meters apart. Traps were checked each morning; they were closed during the day due to high daytime temperatures and opened approximately two hours before sunset. The traps were re-baited every afternoon with a mixture of peanut butter, oats and vegetable oil. All rodents captured were marked with a spot of purple ink before being released, to ensure identification of recaptures (Begg, Begg, du Toit & Mills, 2003). Data for each trapping period were pooled for statistical analyses. The R_a was expressed as the number of individuals caught per 100 trap nights during the trapping period. Recaptures were excluded.

Transect lines: diurnal rodents, reptiles and birds

To monitor seasonal variation in diurnal reptile, bird and rodent, especially whistling rat (*Parotomys brantsii*) numbers, 5 x 100m transect lines in each of the habitats were walked over four consecutive days during each of the three seasons (hot-wet, hot-dry and cold-dry). All rodents, reptiles and birds were recorded.

Prey categorisation

Prey items recorded through direct observations were summarised into seven categories: large mammals (500 - 2000g), small mammals (<500g), birds, reptiles, insects, unknown and other (scorpions and solifugeds). Identification of rodents to the species level was often difficult, as they were consumed whole. Where it was possible to identify a rodent the average body mass of that species presented in the literature was used (Begg *et al*., 2003; Skinner *et al*., 2005). Where rodents could not be identified they were collectively grouped as: *Rodents*, and the body mass used was 50g (calculated as the average body mass of all identified rodent species eaten). The body mass estimates for reptiles, birds and invertebrates were obtained from Begg *et al*. (2003). For prey composition analyses, the three categories: insects, unknown and other were pooled into a single category, *Invertebrates*, to simplify analyses and assigned a mass of 2g.

Prey items are presented as percentage frequency (i.e. the number of food items caught as the percentage of the total number of food items caught) and percentage biomass. The biomass of individual prey items in each prey category was summed to provide an estimate of the biomass contribution of each food category in each season.

Scat analysis

Scat analyses of 52 samples were used to supplement observational feeding data in an attempt to determine unidentifiable prey items. Scats were collected opportunistically while following a focal animal, placed in a brown paper bag, numbered and air dried. Scat analyses followed the methodology of Putman (1984) and Reynolds & Aebischer (1991). The scat was washed in water over a sieve to separate undigested remains and dried for two days in an oven at 30℃. The undi gested remains were separated into a Petri dish and teeth, jaw fragments, bones, feathers, non-digestible plant material and other identifiable remains were separated from the remainder of the scat, which was predominately hair. No attempt was made to identify hair remains. To study the variation in diet composition, the remains were pooled into sub-categories of: large mammal remains, small mammal remains, bird, reptile, invertebrates and plant material. The data were analysed as percentage frequency of occurrence (number of times food category is present in sample/total number of scats analysed x 100) and percentage of occurrence (number of times food category is present/total number of occurrences of all food items x 100) (Manfredi, Lucherini, Canepuccia & Casanave, 2004).

Statistical analysis

An index of dietary diversity for each season from observational data was calculated using Levin's formula for niche breadth (Erlinge, 1981; Lode, 1994): $N_B = 1 / \Sigma\ p_i^2$ where p_i = the proportion of observations in food category *i* of the diet. Results for males and females are presented combined as well as separately. Differences between sexes were tested using the Chi Square test of statistical significance for bivariate tabular analysis (χ^2) (Siegel, 1956). The Spearman Rank correlation coefficient (r_s) was used to investigate relationships between prey abundance and their percentage contribution to diet and small mammal, insect and reptile consumption. The statistical package *Statistica 7.1* (Statsoft, Inc. 1984-2006) was used for all tests, with significance set at $P < 0.05$ for the two-tailed tests.

4. Results

4.1 Overall diet and prey composition

During the study 2,553 prey items were observed to be caught by African wild cats, of which 81% could be identified to one of the five food categories and comprising 26 species (Appendix 2). Nineteen percent of the food items were classified as unknown as they were too small and consumed too quickly to be identified. Rodents, reptiles and invertebrates had the highest percentage occurrence in the scats of African wild cats

(Table 2.2) and confirm visual observations where rodents, insects and reptiles had the highest percentage occurrences.

Vertebrates

Mammals made up 82% of the cumulative prey biomass consumed (73% small mammals and 9% large mammals), followed by 10% birds and 6% reptiles. The remaining 2% consisted of invertebrates (Appendix 2). The most common prey items captured were small mammals (44%) followed by reptiles (23%) (Appendix 2). Small mammals almost exclusively consisted of murids with only one recorded insectivore, a Bushveld elephant shrew (*Elephantulus intufi*).

Invertebrates

Invertebrate prey was difficult to identify from visual observations. Scat analyses suggest that the majority of unidentifiable prey items may be included in the invertebrate category (Table 2.2). If insects, other and unknown prey items are pooled into the single category *Invertebrates*, they contribute 30% to the total number of prey items caught. However, only 2% of the total biomass of the diet of African wild cats comprised invertebrates (Appendix 2).

Plant material

On two occasions cats were observed to consume vegetal material, grass (*Eragrostis* sp.) and leaves of the unpalatable *Radyera urens*. Plant material was not included in the analysis although it was frequently found in the scats of African wild cats (42.3% frequency of occurrence) (Table 2.2). The nutritional value of plants is very low (Kozena, 1990; Moleón & Gil-Sánchez, 2003) and ingestion could have been both incidental (plants sticking to the prey or content of the digestive tract of prey) and intentional, either to supplement micronutrients, or to aid digestion and regurgitation of indigestible parts, particularly fur (see Sladek (1972) in Kozena (1990)).

Table 2.2 Frequency of occurrence of the main food categories in the scats of African wild cats (scat: n = 52)

Food category	Percentage frequency of occurrence	Percentage of occurrence
Large mammals	3.8	1.5
Small mammals	88.5	33.4
Reptiles	69.2	26.3
Birds	3.8	1.5
Insects	50	19
Solifuges	5.8	2.2
Plant material	42.3	16.1
Total		100

4.2 Seasonal variation in the diet

When combining data for male and female cats, Levin's measure of niche breadth, as well as species richness were highest in the hot-dry and hot-wet seasons with the cold-dry season the lowest. This is in contrast with optimal foraging theory since it is expected that niche breadth and species richness should be higher in the cold season. However, when the lean period (the cold-dry season from 2003 to the end of the hot-wet season in 2004 (Fig. 2.2)) was excluded a dramatic decrease in Levin's measure of niche breadth in both the hotter seasons of the year was detected (Table 2.3).

Small mammals and reptiles were the most numerous prey items and together contributed more than 57% of the prey numbers eaten in each season (Table 2.4). Small mammals contributed to more than 65% of the cumulative biomass consumed by African wild cats in any season, but show significant variation between seasons (χ^2 = 275.26, d.f. = 2, P < 0.001) (Table 2.4). The frequency of reptile consumption also showed significant seasonal variation, being most common in the hot-wet season (χ^2 = 326.01, d.f. = 2, P < 0.001) when they contributed 18% to the biomass of the diet, compared to less than 1% during the cold months.

The percentage biomass contributed by birds ranged from 17% during the cold-dry months to 1.6% in the hot-wet season also indicating significant seasonal variation (χ^2 = 75.95, d.f. = 2, P < 0.001). During the hot-dry season birds and reptiles contributed

12.8% to the overall biomass of the diet of African wild cats. Although the relative frequency of unidentifiable prey items was high, especially during the hot seasons, the contribution to the total biomass cat's diet was low (< 4%).

No significant seasonal variation was observed in large mammals (χ^2 = 2.51, d.f. = 2, P = NS). Large mammals were rare in the diet (<1%) (Table 2.4). Four out of 16 hunting attempts on large mammals were successful and contributed 9% to the total biomass of prey consumed.

Insects, other (scorpions, solifugeds) and unidentifiable prey items (all invertebrates) did not contribute more than 4% of total prey biomass in any single season (Table 2.4). Almost all unidentified prey items (97%) observed during the study was recorded within a single year between the hot-dry season of 2003 and the cold-dry season of 2004. During this period, rodent numbers were at their lowest (Fig. 2.2). In addition, the consumption of these three categories showed significant seasonal variation (insects: χ^2 = 93.51, d.f. = 2, P < 0.001; other: χ^2 = 147.06, d.f. = 2, P < 0.001; unknown: χ^2 = 86.61, d.f. = 2, P < 0.001), being most highest during the hot-wet and hot-dry seasons.

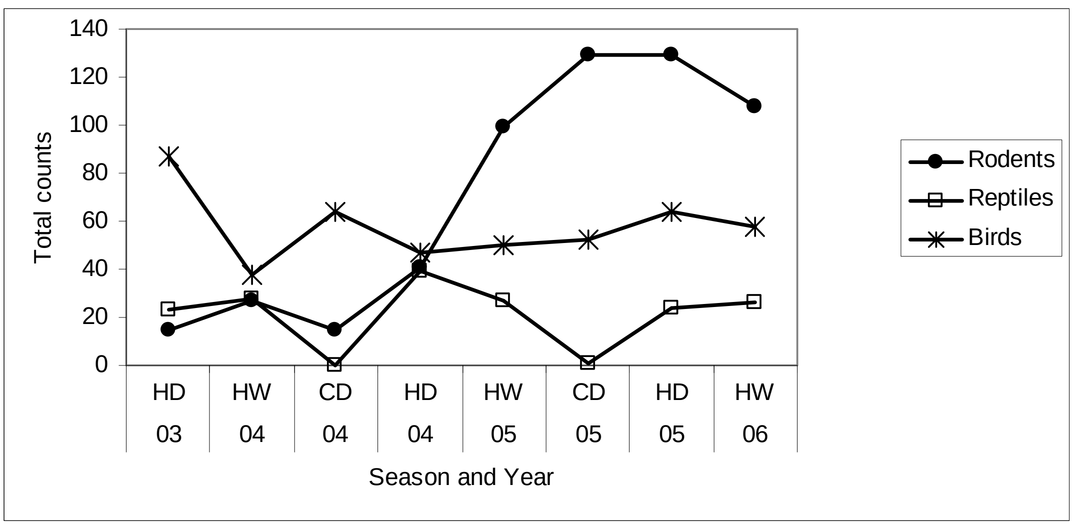

Figure 2.2 Total counts for small rodents, reptiles and birds on transect lines in all habitats pooled together for each season (HD = hot-dry, HW = hot-wet, CD = cold-dry) in the KTP from 2003 to 2006

Table 2.3 Seasonal differences in the niche breadth (Levin's niche breadth) and species richness of the diet of African wild cat (male and female pooled) in the KTP

	Season		
	Hot-wet	Cold-dry	Hot-dry
Niche breadth	3.0	1.4	3.5
Niche breadth (excluding lean season)	1.1	1.3	1.6
Species richness	20	16	23

Table 2.4 Seasonal differences in diet, expressed as percentage presence and percentage biomass contributed by each prey category to the overall diet of African wild cats in the KTP (CD = cold-dry, HD = hot-dry, HW = hot-wet) from direct observations

Prey category	Prey consumed					
	% Frequency			% Biomass		
	CD	HD	HW	CD	HD	HW
Large mammals	0.2	0.3	0	2.3	18.6	0
Small mammals	83.6	42.3	22.4	80.2	65.9	75.7
Reptiles	1	14.9	45.4	0.2	6.6	18.1
Birds	8.3	2.2	0.2	17	6.2	1.6
Insects	2.3	15.6	4.7	0.2	1.1	0.9
Other	0	0.7	0.1	0	0.1	0.04
Unknown	4.6	24.1	27.2	0.2	1.5	3.6

4.3 Influence of changes in prey availability in the diet

Although the consumption of small mammals varied markedly during the course of the study, no clear seasonal pattern was evident. The study period (2003 – 2006) was characterised by initial low rodent densities followed by an increase in numbers when rainfall was higher and a slight decline in numbers towards the end (Fig. 2.3).

Reptile, insect and bird consumption were significantly negatively correlated with the consumption of small mammals during each season of the study (insects: n = 11, r_s = -0.69, P < 0.05; reptiles: n = 11, r_s = -0.73, P < 0.05; birds: n = 11, r_s = -0.64, P < 0.05; Fig. 4). However, the cold-dry season of 2003 showed a different trend in bird consumption. At that time the only radio-collared cat spent most of her time hunting close to a waterhole, where she caught birds perching on the side of the reservoir or birds sitting around the waterhole. Once the rains came, she remained around the water hole but changed her diet to rodents (Chapter 3). For all radio collared cats the consumption of birds was negatively correlated with rainfall (n = 11, r_s = -0.67, P < 0.05), however, none of the other food categories were.

Between the cold-dry season of 2003 and the hot-wet season of 2004, rodent numbers were low and small mammals contributed less than 10% of the percentage prey caught. During this time reptiles and insects increased in importance as prey items (Fig. 2.4). From the cold-dry season of 2004 until the end of the hot-dry season in 2006, small mammals made up more than 64% of the total diet of African wild cats and contributed more than 68% of the biomass in each season, with a dramatic reduction in other prey selected.

4.4 Sexual differences in body size and diet of African wild cats

Body size

African wild cats show distinct differences in the body mass of sexes, with males being 31% heavier than females. In addition, males exhibit significantly longer head body length and Hf s/u (hind foot, *sine unguis*) than females (Table 2.5).

Diet

Small mammals and reptiles were the two most important prey items for both sexes and when combined contributed more than 55% of the prey items in both males and females (Table 2.6). Small mammals were also the largest contributors to cumulative biomass consumed (males 85%; females 63%). Larger mammals were the second-most important contributor to total prey biomass in the males' diets (11%) but were unimportant for females (only one of the 16 hunting attempts on large mammals was by a female). Birds were the second-most important contributor to total prey biomass in females (15%) (Table 2.6).

In all seasons, the prey diversity was higher for females than males (Table 2.7). For both sexes the highest prey diversity was in the hot dry season (males = 1.73 and females = 3.86). Females exhibited the lowest niche breadth index in the cold dry season, whereas for males the niche breadth index in the hot wet and cold dry seasons was similar.

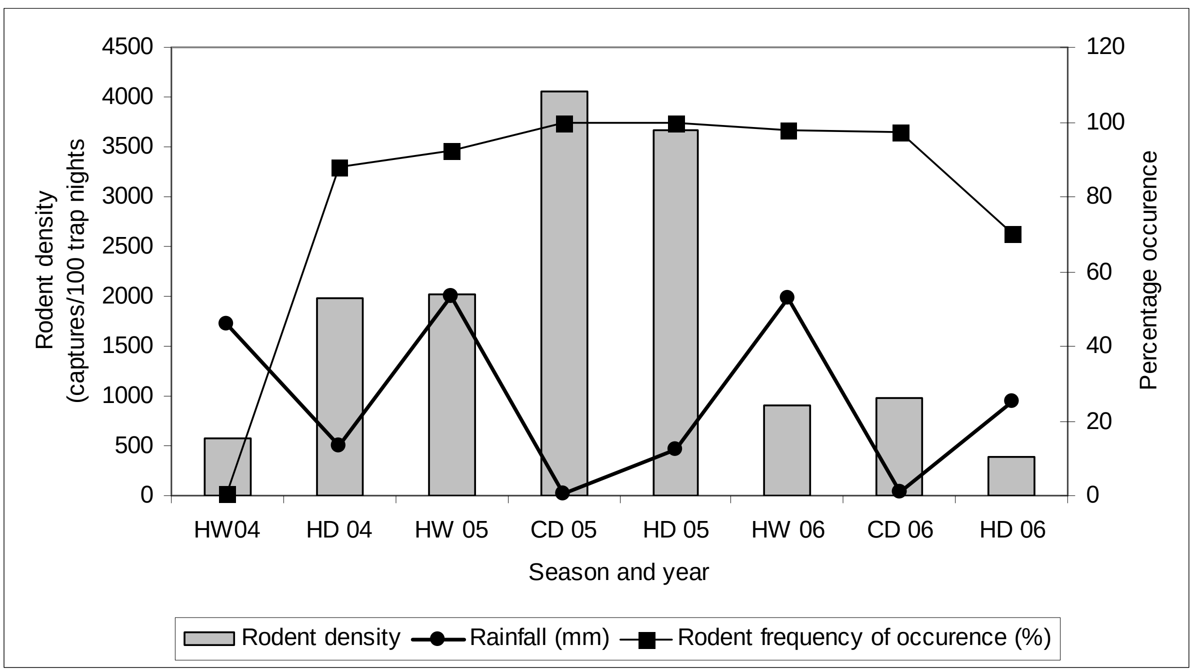

Figure 2.3 The relationship between percentage frequency of small mammals consumed by African wild cats, rainfall and the relative abundance of small mammals estimated from rodent trapping from the hot-wet season 2004 to the hot-dry season 2006

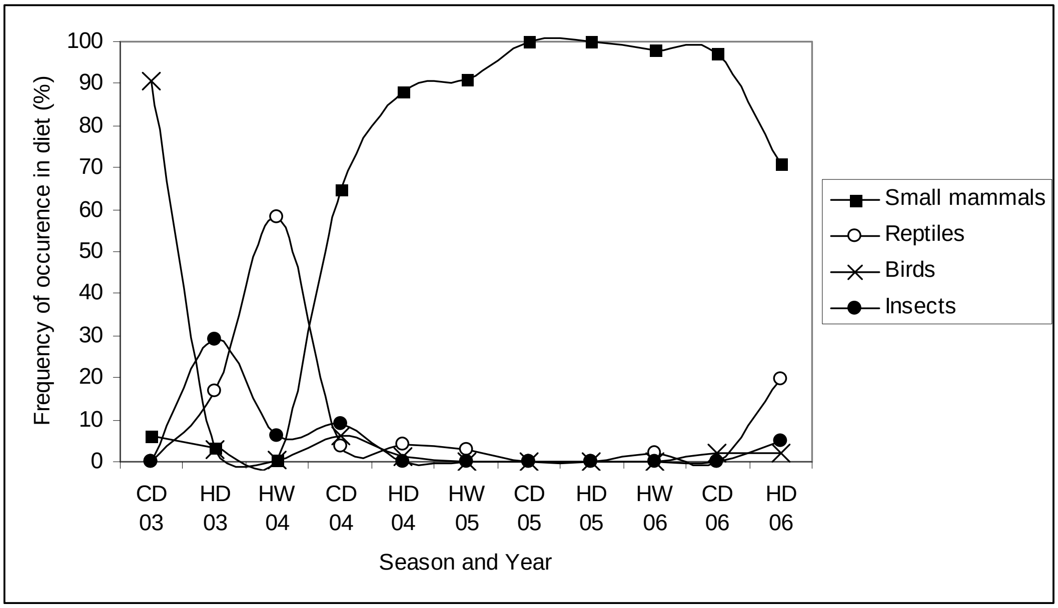

Figure 2.4 Annual and seasonal changes in the proportions of small mammals, insects, reptiles and birds in the diet of African wild cats in the KTP based on visual observations (CD = cold-dry, HD = hot-dry, HW = hot-wet)

Table 2.5 Mean and standard deviation (SD) of standard body measurements of male and female African wild cats in the KTP. Total body length (head body length + tail), Hf s/u (hind foot)

	♂ Overall (n = 13)	♀ Overall (n = 9)	Two-tailed t-test	
Measurement	Mean ± SD	Mean ± SD	t – value	
Total body length (mm)	99.4 ± 4.18	94.8 ± 6.24	2.09	$P < 0.05$
Head – body length (mm)	64.6 ± 2.63	60.4 ± 3.85	3.09	$P < 0.05$
Tail (mm)	34.7 ± 2.46	34.4 ± 3.15	0.31	NS
Hf s/u (mm)	15.7 ± 0.46	14.7 ± 0.74	4.11	$P < 0.001$
Ear (mm)	7.1 ± 0.49	7.1 ± 0.55	0.13	NS
Mass (kg)	5.3 ± 0.67	4.0 ± 0.43	5.22	$P < 0.001$

Table 2.6 Sexual differences in the diet of African wild cats from direct observations (five male and three female) in the KTP expressed as the percentage frequency and percentage biomass contributed by each prey category to the overall diet and ranked accordingly (*n* = total food items). The niche breadth index and species richness of male and female diets are indicated

Prey category	Female diet (*n* = 1649)				Male diet (*n* = 712)				χ^2 (d.f. = 5)	χ^2 (d.f. = 5)
	% Frequency	Rank	% Biomass	Rank	% Frequency	Rank	% Biomass	Rank	% Frequency	% Biomass
Large mammals	0.12	6	6.97	4	0.28	6	11.45	2	-	-
Small mammals	26.32	3	63.46	1	85.53	1	83.45	1	$P < 0.001$	$P < 0.01$
Reptiles	28.87	2	10.41	3	8.85	2	1.64	4	$P < 0.001$	$P < 0.01$
Birds	3.34	5	15.30	2	1.69	4	3.26	3	NS	$P < 0.01$
Insects	12.07	4	1.30	6	2.11	3	0.15	5	$P < 0.001$	$P < 0.01$
Unknown	29.29	1	2.58	5	1.54	5	0.05	6	$P < 0.001$	$P < 0.01$
Niche breadth	2.91				1.35					
Species richness	26				18					

Table 2.7 Seasonal differences in diversity (Levin's niche breadth index) and species richness of the diet of male and female African wild cats separately (HW = hot-wet, CD = cold-dry, HD = hot-dry)

	Season		
	HW	CD	HD
Male	1.03	1.07	1.73
Female	2.97	2.21	3.86
Species richness	15	14	24

5. Discussion

The African wild cat (*F. silvestris*) is a medium sized carnivore in the KTP and, similar to its European counterpart *F. s. silvestris,* prefers to prey on smaller rodents. It is able to supplement its diet with a range of prey species (insects, birds and mammals) (Sarmento, 1996; Moleón & Gil-Sánchez, 2003; Malo *et al*., 2004). In the KTP, prey abundance fluctuates markedly and the cats are able to change their diet according to these changes in prey numbers.

Optimal foraging theory predicts that a predator will choose a prey type that maximises the energetic benefit to the individual in the minimum required time (Perry & Pianka, 1997). Prey abundance, their activity cycles (Zielinski, 1988), accessibility and energy contribution are all important factors that influence prey choice and optimal hunting strategy. These prey parameters are, in turn, influenced by seasonal and annual weather conditions. This appears to be the case for African wild cats in the Kalahari ecosystem. Our initial investigations of annual seasonal differences (hot-wet, cold-dry and hot-dry seasons) were inconsistent. However, when we characterised our early study period (2003 and beginning of 2004) as a lean cycle with below average rainfall and low prey abundances and the latter period (mid-2004 to the end of 2006) as an abundant period a clearer picture emerged. Excluding the lean period leads to a decline in Levine's niche breadth index. Thus our results confirm the optimal foraging theory for African wild cats, as generalists and opportunistic hunters. These predators shift their diet according to food availability. Similar shifts have been documented in other small feline studies (Moleón & Gil-Sánchez, 2003; Malo *et al*., 2004; Sliwa, 2006). Our results show rodents are the preferred prey item, with the highest contribution to biomass consumed throughout the year. The African wild cat thus fits the description of an intermediate specialist carnivore with a likely facultative trophic strategy (Glasser, 1984). Alternative prey items, especially reptiles and birds, change in importance depending on temperature, rainfall variability and consequently rodent abundance.

When rodent densities were low, they were eaten less frequently and the wild cats shifted to less profitable (Konecny, 1987) prey items, in particular reptiles, invertebrates and birds. This switch is apparently not due to a change in the abundance of the less profitable prey item but rather resulting from a decrease in the abundance of the preferred prey. This was evident at the start of the study when small rodent numbers were low and consumption of alternative prey was accordingly high. Following a wet period (2004) and a consequent increase in the abundance of rodents, there was a dramatic shift in the diet to small mammals (cold-dry season of 2004) despite reptiles still being readily available.

An increase in reptile and invertebrate consumption during the warmer months of the year coincides with increased activity of ectotherms and hence, greater availability of alternative prey (Branch, 1988; Begg *et al*., 2003). Of interest is the seasonal shift between bird and reptile consumption. Reptiles contribute greatly to overall biomass consumed by African wild cats, while during cold seasons, cats seem to increase bird consumption. It appears that birds are a substitute prey in colder months when reptile activity is low.

Although large mammals represent a low frequency (<1%) in the diet of wild cats, they contributed 9% to the total biomass of prey consumed, ranking them third after small mammals and birds. Therefore, from an energetic perspective, larger prey might be profitable to hunt. It has been estimated that a wild cat weighing 4 – 5kg needs a daily food intake of 1000g (Carbone, Mace, Roberts & Macdonald, 1999; Malo *et al*., 2004). One hare (*ca.* 1500g) is the energetic equivalent of nearly 20 rodents, and exceeds a cat's daily energetic requirement. Rabbits are an important component of the diet of European wild cats in France and central Spain (Corbett, 1979; Sunquist & Sunquist, 2002; Malo *et al*., 2004).

However, other factors such as catching effort is important (Stephens & Krebs, 1986) and catching rodents may be, proportionate to their smaller size, less energetically demanding than capturing a hare. While rodents can be captured by pouncing, fleeing hares have to be chased, and upon capture, bitten at the nape of the neck and violently shaken until dead. There is also the increased risk of losing the kill of a larger mammal to competitors as two of the six kills were lost to jackals.

Male African wild cats are significantly larger than females and although small rodents were the dominant prey item for both sexes, sexual differences in diet composition were found, both in the frequency of species taken, as well as in the ranking of prey categories. Large mammals were ranked second in male cats' diets, whereas smaller prey items such as birds and reptiles contributed more to the females' diets. It seems that females concentrate on smaller prey, and therefore have a more diverse diet, whereas the larger males can hunt larger prey. This has been explained as a possible means of reducing intra-specific competition between sexes (Fritts & Sealander, 1978; Litvaitis *et al*., 1986; Sliwa, 2006). Females, burdened with the high energy demands resulting from pregnancy, lactation, and provisioning for kittens may well benefit from more profitable, larger prey, but may lack the ability and strength to do so. A more diverse diet of smaller prey species may thus be a more optimal feeding strategy for them.

In conclusion, African wild cats are generalist and opportunistic predators that exhibit a wide dietary niche breadth. They also show evidence of sexual separation in diet composition reflected in the selection of larger prey by the larger males, and greater utilization of more numerous prey items by the smaller females. Southern African wild cats adapt their hunting strategies according to annual and seasonal changes in prey abundances and availability. Small mammals, especially rodents, comprised the bulk of the diet, while birds, reptiles and invertebrates increased in importance when rodent numbers were low. The understanding of these changes is important for the interpretation of multiple predator–prey interactions.

6. References

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