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Behavioural ecology and population genetics of the African wild cat, *Felis silvestris* Forster 1870, in the southern Kalahari

by

Marna Herbst

Submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy (Zoology)
in the Faculty of Natural and Agricultural Sciences
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To my parents and my brother, for their love and support

Radio collared African wild cat, *Felis silvestris*
in the Kgalagadi Transfrontier Park

Behavioural ecology and population genetics of the African wild cat, *Felis silvestris* Forster 1870, in the southern Kalahari

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Summary

The motivation for this study was to increase our knowledge on the natural history of the African wild cat and to investigate the genetic status of the Kalahari population. Hybridisation with the domestic cat is a global threat to the genetic integrity of the species. The Kalahari population was selected due to the isolation of the area and the slight possibility of contact with domestic cats. Radio telemetry and direct visual observations (1,538 hours) of eight habituated African wild cats (five male and three female) were used to address the feeding habits, foraging behaviour, spatial organisation and reproduction in wild cats. Throughout the study small skin biopsies were collected from both African wild cats and domestic cats from surrounding communities in order to address the potential of hybridisation and population genetic structure.

The Kalahari ecosystem not only experience annual dry and wet seasons but also longer lean and abundant periods that in turn influence rodent abundances and hence prey availability for the cats. This plays an important role in nearly all aspects of African wild cat behavioural ecology. The feeding habits of the African wild cat were discussed in the view of the optimal foraging theory. The lean season were characterised by a high species richness and high dietary diversity. African wild cats adapt their diet and foraging behaviour to seasonal prey abundances and availability. Male African wild cats were significantly larger than female cats and both sexes predominantly fed on smaller rodents, although there were differences is diet composition with males hunting larger mammals and females favouring birds and reptiles.

Despite sexual dimorphism male and female cats show little differences in time budgets and both exhibit a two peak activity period with a strong seasonal shift from predominantly nocturnal during the hotter seasons to more diurnal activity in the colder seasons. The major factors influencing activity patterns and habitat use appears to be prey abundances and temperature extremes.

As predicted male African wild cats had significantly larger annual home ranges than female cats (MCP 95%, ♂ = 7.7 ± 3.5 km^2 and ♂ = 3.5 ± 1.0 km^2). Female cats shows extensive overlap of home ranges, however the core areas were mostly exclusive while male-male overlap were limited and show no overlap of core areas. There were no differences in seasonal ranges between male and female cats and thus reproduction seems to be aseasonal and depending on food availability. Urine spray marking in males were prominent with territorial behaviour and aggression observed, while female spray marking seems to be related to their reproductive status.

In our study we report the genetic variation and admixture analysis of 57 wild living African wild cats and 46 domestic cats using 18 microsatellite loci. Bayesian cluster analysis support the classification of African wild cats and domestic cats as two distinct entities and identified four cryptic hybrids among the wild cats. Although all hybrids were outside or on the periphery of the KTP, suggesting that levels of introgression are low, this is still a concern to the genetic integrity of African wild cats as a species.

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To the Kalahari and the African wild cats – it was though but a remarkable journey! Words can not do justice to describe my experiences in the Kalahari.

God is in the details

~ Unknown ~

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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).

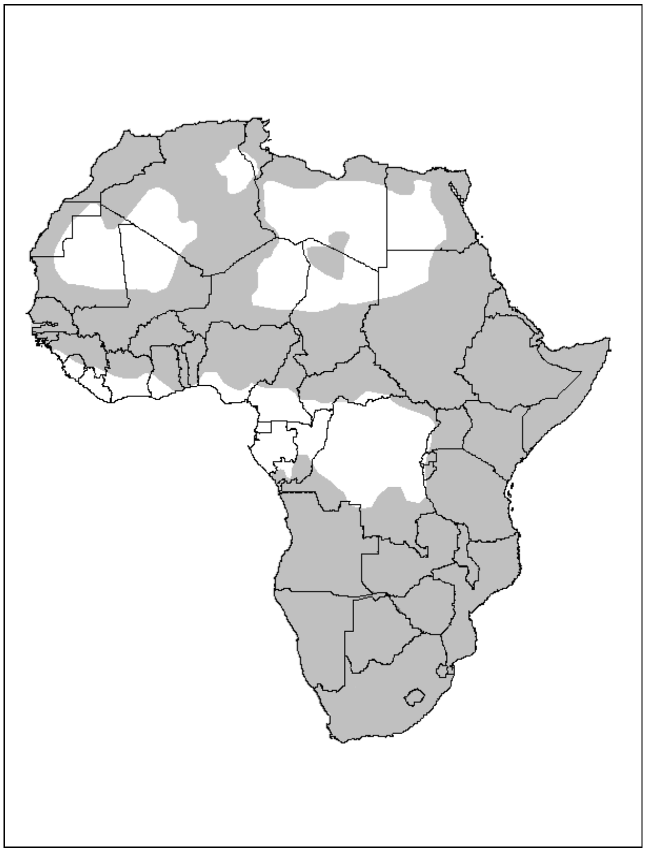

Figure 1.1 The geographical distribution of the African wild cat on the African continent (data from Stuart & Stuart as presented in Wilson & Reeder, 2005)

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, 26º28’17.7”S, 20º36’45.2”E) for the study period (Fig. 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.

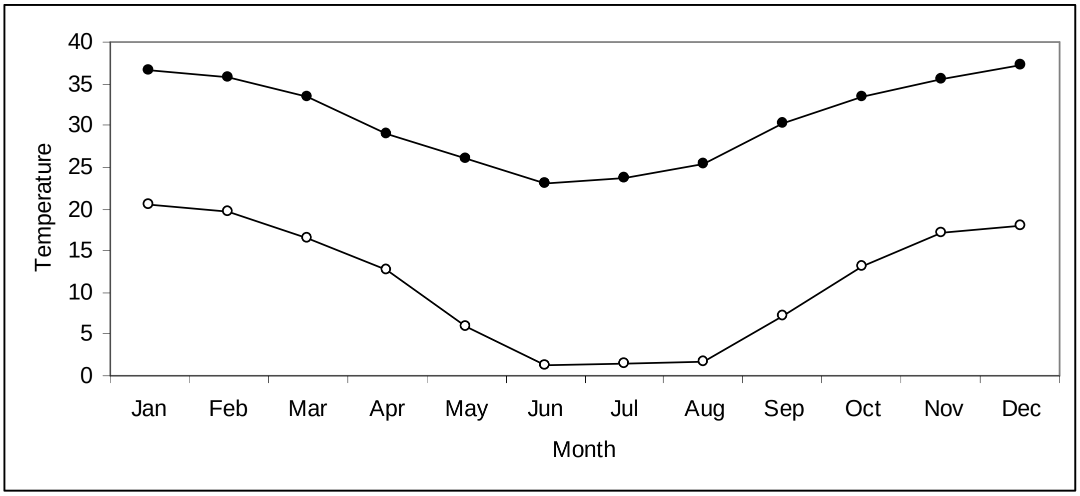

Figure 1.3a Monthly averages of the minimum (○) and maximum (●) temperatures (ºC) at the Twee Rivieren rest camp for the years 2003 to 2006

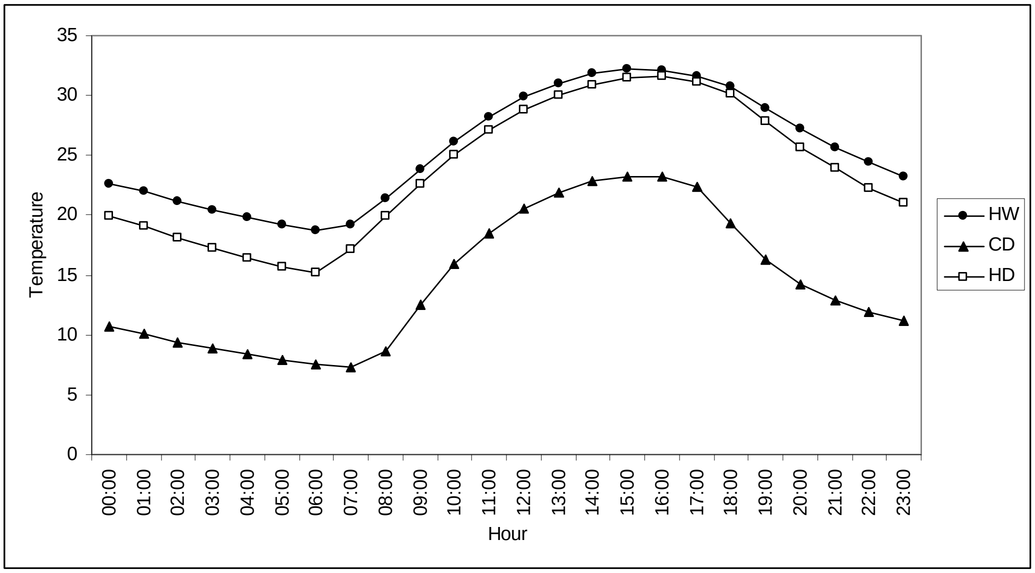

Figure 1.3b Average hourly changes in temperature in the hot-wet (HW), cold-dry (CD) and hot-dry (HD) seasons calculated from the nearest weather station in Upington

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.

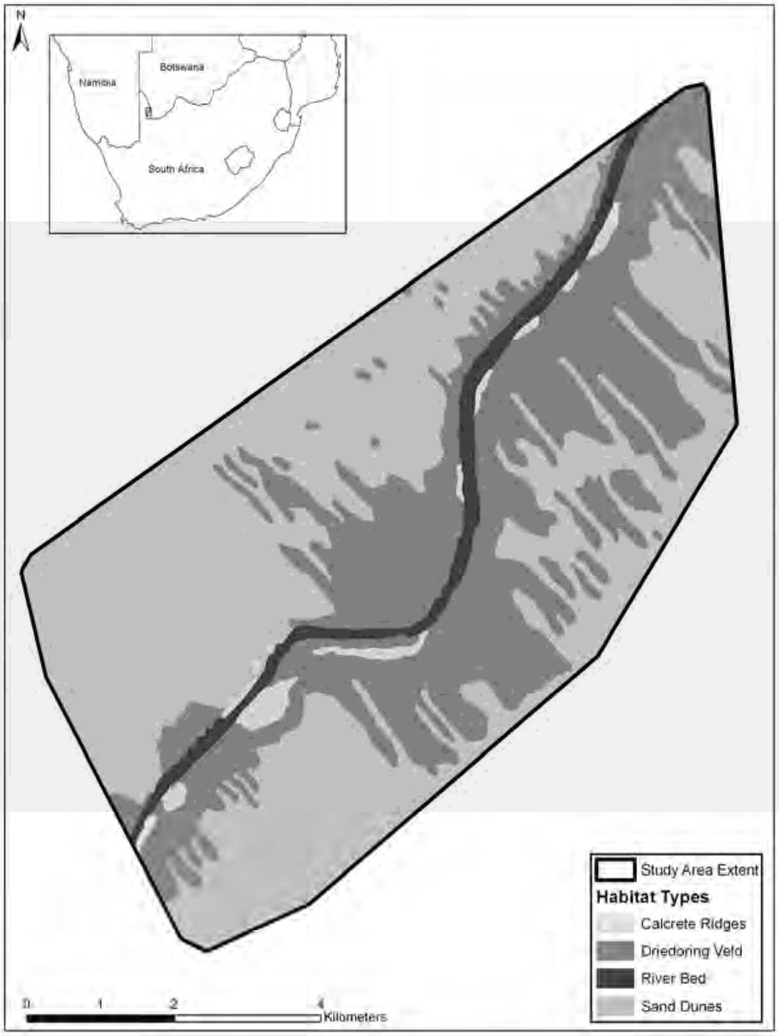

Figure 2.1 Map of the study area in the Kgalagadi Transfrontier Park indicating the different habitat types

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 rainfall; (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 undigested 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 ($\chi^2 = 2.51$, 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: $\chi^2 = 93.51$, d.f. = 2, $P < 0.001$; other: $\chi^2 = 147.06$, d.f. = 2, $P < 0.001$; unknown: $\chi^2 = 86.61$, d.f. = 2, $P < 0.001$), being most highest during the hot-wet and hot-dry seasons.

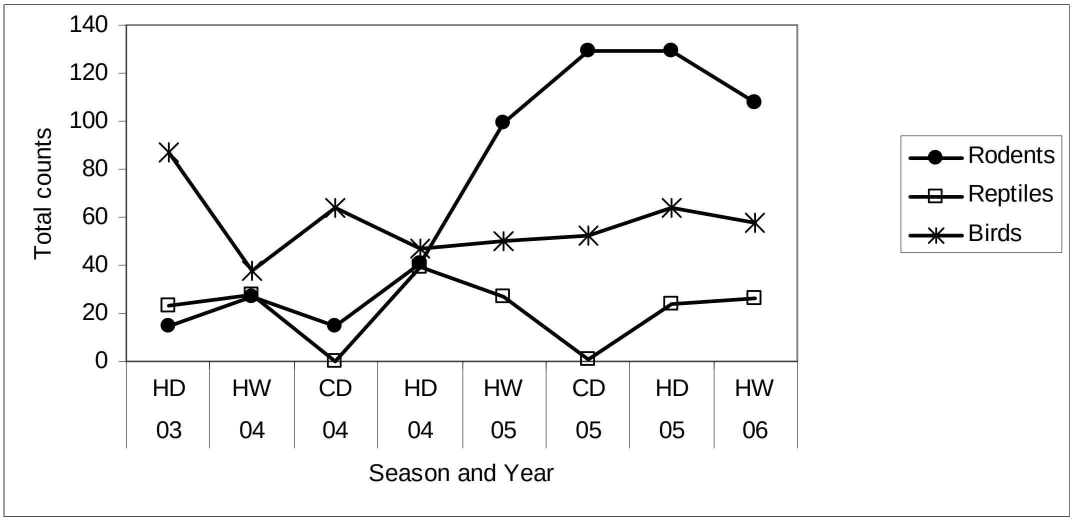

Figure 2.2 Total counts for small rodents, reptiles and birds on transect lines in all habitats pooled together for each season (HD = hot-dry, HW = hot-wet, CD = cold-dry) in the KTP from 2003 to 2006

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.

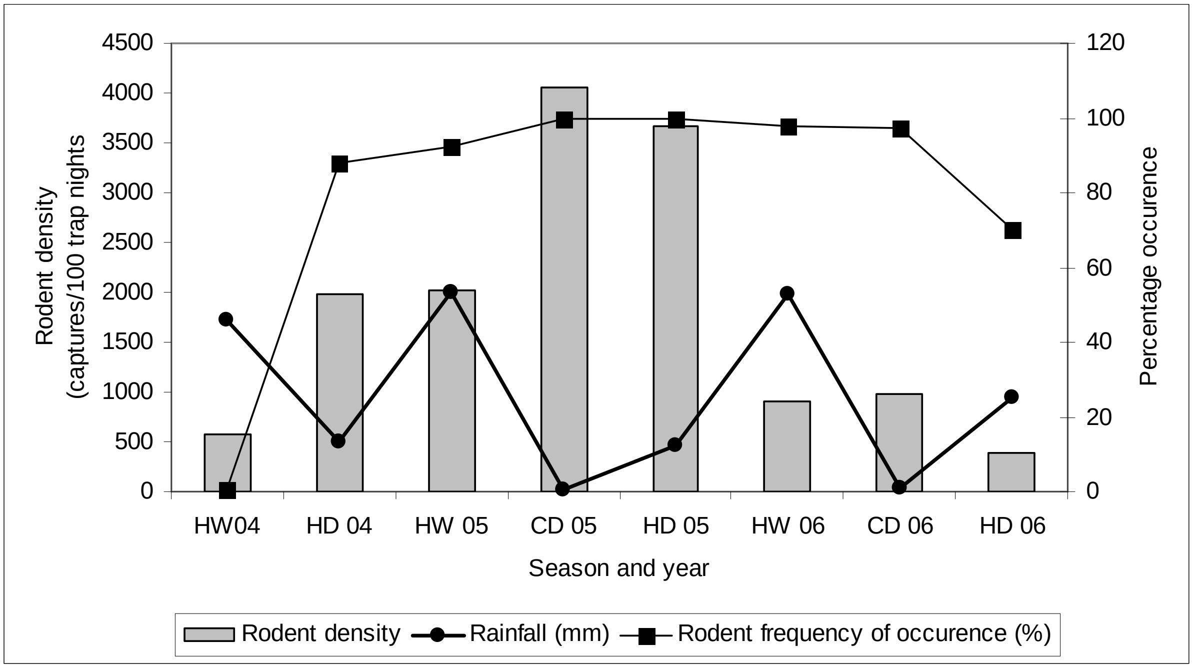

Figure 2.3 The relationship between percentage frequency of small mammals consumed by African wild cats, rainfall and the relative abundance of small mammals estimated from rodent trapping from the hot-wet season 2004 to the hot-dry season 2006

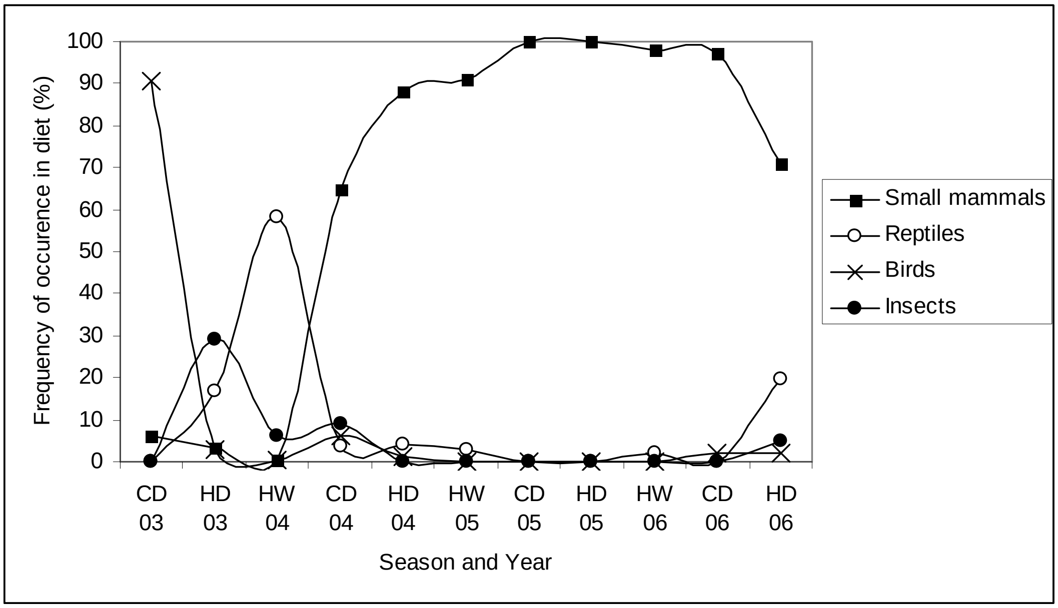

Figure 2.4 Annual and seasonal changes in the proportions of small mammals, insects, reptiles and birds in the diet of African wild cats in the KTP based on visual observations (CD = cold-dry, HD = hot-dry, HW = hot-wet)

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.

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CHAPTER 3

Foraging behaviour and habitat use of the African wild cat, *Felis silvestris* in the Kgalagadi Transfrontier Park

1. Abstract

The foraging behaviour and habitat use of eight habituated African wild cats (*Felis silvestris*) were investigated over 46 months in the Kgalagadi Transfrontier Park through direct observations. Hunting was typically felid with three distinct hunting behaviours identified: (i) a slow winding walk while inspecting holes and scent trails, (ii) sitting and looking around for prey, or (iii) fast walking while spray marking with opportunistic killing of prey, typical of male cats. Both sexes show two daily peaks of activity, in the early morning and the evenings. The timing of the two active periods shows strong seasonal shifts from predominantly nocturnal during the hotter seasons to more diurnal during the colder seasons. A longer period of activity during the day was observed during the cold-dry season with corresponding low food availability, apparently a behavioural response to low prey abundances. Male and female African wild cats differed very little in their activity budgets, with hunting taking up most of their time. African wild cats are solitary and socialising between individuals is minimal. Cats show gender-specific preferences for specific habitat types, with the number of prey captured corresponding closely to the time spent in each habitat. It appears that the major factors influencing the activity patterns and habitat use of the African wild cat in the southern Kalahari are prey abundance and temperature extremes.

Key words: foraging behaviour, activity patterns, time budgets, African wild cat, *Felis silvestris*, southern Kalahari

2. Introduction

Time and energy budgets vary widely between mammals and the time allocated to foraging is important (Bekoff & Wells, 1981; Armitage, Salsbury, Barthelmess, Gray & Kovaach, 1996), although sufficient time is also necessary for other activities for example, mating, defence of resources and predator avoidance (Bekoff & Wells, 1981; Armitage *et al*., 1996). Even periods of inactivity may be adaptive (Herbers, 1981) and essential for digestion (Diamond, Karasov, Phan & Carpenter, 1986), energy conservation and avoidance of potentially dangerous situations (Meddis, 1983). Time allocated to specific activities may be influenced by environmental conditions (Armitage *et al*., 1996). For example, raccoon dogs (*Nyctereutes procyonoides*) may hibernate where they occur in habitats with harsh winters like Finland and Russia, but remain active during milder winter conditions in Japan (Kauhala & Saeki, 2004). Animals may also synchronize their predatory activities with the activity periods of their primary prey (Curio, 1976), for example pine marten (*Martes americana*) activity appears to follow that of their primary prey rather than ambient temperature (Zielinski, Spencer & Barrett, 1983).

All animals show some form of regularity in their daily behavioural patterns and habits (Manning & Dawkins, 1995). Wild cats are described as either strictly nocturnal (Smithers, 1983; Sunquist & Sunquist, 2002) or arrhythmic (Gittleman, 1989). However, despite their wide distribution very little is known about their free-ranging activities and time budgets in the wild. By contrast, detailed studies on the foraging behaviour of larger felids exist, for example: lion, *Panthera leo* (Eloff, 1984; Stander, 1992), leopards, *Panthera pardus* (Bailey, 1993) and cheetah, *Acinonyx jubatus* (Caro, 1994) and even for some smaller cats like feral domestic cats, *Felis silvestris catus* (Panaman, 1981; Dards, 1983); black-footed cats, *Felis nigripes* (Sliwa, 1994) and bobcats, *Lynx rufus* (Rollings, 1945; Beasom & Moore, 1977).

The African wild cat (*Felis silvestris cafra*) is an opportunistic predator and although rodents are the preferred prey, a variety of other prey may be taken, depending on prey availability (Chapter 2). African wild cats are sexually dimorphic, with male cats approximately 31% larger than females (Chapter 2). In carnivores, the limiting resource for females is usually food, while the limiting resource for males is receptive females (Sandell, 1989). Therefore, it may be expected that males and females will partition their time differently, especially as a result of different energetic demands of reproduction and parental care. This has been shown to be the case in the domestic cat (*F. s. catus*) (Turner & Meister, 1988); the black-footed cat (*F. nigripes*) (Sliwa, 2006) and leopards (*P. pardus*) (Bothma & Coertze, 2004).

By shifting the timing of a specific activity period, animals might also influence the costs and benefits of that particular activity (Begg, 2001). If foraging costs change as a function of the time of day of an activity, the predators should distribute their activity periods to maximise the net foraging benefits (Pyke, Pulliam & Charnov, 1977). Prey may exhibit a daily cycle of activity (nocturnal, diurnal and crepuscular) (Zielinski, 1986) and carnivores that are able to anticipate circadian peaks in prey activity can be expected to be more successful at foraging than carnivores that forage randomly (Zielinski, 1986). Numerous studies have shown predators to synchronize their activity with prey activity, for example, in American marten, *Martes martes* (Zielinski *et al*., 1983; Clevenger, 1993); American kestrel, *Falco tinnunculus* (Rijnsdorp, Daan & Dijkstra, 1981); Ethiopean wolf, *Canis simensis* (Sillero-Zubiri & Gotelli, 1995); pangolin, *Manis temminckii* (Swart, Richardson & Ferguson, 1999) and leopard, *P. pardus* (Jenny & Zuberbühler, 2005).

On a seasonal scale, the daily routine of animals and the time spent on different activities may be seen as strategies for coping with changes in the environment, for example changes in prey numbers or habits, variation in temperature, vegetative cover, and activities of predators (Gittleman & Thompson, 1988; Manning & Dawkins, 1995). In a multi-prey system, predators select different kinds of prey according to their availability where availability is a function of both prey abundance and anti-predator behaviour or vulnerability. Prey availability is likely to fluctuate as a result of seasonal changes in abundance, through reproduction or migration, but also through temporal or seasonal changes in behaviour that make prey more vulnerable, for instance during the mating season (Caro & FitzGibbon, 1992). Prey preferences are expected to mirror these fluctuations.

Habitat selection by animals can be described on three different spatial scales (Johnson 1980): (i) the geographic distribution of the species, (ii) the habitat selection within home ranges, and (iii) the habitat choice or preference for the individual (Neu, Byers & Peek, 1974; Dunstone, Durbin, Wyllie, Freer, Jamett, Mazzolli & Rose, 2002). In our study we focussed on the habitat selection within the study site and the individual animal and sexual differences in habitat choice and utilisation. It is widely accepted that habitat preferences and utilisation by predators are predominantly determined by their primary prey abundances (McNab, 1963; Bailey, 1979; Knick, 1990; Morrison, 2001) and climatic conditions as well as the availability of protective cover (Bushkirk, 1984; Johnson & Franklin, 1991; Fernandez & Palomares, 2000; Palomares, 2001). In general, movement patterns between genders differ, with males moving further and at greater rates than females for example, the bobcat, *Lynx rufus* (Bailey, 1974; Chamberlain, Leopold & Conner, 2003); Geoffroy's cat, *Felis geoffroyi* (Johnson & Franklin, 1991) and the African wild cat *F. s. cafra*, (Chapter 4). Therefore, we would expect that in the African wild cat, sexual differences in habitat use will be evident.

The aim of this chapter is to analyse: (i) the foraging behaviour of free-ranging African wild cats in their natural habitat, (ii) their activity patterns, particularly pertaining to changes in prey abundance, seasonal climatic influences and differences between male and female cats and (iii) habitat utilisation in their natural surroundings.

3. Material and Methods

3.1 Study area

The study was conducted in the Kgalagadi Transfrontier Park (KTP) from March 2003 to December 2006 (46 months). The study area was along the southern part of the Nossob riverbed and surrounding dune areas (26°28'17.7"S, 20°36'45.2"E) (Fig. 3.1). The KTP, incorporating the Kalahari Gemsbok National Park (South Africa) and the neighbouring

Gemsbok National Park (Botswana), is a 37,000 km^2 area in the semi arid southern Kalahari system.

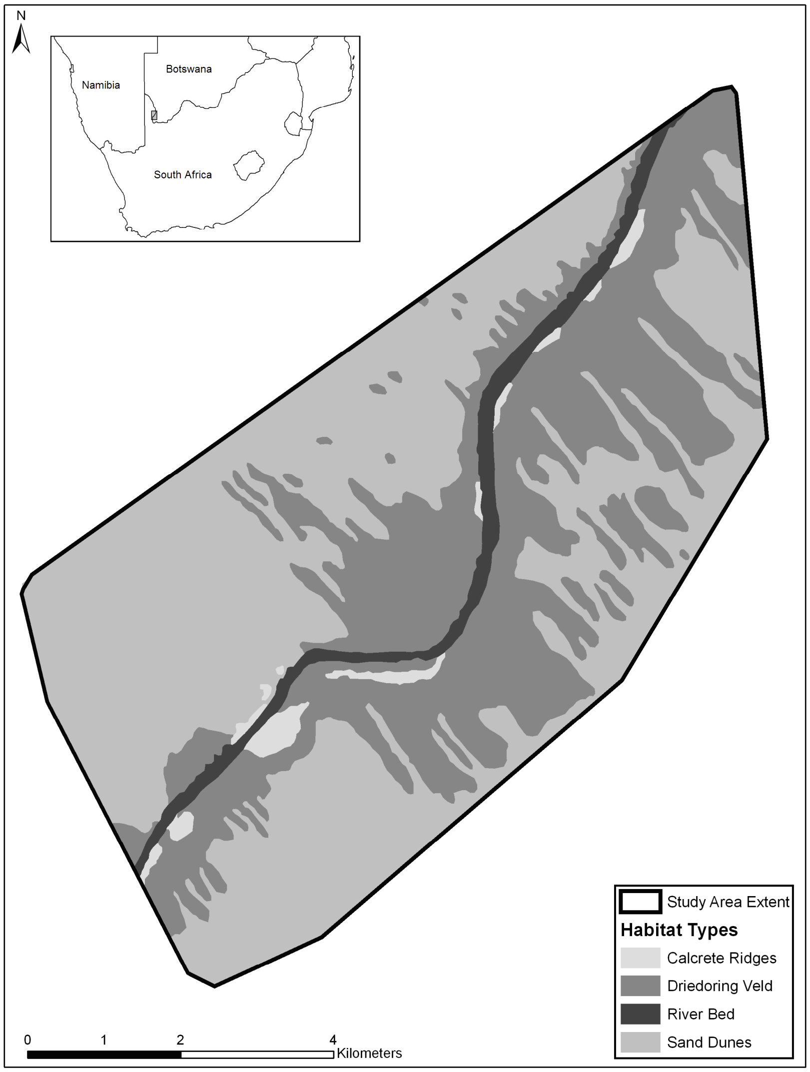


Figure 3.1 Map of the study area in the Kgalagadi Transfrontier Park indicating the different habitat types

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 and described as: (i) the dry riverbeds and immediate riparian surroundings, (ii) the adjacent *Rhigozum* veld, (iii) calcrete ridges and limestone plains and (iv) sandy dune areas (Fig 3.1).

The dry fossil riverbeds are dominated by large camelthorn trees *Acacia erioloba*, smaller *A. haematoxylon*, bushy *A. mellifera*, the scrub *Galenia africana* and perennial grasses. Although the rivers usually contain no surface water and only cover a small percentage of the area, they are very important in the ecosystem. They sustain a diverse animal life in the Kalahari by providing suitable grazing, water and habitat diversity (Van Rooyen, 2001).

Located adjacent to the riverbeds, are thick stands of *Rhigozum trichotomum* and large limestone plains compacted with pink to white sands. These plains are characterised by a scrub savanna cover, it is dominated by dense dwarf scrubs of *Rhigozum trichotomum* (driedoring), *Monechma incanum* (blouganna), *Aptosimum albomarginatum* as well as dominant grass species such as the perennial small bushman grass (*Stipagrostis obtusa*), Kalahari sour grass (*Schmidtia kalihariensis*), tall bushman grass (*Stipagrostis ciliata*) and silky bushman grass (*Stipagrostis uniplumis*), interspersed with scattered camel thorn (*A. erioloba*) trees. The calcrete ridges were sloping slides adjacent the riverbed with rocky stretches into the *Rhigozum* veld.

The dune habitat consists of loose sand and tall perennial grasses, such as, *Stipagrostis amabilis, Eragrostis trichophora,* and *E. lehmanniana.* Dominant scrub species in the dune areas are the dune bush (*Crotalaria spartioides*), lusern bush (*Hermannia tomentosa*) and the gemsbok cucumber (*Acanthosicyos naudinianus*). 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 Bothma & De Graaf (1973) and van Rooyen, van Rensburg, Theron & Bothma (1984).

3.2 Climate and rainfall

The study site is characterised by low, irregular annual rainfall (Mills & Retief, 1984), receiving between 200mm 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). Rodent numbers in the Kalahari fluctuate seasonally, slowly increasing as rainfall increases, followed by rapid declines (Nel, Rautenbach, Els & De Graaf, 1984). These rodent fluctuations are driven by indirect effects of rainfall, primarily on seed production and vegetation cover (Nel *et al*., 1984).

Three seasons are recognized in the KTP: (i) A hot-wet season (HW) from January to April, characterised by mean monthly temperatures equal to or greater than 20ºC and 70% (± 175 mm) of the annual rainfall, (ii) a cold-dry season (CD) from May to August with mean monthly temperatures below 20ºC and little rainfall and (iii) a hot-dry season (HD) from September to December with mean monthly temperatures of approximately 20ºC and about 20% (or ± 50 mm) of annual rainfall (Mills & Retief, 1984).

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 (Fig. 3.2a) 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. 3.2b). The mean maximum temperature for December is estimated at 37.3ºC and the mean minimum for July at 1.4ºC. Monthly rainfall records for the KTP for the period of the study are illustrated in Chapter 1. Field observations commenced in 2003, which was a year with below average rainfall. All subsequent years (2004 – 2006) had average or above average rainfall (see Chapter 1).

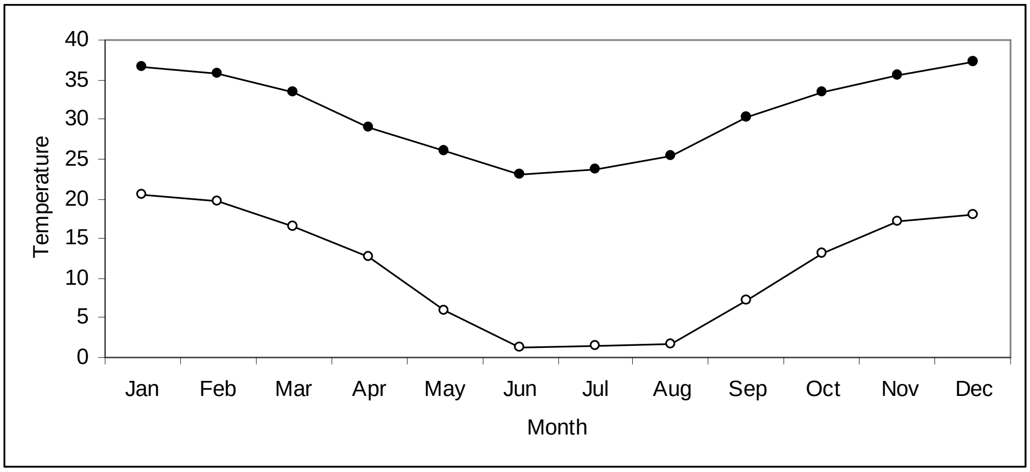


Figure 3.2a Monthly averages of the minimum (○) and maximum (●) temperatures (ºC) at the Twee Rivieren rest camp for the years 2003 to 2006

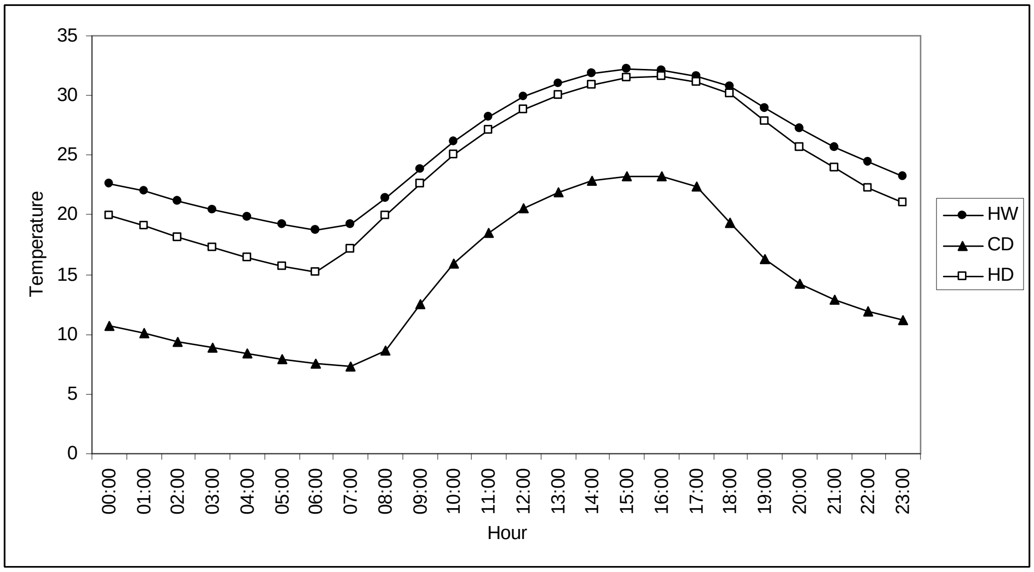


Figure 3.2b Average hourly changes in temperature in the hot-wet (HW), cold-dry (CD) and hot-dry (HD) seasons calculated from the nearest weather station in Upington

3.3 Data collection

3.3.1 African wild cat trapping

African wild cats were either caught in cage traps (eight cats), or by darting (two cats). In total, five male and five female cats were caught and radio collared. Sufficient data from only three females are presented since one female died of predation and the other female disappeared from the study site. The capture methodology is described in more detail in (Appendix 1).

3.3.2 Behavioural observations

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 positively, where prey were blinded by lights and thus easier to catch, or negatively where prey were startled into fleeing, disrupting a stalking approach by a cat. Such effects are difficult to quantify, but our results may show a slight bias, with larger prey being underrepresented.

After an initial habituation period of approximately a week, during which the cats were followed in a vehicle using radio telemetry at a distance of 50 to 100m, visual contact was gradually established until the cats could be followed at 10 – 30m depending on visibility without any obvious influence on their behaviour. During the course of the study 1,538 hours were spent observing habituated cats (499 hours of diurnal and 1,039 hours of nocturnal observations). Different cats were observed on successive nights on a rotating system and followed for 6.0 ± 3.2 hours of direct observation per observation period (*n* = 382 observation periods). Thick vegetation and long grass sometimes precluded direct visual contact with the cats for short periods.

A 1,000,000 candle power spotlight was used occasionally during night observations, although the light provided by the vehicle was generally sufficient to allow observations and recording of the prey type. When used, the beam of the spotlight was directed slightly behind the cat to avoid illuminating the cat or prey item.

3.4 Definition of terms

A cat was considered to be active when engaged in actions requiring physical action, i.e. not sleeping or resting. All behaviours were divided into five categories (resting, foraging, eating, social and other) and were recorded to the nearest minute. These activities are described as follows:

3.4.1 ***Resting***: Resting or sleeping or out of sight, inactive.

The cat lying on its side with head resting on body, or head up with eyes closed or out of sight in thick vegetation or a hole in the ground without emitting a sound or sign of movement.

3.4.2 ***Foraging***: Moving stealthily through its territory while watching and listening for signs of prey activity, or obviously waiting in ambush (Sunquist & Sunquist, 2002).

(i) Searching/travelling: Actively looking for prey, walking fast or slowly winding around with frequent investigation of holes and scent trails.

(ii) Sitting: Sitting down and scanning its surroundings for movement.

(iii) Stalking: A stealthy approach of a visible prey item, generally with its body close to the ground.

3.4.3 ***Eating***: Obviously chewing or ingesting a food item or actively engaged in subduing a prey item.

3.4.4 ***Social activities***: Intraspecific activities and scent marking.

(i) Intraspecific interactions: any activity where two adult African wild cats responded to each other's actions directly or staring over a distance. This includes male-male, male-female and female-female interactions and may be hostile or friendly.

(ii) Scent marking: Specific behaviour associated with depositing scent marks on objects in the environment. This includes rubbing of face and cheek on objects, urinating and defecation.

3.4.5 ***Other activities***: Grooming, playing, rolling in sand, predator avoidance and interspecific interactions.

(i) Grooming: Periods spent licking and cleaning fur. Grooming events of less than one minute were not included.

(ii) Playing: Actively playing and hitting a prey item, throwing it into the air but not eating the prey item.

(iii) Rolling in sand: Rolling in sand several times before standing up, shaking the sand off and continuing.

(iv) Predator avoidance: When a cat hides in thick vegetation or runs away from a potential dangerous situation or approaching predator.

(v) Interspecific interactions: any interaction between cats and other small predators such as, black-backed jackals (*Canis mesomelas*), Cape foxes (*Vulpes vulpes*) and small spotted genet (*Genetta genetta*).

A *hunting attempt* is defined as one or all of the following events: moving towards a prey item either with increased speed and attentiveness or at a slow, stealthy stalk; and the settling of the back feet and pouncing or chasing of a prey item. A hunting attempt may be either successful or unsuccessful.

3.5 Data analysis

Unequal periods spent observing different cats were standardised by converting each activity type to a percentage time spent on that activity per hour and deriving mutually comparable activity schedules from this. Appendix 3 shows the overall amount of time spent observing habituated African wild cats for each hour of the day in each season. The average time of sunset and sunrise for each season was calculated from a GPS location (Leeudril waterhole) in the centre of the study area and activities were denoted as nocturnal and diurnal depending whether they took place after or before sunset, respectively. A Spearman rank (r_s) correlation was used to assess if the time an activity started or ended correlated with the time of sunset or sunrise. Throughout the analyses differences between sexes were evaluated and where no differences were found (significance set at $P \leq 0.05$) data for the sexes were pooled.

For the analysis of time budgets and active periods only data from observation periods lasting at least eight continuous hours or more were used (female: n = 54 observation periods and male: n = 53 observation periods). The time spent engaged in each category (minutes) is represented as a proportion of the cumulative observation period. The total number of minutes active ($\log_{10}$) were normally distributed but the variances were not homogenous. Thus, to compare differences in seasonal activity for both sexes a general linear factorial ANOVA was used (Zar, 1999) and analysed statistically with two sided t-tests (here time spent (minutes) were used instead of proportions) (Statistica 7.1 StatSoft, Inc. 2006). The means were back transformed for presentation (Zar, 1999). The difference in habitat utilisation between male and female cats was tested with a general linear analysis of covariance (Zar 1999). The time spent in the different habitats (minutes) were normally distributed (Statistica 7.1 StatSoft, Inc. 2006).

A 2.5m resolution satellite SPOT5 image (from CSIR, 2005 series) was used to map the vegetation boundaries and features of the terrain. Habitat patches were categorised and areas (m^2) calculated on the satellite image, which was digitised on-screen with ArcGIS 9.0, projection WGS84 (ESRI software). Non-parametric tests (Kruskal Wallis test and Mann Whitney U-test) were used to test seasonal and sexual differences in hunting behaviour (Siegel, 1956). Consumption rate was determined as the total biomass consumed per night in grams, expressed as the total distance travelled that night to allow comparisons with other studies.

4. Results

4.1.1 Feeding and foraging behaviour

Results on the diet and feeding habits of African wild cats are described in Chapter 2. During the 1,538 hours of direct observation of eight African wild cats (three females and five males), 3,676 hunting attempts on prey ranging from invertebrates to mammals were recorded, of which 2,553 (80%) were successful. In all, 2,050 hunting attempts by female cats were recorded of which 87% were successful, while 1,123 were recorded for males of which 69% were successful (Table 3.1). After a successful hunt the prey was either consumed on the spot or carried away into cover and then eaten. The remains of larger prey such as hares were cached and returned to later.

Table 3.1 Number of hunting attempts, the number and percentage of successful hunting attempts on prey species from direct observations of five male (657 hours) and three female (881 hours) African wild cats and the percentage successful hunting attempts pooled for both sexes in the KTP

	Male			Female			Pooled
Prey category	Number of attempts	Number successful	%	Number of attempts	Number successful	%	%
Rodents	961	661	69	790	612	77	72
Inverts	53	45	85	742	689	93	92
Reptiles	54	53	98	487	456	94	95
Birds	40	12	30	30	19	63	63
Large mammals	15	5	33	1	1	100	38
Total	1123	776	69	2050	1777	87	80

4.1.2 Descriptions of hunting behaviour

African wild cats are solitary hunters and on no occasion were two adult cats observed to hunt cooperatively. Their most important senses in finding food appeared to be first visually, followed by auditory and then olfactory cues. Individuals frequently stopped a winding foraging walk to visually investigate, or sniff, at rodent holes and then either continued the walk or lay in ambush. Although the cats often closed their eyes during such periods, they remained alert to their surroundings, with their heads up and their ears constantly moving. Of 344 observations of cats lying in front of holes, 27% resulted in successful kills, 9% in unsuccessful hunting attempts and for 64% no kill attempts were made.

Upon detection of prey, African wild cats crouched down and approached with a low stalking run, while appearing to use every available piece of cover to move forward to within striking distance. They darted forward (when ± 2m from the prey) and struck prey with their paws and delivered an immediate bite to the nape of the neck.

Rodents

A total of 69% of all recorded hunting attempts by male and female African wild cats were on rodents, with a 72% success rate (Table 3.1). Rodents were killed quickly with a swift head or neck bite after a stalk, followed by a rush (89.5% of all kills), or by waiting in front of a hole for up to 30 minutes (10% of all kills). Cats were observed to hunt opportunistically when they were resting and would rush over when rodents venture too close to the resting cat (0.5%). Rodents were eaten whole within 10 seconds to three minutes, depending on size. The heads were eaten first and tails swallowed at the end. Larger rodents were sometimes eviscerated, the stomach and intestines not being eaten. In <1% of all rodent prey the entrails and stomach were buried: females in the presence of kittens always buried the remains. Females with dependant kittens (2 – 3 months old) had a 78% success rate in catching prey, of which 54% of their kills were carried to the kittens (number of kills *n* = 168).

Damaraland mole-rats (*Fukomys damarensis*) were caught on three occasions. Mole-rats seldom venture above ground and are easy prey when they do, having poor vision and responding to perceived threats by remaining stationary and making threatening displays with their large incisors (Bennett & Faulkes, 2000). Mole-rats were simply picked up and eaten from the tail end forwards, leaving the heads with large incisors behind. This is in contrast with the feeding behaviour on other rodents and probably due to the incisors of mole-rats being too large to digest.

Invertebrates

Invertebrates were primarily consumed when rodent numbers were low and consisted of lace wings (Neuroptera), locusts (Orthoptera), moths (Lepidoptera) and scorpions (Scorpionidae) (see Chapter 2). Insects were caught by being pinned to the ground or removed from grass stalks with paws and then grabbed with the mouth. On three occasions a large scarab beetle (Coleoptera) was encountered and left after some handling. The beetles were not killed but investigated, sniffed and picked up and then left behind. Scorpions (*n* = 5) were caught by repeated paw strikes alternated with jumping retreats until they could be pinned to the ground. Our data might indicate that females were catching more invertebrates than male cats, however, with the onset of the study in 2003 when rodent numbers were low, only female cats were radio collared and observed.

Reptiles

African wild cats had a 95% success rate in catching reptiles. Reptiles were spotted when they moved, cats rushed at them and smaller reptiles like barking geckos, *Ptenopus garrulous* (*n* = 488) were simply picked up and consumed whole. Larger geckos and agamas (ground gecko, *Chondrodactylus angulifer* (*n* = 34), ground agama, *Agama aculeate* (*n* = 13) and Kalahari tree skink, *Mabuya occidentalis* (*n* = 5)) were chased, pinned to the ground and then eaten alive. Sand snakes (*Psammophis* sp.) (*n* = 5) were chased and grabbed in the middle of the body and bitten in two. Snakes were consumed whole, although they were regurgitated on two occasions. On one of these occasions, the cat returned after 20 minutes and continued eating the remains. Most of the reptiles were caught in the warmer seasons when reptiles are known to be more active (see Chapter 2).

Birds

Female cats had a 63% (*n* = 30) success rate when catching birds while male cats had a 30% (*n* = 40) success rate. Birds were caught either when they were flushed out by the approaching cat or stalked when sitting on the ground. This excludes the observations on one individual female specialising in hunting birds at a man-made reservoir during a period of low rodent numbers. From 41 daily sightings at the waterhole she was observed actively hunting on 21 occasions and catching 45 birds during this period, with a 40% success rate. Once rodent numbers increased she was recorded hunting only twice at the waterhole, with one successful and one unsuccessful attempt. In all cases hunting was a combination of waiting in ambush at potentially profitable spots by the reservoir and then pouncing. Birds were normally knocked to the ground while perching or when taking off. On three occasions Namaqua sandgrouse (*Pterocles namaqua*) were caught in mid air while descending to water. Birds would be pinned directly to the ground with the front paws and killed by biting. Smaller birds were always consumed whole. Larger birds such as Namaqua sandgrouse and doves (*Streptopelia capicola* and *Oena capensis*), were plucked first and then eaten.

Large mammals

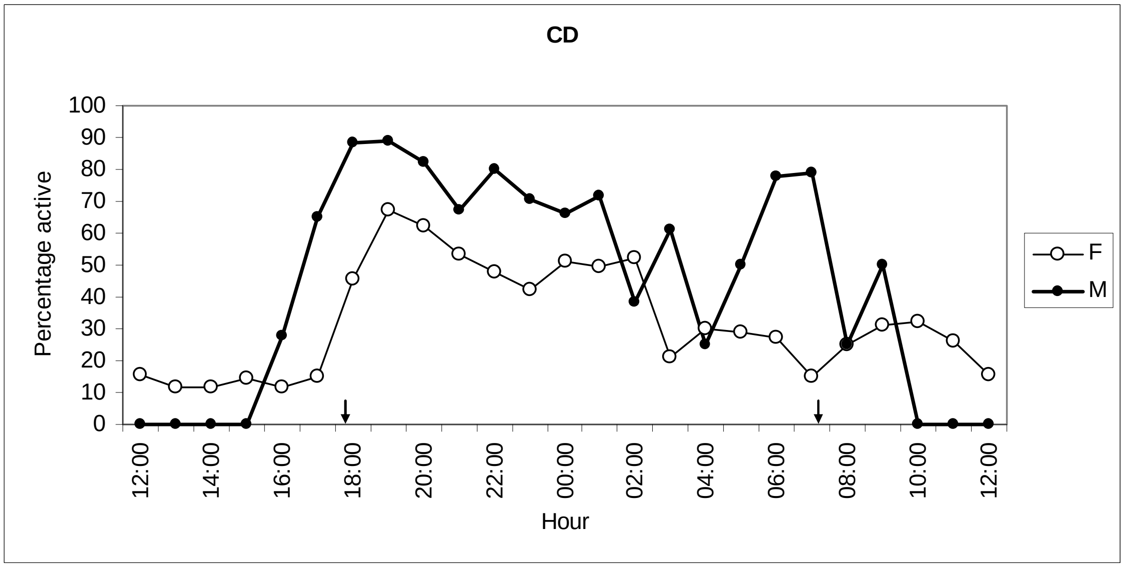
The hunting technique for large mammals comprised typical feline behaviour with stalking, chasing over a distance (± 30m), jumping on prey and killing it with a single bite to the neck (Sunquist & Sunquist, 2002). On one occasion the hare was vigorously shaken until dead. Female cats rarely hunted larger mammals (500 – 2000g, see Chapter 2) with only one successful attempt on a hare (*Lepus* sp.) being observed. Male African wild cats made 15 hunting attempts and had a 33% success rate. Unsuccessful attempts were characterised by the prey outrunning the cat and in one case the springhare fled into a hole. The cat lay in front of the hole for 45 minutes before leaving. Two kills were stolen by black-backed jackal within minutes after being caught. It seems males are able to catch larger prey than females, which tended to prefer smaller rodents. After killing a larger mammal, the female remained inactive for the rest of the night, sleeping and grooming while the male cats tended to consume their prey, stash the remains and then continued with foraging and spray marking activity. The male cats did not return to the prey during the observation periods, however, it is possible that they returned after the researchers left.

4.2.1 Activity periods and distances travelled

Both male and female African wild cats showed a bigeminus (two peak, Aschoff, 1966) activity pattern, with females having a smaller morning peak (Fig. 3.3). During the hot seasons the daily activity peaks were significantly correlated with the time of sunset, however the time activities ended were not correlated with the time of sunrise (Table 3.2).

Male cats were significantly more active than females at night during each season (cold-dry: $t = -3.7$, $P < 0.05$, observation periods: ♂ = 52, ♀ = 106; hot-dry: $t = 3.7$, $P < 0.05$, observation periods: ♂ = 58, ♀ = 91; hot-wet: $t = 3.0$, $P < 0.05$, observation periods: ♂ = 27, ♀ = 48) (Fig. 3.3). There were no differences in activity between seasons for male and female African wild cats (Factorial ANOVA: $F_{2,138} = 0.2$, d.f. = 2, $P = 0.8$). However, during the cold-dry season cats were active for longer periods in the mornings as well as earlier in the afternoons (Fig. 3.3a). The period of elevated nocturnal activity was more protracted during the hot-wet season, lacking the gradual tapering off evident in the dry seasons (Fig. 3.3c). This was coupled to virtually complete inactivity during daylight hours in both sexes (Fig. 3.3c).

a).



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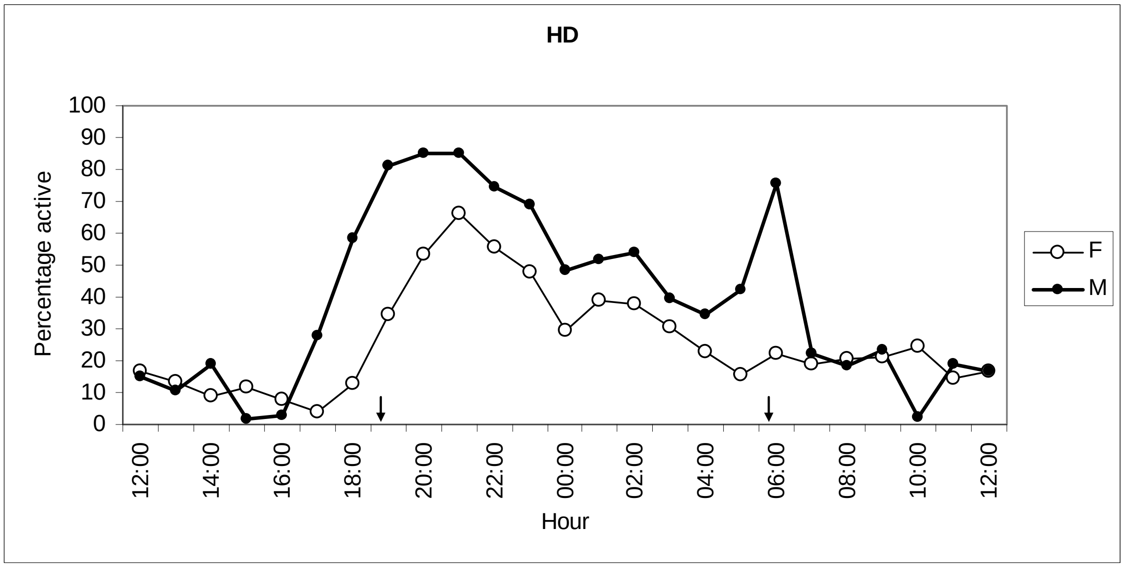

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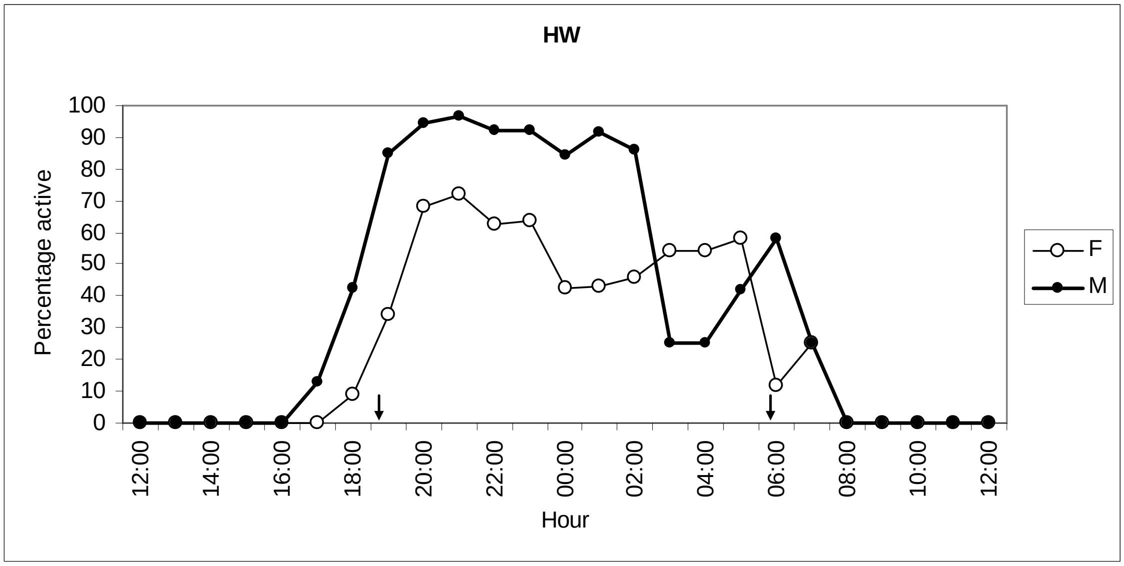

Figure 3.3 Daily activity schedules of male and female African wild cats in the (a) cold-dry, (b) hot-dry and (c) hot-wet seasons. Data were calculated as the mean percentage of observation time that individual African wild cats were active for each hour of the day. The two arrows indicate sunrise and sunset for midpoints of the season

Table 3.2 Seasonal changes in the average time that an activity period begins and end for African wild cats and the correlation (r_s) with sunset and sunrise in the KTP

Season	Average time sunset	Average time begin (*n*)	r_s	*P*	Average time sunrise	Average time end (*n*)	r_s	*P*
Hot-dry	18:48	18:40 (52)	0.65	$P < 0.05$	05:58	07:02 (16)	0.23	NS
Cold-dry	18:01	18:06 (56)	0.27	NS	07:15	10:15 (25)	0.22	NS
Hot-wet	19:00	19:28 (35)	0.37	$P < 0.05$	06:26	07:10 (20)	0.23	NS

Male African wild cats (1.2 ± 0.9 km/h) travelled significantly longer distances than females (0.4 ± 0.2 km/h) during an eight hour or more observation period (Mann-Whitney U-test: Z = 6.94; $P < 0.0001$, observation period: ♂ = 42, ♀ = 49). The percentage activity of both sexes, as well as the distances travelled by male and female cats, where they were observed for eight hours or more, is presented in Fig. 3.4. The increase in distances travelled in the early morning hours of female cats can be explained by the increased diurnal activity during 2003 when female cats continued to forage late in the mornings. Only female cats were followed in 2003 and we suggest that this increase in activity is due to low food availability during the lean period (Chapter 2) and not a difference between sexes.

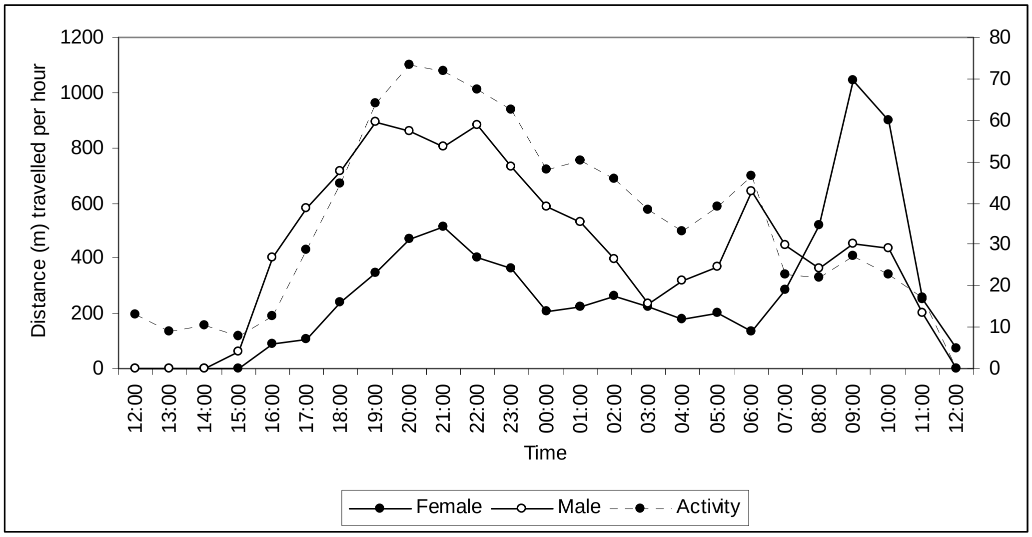

Figure 3.4 The distance travelled (m) and the percentage active per each hour of observation for male and female African wild cats during the study in the KTP. Observation periods = 8 hours or more (males: n = 42 observation periods; females: n = 49 observation periods)

The activity pattern of a female, the only wild cat radio collared during the lean period (cold-dry 2003 to hot-wet 2004) showed a marked difference from the activity patterns observed during the rest of the study when rodent numbers were abundant (cold-dry 2004 to hot-wet 2006). During the former period she actively hunted at a waterhole late in the mornings and afternoons (Fig. 3.5). With the subsequent increase in rodent numbers her behaviour changed. She became more active during the nocturnal hours and switched her diet from hunting birds to rodents (Chapter 2).

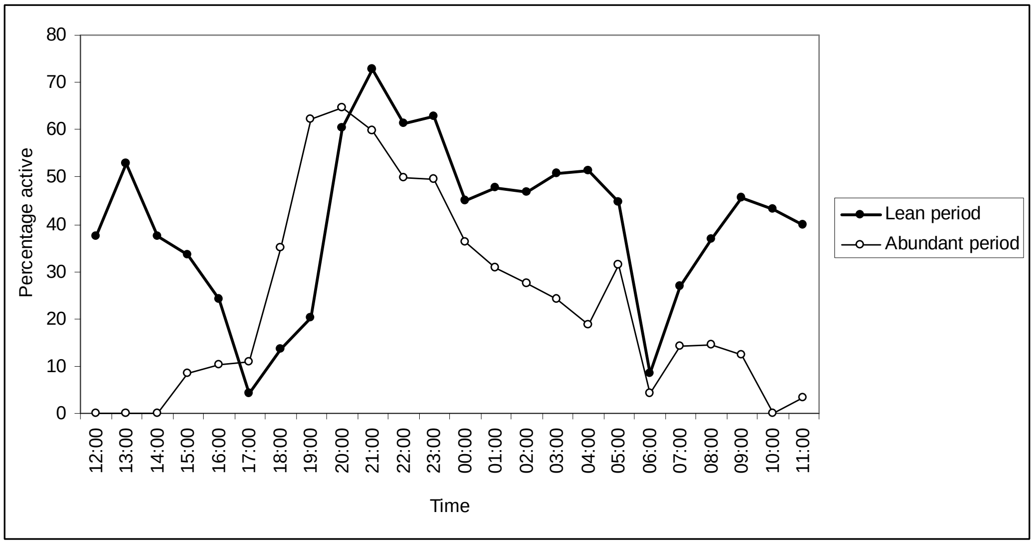

Figure 3.5 Percentage activity of a single African wild cat female over a twenty four hour period, indicating the change from the lean period (●) (cold-dry 2003 to hot-wet 2004) in comparison to the abundant period (○) (cold-dry 2004 to hot-wet 2006)

4.2.2 Time budgets

There were no significant differences in the percentage of time that male and female African wild cats spent on different activities during the first eight hours of observations (t-test: *t* = -0.49, *P* = 0.67, observation periods: ♂ = 53, ♀ = 54) (Table 3.3). African wild cats spent most of their time foraging (68%) and resting (26%), with little time spent on social activities (3%) (Fig. 3.6). However, resting time is underrepresented as our observations were biased towards the time of day that cats were most likely to be active and do not cover the twenty four hour daily cycle.

Table 3.3 A comparison of activities during the first eight hours of an activity period of male (*n* = 53) and female (*n* = 54) cats expressed as the proportion and percentages of each activity

Activity	Male		Female		*t-test*
	Proportion	Percentage	Proportion	Percentage	
Foraging activities		*71*		*65*	NS
Foraging	36.42	69	32.50	60	
Eating	0.98	2	0.63	1	
Sitting	0.21	<1	2.18	4	
Resting activities		*24*		*28*	NS
Resting	8.52	16	11.91	22	
Lying	4.16	8	3.10	6	
Social	*1.52*	*3*	*2.09*	*4*	NS
Other activities		*2*		*3*	NS
Other	0.27	<1	0.08	<1	
Groom	0.99	<1	1.51	3	

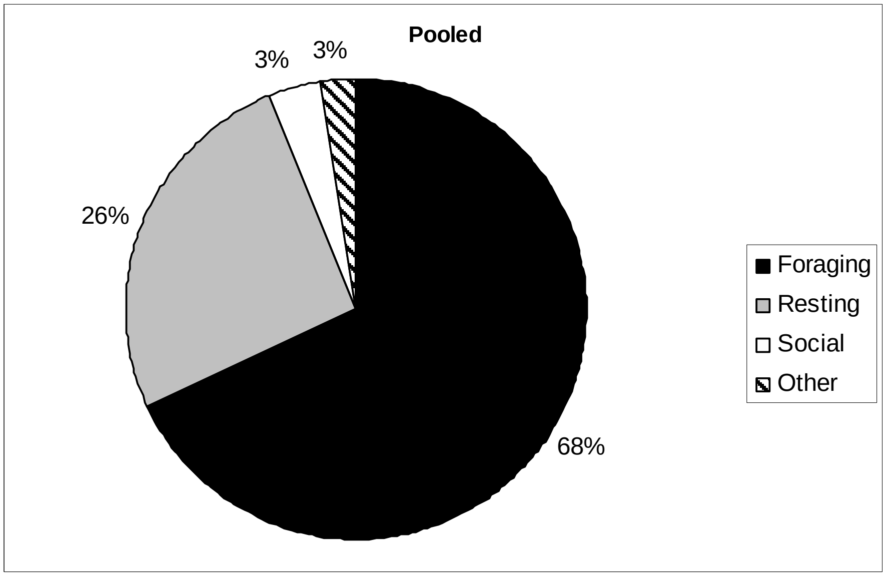

Figure 3.6 Overall time budget of African wild cats calculated from the first continuous eight hours of an observation period of habituated individuals (♂ = 53 observation periods, ♀ = 54 observation periods) in the KTP

4.2.3 Consumption rate

Male and female African wild cats show no significant seasonal differences in consumption rate (g/km) (General linear model: F = 1.65, d.f. = 2, *P* = 0.20) and there is no significant difference between seasonal consumption rates (g/km) (Kruskal Wallis: $H_{2,39}$ = 2.3, *P* = 0.32) when male and female data were pooled (Table 3.4). On average male African wild cats consumed more food than females (male = 473 ± 389 g, female = 339 ± 320 g) (Mann-Whitney U-test: Z = 2.10; *P* < 0.05), however, in biomass eaten per kilometre moved, females consumed significantly more than males (male = 85. ± 146.4 g/km, female = 127 ± 120.1 g/km) (Mann-Whitney U-test: Z = 3.15, *P* < 0.01).

The consumption rate of lactating females was 152.0 ± 79.0 g/km (observation periods: *n* = 5), an increase of 19.6% compared to when they foraged alone. Occasionally cats played with prey items by hitting them with their paws, chasing or throwing them into the air until they escaped or died, in which case the prey was not eaten. Male cats played with prey on 39 occasions after consuming an average of 8.6 ± 6.1 prey items (observation periods: *n* = 12) and females played with prey on six occasions after consuming an average of 6.5 ± 3.8 prey items (observation periods: *n* = 6).

Table 3.4 The average seasonal consumption rate of male and female African wild cats from continuous 8+ hours of observation periods (*n*) and expressed as the mean ± SD biomass of food eaten per kilometre and the average ± SD distances travelled during the observation periods

Season	Observation periods (*n*)	Consumption (g/km)	Distance travelled (km)
Hot-dry	43	130.3 ± 177.0	4.2 ± 2.5
Hot-wet	20	107.8 ± 105.6	4.8 ± 4.2
Cold-dry	30	75.8 ± 48.4	6.5 ± 3.4
All seasons	93	107.9 ± 133.8	5.1 ± 3.4

4.3 Habitat utilisation

The study area comprised of 61% sand dunes, 37% *Rhigozum* veld, 1.8% calcrete ridges and 0.2% riverbed habitat (Fig. 3.1). There was no correlation between the time spent in each habitat and the availability of the habitat in the study site (r = 0.9 p = 0.1) (Fig. 3.7), although the riverbed was utilised far more by both sexes than would be expected given its availability. Male and female cats showed different habitat preferences: males spent more time in the dunes (63%) than in the *Rhigozum* veld (19%), while females show the opposite, spending more time in the *Rhigozum* veld (53%) than in the sand dunes (26%) (General linear model: $F_{3,24} = 7.8$ $P = 0.0008$) (Fig. 3.7).

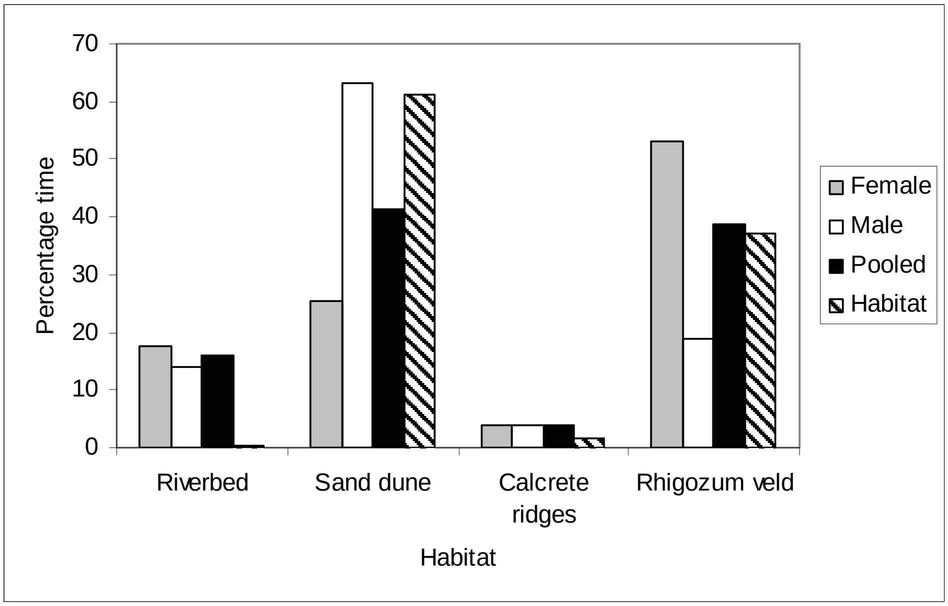

Figure 3.7 The percentage time that males, females and both sexes combined spent active in the different habitats in the KTP. The percentage that each habitat comprised in the study site is included

Data from rodent trapping for food availability analysis (Chapter 2) showed that 43% of all rodents were trapped in the sand dunes, 34% in the *Rhigozum* veld, 17% in the riverbed and 6% on the calcrete ridges. The cats caught most of the rodents in the sand dunes (51%) or the *Rhigozum* veld (42%) (Table 3.5). There was a significant difference between the observed frequencies of rodents caught and the expected availability of rodents in each habitat ($\chi^2 = 14.15$, d.f. = 3, $P < 0.01$). African wild cats caught significantly less rodents in the riverbed than expected. The observed time spent in each habitat differ significantly from the expected frequency of rodents caught in the habitats ($\chi^2 = 16.18$, d.f. = 3, $P < 0.001$). There was no significant difference between the availability of rodents in each habitat and the time spent in those habitats ($\chi^2 = 6.16$, d.f. = 3, P = NS).

Table 3.5 The percentage prey caught in the different habitats by habituated male and female African wild cats in the KTP (observation periods: ♂ = 137, ♀ = 155)

	Male				Female			
Prey item	Riverbed	Sand dune	Calcrete ridges	*Rhigozum* veld	Riverbed	Sand dune	Calcrete ridges	*Rhigozum* veld
Inverts	3	83	3	10	2	28	0	69
Birds	0	83	17	0	80	3	17	0
Reptiles	0	80	2	18	9	27	1	63
Rodents	3	69	2	26	9	27	1	63
Total	3	70	2	25	6	30	1	64

Cats caught most of the reptiles in the *Rhigozum* veld (57%) and in the sand dunes (42%). However, 37% of all reptiles surveyed were trapped in the dunes, 27% in the *Rhigozum* veld, and 18% on both the calcrete ridges and in the riverbed (Chapter 2). There were significant differences in the observed frequencies of reptiles caught and the availability of reptiles in each of the habitats ($\chi^2 = 68.05$, d.f. = 3, *P* < 0.001). Invertebrates were mostly caught in the *Rhigozum* veld (66%) and sand dune habitat (31%). The large percentage of birds caught in the riverbed (66%) may be biased, and can be ascribed to the female who specialised at catching birds at a man made waterhole and reservoir. Birds were also caught on the calcrete ridges (17%) or in the sand dunes (17%) (Fig. 3.8).

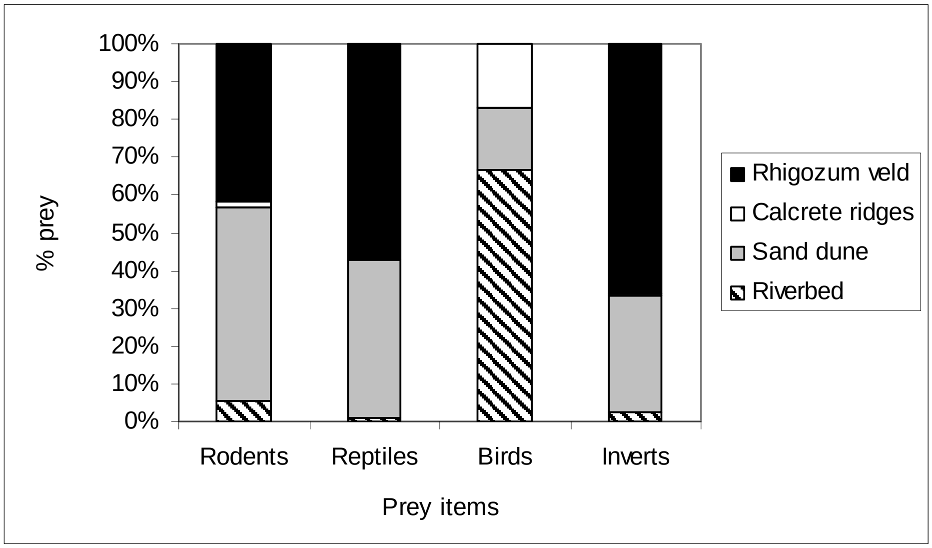

Figure 3.8 The percentage of prey caught in each of the habitats for male and female African wild cats (data pooled)

4.4 Social and other behaviours

Very little social behaviour by both sexes was observed, except for the short periods (2 – 4 months) that females cared for kittens or during the brief mating periods when males trailed receptive females (1 – 2 days). In all cases where females increased urine spray marking kittens were born within 3 months. Therefore we argue that urine spray marking in females was related to their reproductive status. Male cats marked more regularly with an average of 13.6 ± 23.5 sprays per kilometre moved (Chapter 4).

Extensive grooming was usually observed before (15.6 ± 11.4 minutes) and after (20.4 ± 12.9 minutes) a nightly activity period. Shorter grooming periods of less than one minute between hunting activities were often seen. Grooming bouts lasted between 1 – 40 minutes. Rolling in sand was observed in both sexes. Leyhausen (1979) describes rolling as a sexual behaviour in females as they came into oestrus as well as during the courting period. We observed both male and female cats rolling to and fro with snakelike twists (see description in Leyhausen 1979) followed by continued foraging.

5. Discussion

Feeding and foraging behaviour

Like most cats (Sunquist & Sunquist, 2002), the African wild cat is a solitary hunter and no cooperative hunting between adults was observed. The species has an extensive geographic range (Nowell & Jackson, 1996) and is able to live and hunt in a wide variety of habitats (Sunquist & Sunquist, 2002). Throughout its range it requires cover for hunting and resting sites, from rocks to scrubby undergrowth, holes in the ground and thick vegetation (Sunquist & Sunquist, 2002). The most important senses in finding food appear to be mostly visual and auditory followed by olfactory cues. Although it is an excellent tree climber it mostly hunts on the ground. Its hunting techniques are typical feline; moving slowly and quietly, watching and listening for signs of prey activity and investigating scent trails. Like most other cats it also sits and waits in ambush (Sunquist & Sunquist, 2002) before a surprise attack on its prey. The African wild cat is highly adaptable and although it prefers rodents, it is capable of hunting a wide range of prey species (Chapter 2; Sarmento, 1996; Moleón & Gil-Sanchez, 2003; Malo, Lozano, Huertas & Virgós, 2004). Playing with a prey item was often seen, especially after a few successful hunting attempts.

Activity periods

The effect of human interference on the behaviour of the wild cats in our study is thought to be minimal as the cats were completely habituated to the research vehicle and the study site was far from the activities of tourist camps. The African wild cat is considered to be strictly nocturnal (Smithers, 1983), however our results clearly showed that a decrease in rodent densities and availability lead to increased hunting during late mornings and early afternoons, as well as opportunistic hunts during the middle of the day on rodents close to their resting sites. However temperature also has an influence and the cats showed a seasonal shift from predominantly nocturnal activity in the hot seasons to increased diurnal activity in the cold seasons. Therefore, the African wild cat shows an activity pattern that could describe it as predominantly nocturnal, however, depending on food availability and temperature the species also shows crepuscular characteristics. Both male and female cats showed an increase in activity during the early evenings and again in the early mornings. Two peak activity patterns are common in many carnivores (Aschoff 1966) for example, the Cape fox, *Vulpes vulpes* (Smithers, 1983), spotted hyaena, *Crocuta crocuta* (Kruuk, 1972), honey badger, *Mellivora capensis* (Begg, 2001), ocelot, *Leopardus pardalis* (Weller & Bennett, 2001) and leopard, *Panthera pardus* (Jenny & Zuberbühler, 2005).

The time of emergence from resting sites was significantly correlated with the time of sunset during the hot seasons, however, the time an activity ended was not correlated with the time of sunrise. It is probable that physiological state (such as hunger), ambient temperature, rain and wind (sand storms) are the important variables determining activity. In addition predators may synchronize their foraging behaviour with the activity of their main prey (Schuh, Tietze & Schmidt, 1971; Curio, 1976; Armitage *et al*., 1996) and for the African wild cat seasonal food availability and daily prey activity might also play a role in determining their activity patterns.

Foraging theory predicts that predators should distribute their activity patterns to maximize the net foraging benefits (Pyke *et al.,* 1977). This theory is supported by bat-eared fox foraging behaviour on termites (Nel, 1990) and the seasonal prey preferences in the pine marten (Zielinski *et al.,* 1983). Our results support a shift in activity patterns in relation to increases or decreases of prey numbers. This is illustrated by the behaviour of a female cat at a water hole that specialised in hunting diurnal birds during a lean period in 2003. Birds may become an important food resource for cats when mammalian prey numbers are low (Fitzgerald & Veitch, 1985; Kirkpatrick & Rauzon, 1986), and individual cats may also become particularly skilled at hunting birds (Molsher, 1999). With the increase in rodent numbers, this female changed her foraging behaviour and diet accordingly and became more nocturnal. Samson & Raymond (1995) hypothesized that when prey are active they could easily be detected by predators and foraging time can be minimized if the predator hunts during prey activity bouts. On a seasonal basis the lower numbers of reptiles caught in the cold dry season when reptiles are inactive with an increase in the warmer months suggest that this is the case (Chapter 2). Zielinski (1988) reported that small carnivores can be sensitive to within day variation in foraging costs, however that is not the only criteria that influence seasonal foraging patterns in predators. It is thus unlikely in the African wild cat that prey activity is the only driving force in their activity patterns.

A decrease in activity in the middle of the day in the hot seasons as well as a decreased activity from midnight and early mornings suggest that temperature might also be an important factor in the activity schedule of the African wild cat. This is expected given the temperature extremes in the southern Kalahari. African wild cats appear to avoid extreme day time temperatures by sleeping and resting in thick vegetation and consequently shift their active periods to strict nocturnal hours in the hot seasons and include more diurnal hours in the cold seasons in order to satisfy their energy requirements. This has also been described in other small carnivores, i.e. the honey badger (Begg, 2001) and the black-backed jackal, *Canis mesomelas* (Ferguson, Galpin & De Wet, 1988). Although one would expect that night time activity would decrease in the cold seasons due to the cold temperatures there were no significant seasonal differences in activity. However there was a clear decrease in the distances travelled in the early cold mornings (around 02:00) since cats moved more slowly in the cold (Fig. 3.5).

There were no significant differences between time budgets of male and female cats during the first eight hours of observations. Foraging was the most important activity and since African wild cats are solitary, little time would be expected to be devoted to socialising. For females the time available for foraging is likely to be critical to meet the high energy demands when they are pregnant, lactating and raising their young. Males would be expected to forage for longer periods than females since they are significantly larger than females (Chapter 2), also they need to patrol and advertise their presence in their territory. However, increased cost of reproduction in females and rearing kittens on their own may increase their energetic demand to similar levels of that of male cats. Indeed, female consumption rate (g/km) is higher than male cats indicating that the raising of young is more energetically costly for females than the covering of long distances and marking of territories by male African wild cats.

Habitat utilisation

Male and female wild cats show different habitat preferences, with males mostly using the dune habitat and females the *Rhigozum* veld. The use of specific habitats is associated with the availability of the key prey resources, for example as shown in studies on the kodkod, *Oncifelis guigna*, (Dunstone *et al*., 2002) and their preference for rodents in specific habitat types (Fernandez, Evans & Dunstone, 1994, 1996; Fernandez, Dunstone & Evans, 1999).

Like many small felids, rodents are the major prey resource for African wild cats (Chapter 2). Our study clearly showed that the habitats where the cats spent most of their time are the habitats where they catch most of their prey. Seasonal prey surveys confirmed that rodents had high densities in the sand dune and *Rhigozum* veld habitats.

The difference in habitat preferences between male and female cats suggest that females use denser habitats (*Rhigozum* veld) when active, especially when they have kittens. Male cats cover larger areas and longer distances and therefore spend more time in the sand dunes since the dune area covers a large part of the study site. Thus our results confirm that during active periods cats prefer habitats with high prey abundances and that resting sites might be chosen for their vegetation cover and shelter. Sexual differences in habitat use are well recorded in felid literature (Sandell, 1989; Broomhall, Mills & Du Toit, 2003; Chamberlain *et al*., 2003).

In conclusion the African wild cat is a successful predator with a hunting style typical of a solitary felid. They are able to change their foraging behaviour according to seasonal prey availability, density and environmental conditions. It is mainly nocturnal but exhibits some crepuscular and diurnal activity when needed. Although sexual dimorphism is evident (Chapter 2), male and female wild cats show little differences in time budgets, however, male cats travel over longer distances and have a higher consumption rate than females. Habitat utilisation between sexes differs and habitat preferences appear to be based on suitable shelter and cover, as well as prey abundances in these habitats.

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CHAPTER 4

Aspects of the social organisation of the African wild cat, *Felis silvestris* in the southern Kalahari: Factors affecting home range size and movement patterns, and a basic description of scent marking behaviour and reproductive biology

1. Abstract

Eight African wild cats, *Felis silvestris* (three female and five male) were radio collared from 2003 to 2006 (46 months) in the Kgalagadi Transfrontier Park. Minimum convex polygon (95% MCP) estimates show male cats had larger annual home ranges (7.7 ± 3.5 km^2) than female cats (3.5 ± 1.0 km^2). No differences were detected in seasonal home ranges. Female home ranges overlapped extensively, whereas male home ranges indicated smaller overlap with exclusive core areas, but extensive overlap with the ranges of several females. Male cats travelled significantly further than female cats during an observation period. Male cats scent marked frequently to mark their home ranges, while female spray marking appeared to be related to their reproductive status. The cats displayed an aseasonal breeding strategy related to food abundance.

Key words: African wild cat, *Felis silvestris*, home range, overlap, scent marking, reproduction

2. Introduction

Spatial organisation in a population is the result of conspecifics distributing themselves in a manner which maximises individual survival and reproductive success (Sandell, 1989). Spacing patterns and mating systems are closely interrelated (Clutton-Brock & Harvey, 1987; Sandell, 1989; de Azevedo & Murray, 2007; Schmidt, 2008). Social spacing includes the maintenance of core areas, home ranges and territories (Mares & Lacher, 1987). A home range is defined without reference to defence, advertisement or reaction to intrusion by neighbouring individuals, only the presence of the individual is required (Brown & Orians, 1970; Börger *et al*., 2008). In the contrary, a territory arises when individuals exhibit spatially orientated aggressive behaviour towards competitors and prevents intrusion to the defended area (Brown & Orians, 1970; Maher & Lott, 1995). For most animals, spatial requirements, movement patterns and distribution are mainly influenced by the abundance and distribution of food and other key resources such as reproductive requirements, intra- and interspecific relations and habitat requirements (Macdonald, 1983; Litvaitis, Clark & Hunt, 1986; Sandell, 1989; Ranta, Lundberg & Kaitala, 2006).

With the exception of the African lion, *Panthera leo* (Schaller, 1972) and cheetah, *Acinonyx jubatus* (Caro & Collins, 1987), all wild felids are solitary hunters. However, studies on feral domestic cats, *Felis silvestris catus*, show variation in their use of space (Liberg & Sandell, 1988), from strict territoriality (Davies & Houston, 1984) and active defence of borders (Leyhausen, 1965; Liberg, 1980, 1984; Langham & Porter, 1991), to limited mutual tolerance (Apps, 1986). Females might be either solitary or group living and may or may not tolerate dominant males in their territories (Liberg & Sandell, 1988). The African wild cat, *F. s. cafra*, ancestor of the domestic cat, has been described as a solitary hunter (Smithers, 1983; Chapter 3), however, there is a paucity of information about its spatial requirements, movement patterns and reproductive biology.

The general explanations and mechanisms of animal home range behaviour is still lacking and research is split into three areas of investigation: (i) the movement models based on random walks, (ii) individual home range models based on optimal foraging theory, and (iii) a statistically modelling approach (see review by Börger, Dalziel & Fryxell, 2008). However, the distribution and abundance of food resources are among the most important factors influencing animal distribution,spatial requirements, movement patterns (Macdonald, 1983; Ranta *et al*. 2006) and prey densities (Hayward, O'Brien & Kerley, 2007). Animals may use different strategies in exploiting available resources to satisfy their survival or reproductive requirements, but the quality and quantity of resources should chiefly determine their home ranges (Mitchell & Powell, 2004).

Animals may select home range sizes to meet their metabolic requirements over a critical biological time period (Lindstedt, Miller & Buskirk, 1986). Several studies on carnivores have investigated the relationship between home range sizes and different functions of body weight. These studies have postulated that body weight differences, and specifically metabolic differences, account for much of the difference between male and female home range size (McNab, 1963; Harestad & Bunnell, 1979; Gittleman & Harvey, 1982; Lindstedt *et al*., 1986; Litvaitis *et al*., 1986; Swihart, Slade & Bergstorm, 1988; Jetz, Carbone, Fulford & Brown, 2004; Ferguson, Currit & Weckerly, 2009). In the African wild cat, males are 31% larger than females (Chapter 2), and based purely on the above, it is expected that males will have larger home ranges than females.

Metabolic differences between sexes may only be relevant during specific periods. In solitary carnivores, female spatial organisation is generally determined by the abundance and distribution of food resources and habitat quality, but male spatial organisation, at least during the breeding season, may be determined instead by the distribution and availability of receptive females (Erlinge & Sandell, 1986; Sandell, 1989; Johnson, Macdonald & Dickman, 2000).

Furthermore, theory predicts that home range size should increase with decrease in quantity and density of food resources, showing a seasonal, possibly cyclical contraction and expansion (Mitchell & Powell, 2004; Herfindal, Linnell, Odden, Nilsen & Andersen, 2005). In carnivores, spatial dispersion patterns of prey animals may affect foraging patterns and hence, home range (Andersson, 1981; Stephens & Krebs, 1986; Brandt & Lambin 2007). However, studies on carnivores provide inconsistent results on the relationship between home range size, prey abundance and density. A negative relationship between home range size and prey availability was found in the European lynx, *L. lynx* (Herfindal *et al*., 2005), wolves, *Canis lupus* (Fuller, 2003; Jedrzejewski, Schmidt, Theuerkauf, Jedrzejewska & Kowalczyk, 2007) and bobcats, *L. rufus* (Litvaitis *et al*., 1986), while no relationship was found in puma, *Puma concolor* (Logan & Sweanor, 2001) and Iberian lynx, *L. pardinus* (Palomares, Delibes, Revilla, Calzada & Fedriani, 2001).

If the key resource is predictable in space and time and is concentrated within a restricted area it can be defended and therefore development of territorial behaviour and aggression is favoured (Brown & Orians, 1970; Hixon, 1980; Lindzey, van Sickle, Ackerman, Barnhurst, Hemker & Laing, 1994; Pierce, Bleich & Bowyer, 1999; Adams, 2001). A system of overlapping ranges is possible when the availability and spatial distribution of resources vary (Erlinge & Sandell, 1986; Sandell, 1989), resulting in less competition for food (Mech, 1977). The spatial distribution of many felids is related to this, for example the European lynx (Poole, 1995), puma (Pierce, Bleich & Bowyer, 2000) and bobcat (Benson, Chamberlain & Leopold, 2004, 2006).

It is predicted that in the Kalahari, African wild cat female home ranges should be large enough to include sufficient food resources to meet energetic requirements (Goodrich & Buskirk, 1998; Sandell, 1989), and may fluctuate seasonally according to food availability. If available females are the limiting resource for adult male African wild cats, their home ranges should be larger than predicted purely on metabolic requirements (Sandell, 1989). Furthermore, if available females are the limiting resource for adult male African wild cats and since breeding in the southern Kalahari seems to be aseasonal, there should be no seasonal variation in home range size, since receptive females should be available throughout the year (Goodrich & Buskirk, 1998).

With most solitary felids, adults of the same sex exhibit a spatially and temporally dispersed social organisation (Beckoff, Daniels & Gittleman, 1984). However, all felids still posses a rich repertoire of communication signals (Leyhausen, 1965; Seidensticker, Hornocker, Wiles & Messick, 1973). Although information on communication is limited in small cats due to their mostly nocturnal activity patterns, the densely vegetated habitat that many of them inhabit, their wide ranging movement patterns and their extreme wariness to observers (Mellen, 1993; Nowell & Jackson, 1996), it seems that all felids possess very similar behavioural mechanisms and communication patterns (Mellen, 1993). Transmission of information by individuals can be visual, through sound and odour (Gorman & Trowbridge, 1989). Odours are deposited in the environment as scent marks and therefore provide a spatial and historical record of the animal's movement and behaviour patterns (Gorman & Trowbridge, 1989).

The aim of this chapter is to describe the spatial organisation of free-living African wild cats in the southern Kalahari and to investigate factors affecting the home range size and movement patterns of males and females such as dispersion of resources. Specific questions about spatial organisation include: (i) How large is the home ranges of male and female African wild cats in the Kalahari and do they differ between sexes? (ii) What level of overlap exists between neighbouring ranges and is core areas exclusive? (iii) Is there spatial or temporal avoidance among wild cats? We also describe aspects of the reproductive biology of the species and some basic communication and behavioural patterns.

3. Materials and Methods

3.1 Study area

The study was conducted from March 2003 to December 2006 (46 months) in the Kgalagadi Transfrontier Park (KTP). The main study area included the southern part of the Nossob riverbed and surrounding dune areas centred around Leeudril waterhole (26º28'17.7 S, 20º36'45.2 E) (Fig. 4.1). The KTP, shared between South Africa and Botswana, is a 37,000 km^2 area in the semi arid southern Kalahari system. The study area is characterised by low rainfall (between 200 - 250mm annually). Three seasons are recognised, the hot-wet season (January to April) the cold-dry season (May to August) and a hot-dry season (September to December). However, for the purpose of home range analyses two seasons were distinguished, the hot-wet season (September to April) when the majority of the rainfall occurs and a cold-dry season (May to August) characterised by limited rainfall and low temperatures (Begg, Begg, Du Toit & Mills, 2005). The main study area comprised four broad habitat types: (i) the dry riverbed, (ii) the adjacent *Rhigozum* veld, (iii) calcrete ridges, and (iv) the surrounding dune areas. See detailed description of the study area in Chapters 1 and 3.

3.2 Data collection

Details of the capture, radio collaring and habituation techniques on African wild cats are described in (Appendix 1). A total of eight cats (three female and five male) were fitted with radio collars (*African Wildlife Tracking CC*) with a battery life of approximately 18 months. The radio collars were replaced in three cats before the battery life expired, to ensure continuous visual observations. All radio collars were removed at the conclusion of the study. All individuals were weighed, measured and a small skin sample was collected for DNA analyses (Appendix 1, Chapter 5).

Radio collared animals were located by ground based tracking using a two or three element antenna. As soon as the wild cat was sighted the geographic co-ordinates (using a Garmin GPS), time, activity and habitat were recorded. Two types of data were collected: (i) radio-location observations, when only a radio-fix of the animal was recorded; and (ii) continuous observations, when radio collared wild cats were followed by a vehicle for varying periods of 1 – 14 hours (an average of, male: 6.0 ± 3.4 hours and female: 4.7 ± 3.7 hours). A rotation system was followed in order to obtain equal observation records for all cats (Appendix 3). Over the course of the study 1,538 hours were spent with habituated wild cats (females = 881 hours (n = 3) and males = 657 hours (n = 5)). One sub-adult male (VLO1665) became an adult with an established home range and was then included in the calculations for adult cats (Table 4.1). At the start and end of each activity period the GPS position of the individual were noted. The first GPS position was noted when the cat was less than 30m from the vehicle. Since all cats were habituated (Appendix 1), the approaching research vehicle had no influence on their behaviour and they were not disturbed from their resting position. GPS positions were also taken at certain behavioural actions such as spray marking or at 5 minute intervals if the behaviour did not change and distances covered by the cats were determined from these GPS positions.

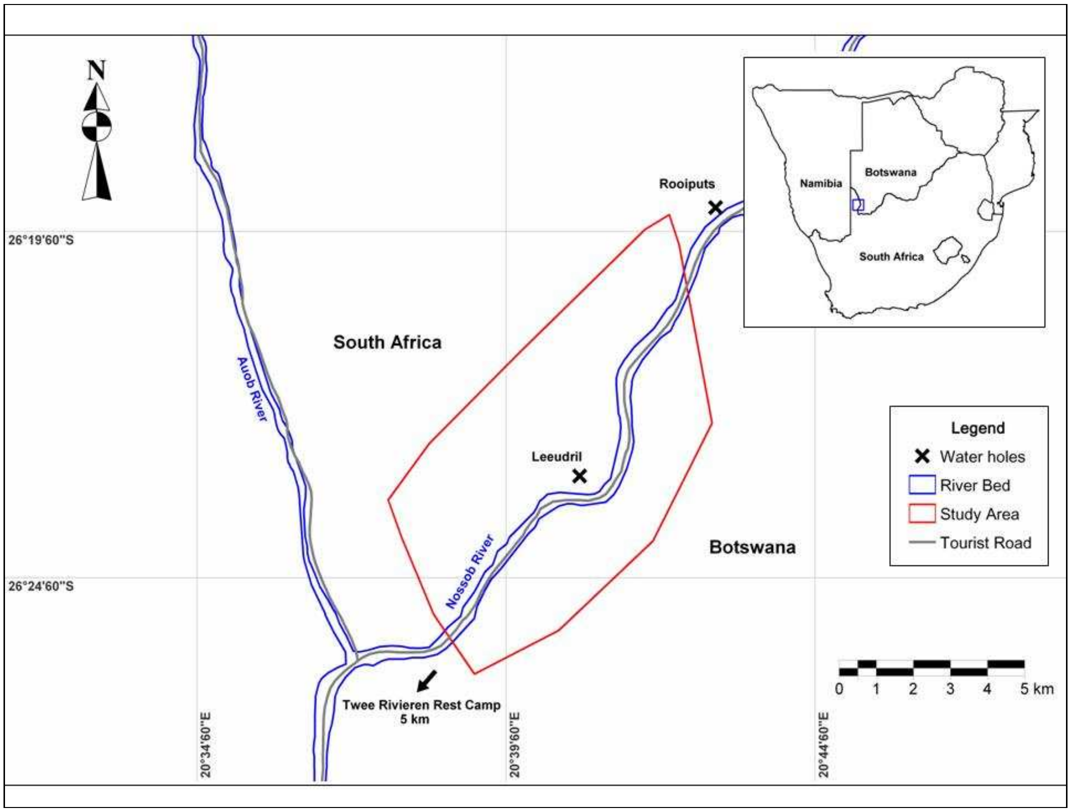

Figure 4.1 Map of the study area in the Kgalagadi Transfrontier Park

Table 4.1 Individual African wild cats (3♀ and 5♂) used for home range analysis showing the seasons that each individual was radio tracked and the number of hours of observations on habituated individuals from March 2003 until December 2005. Black blocks indicate adult cats and grey blocks indicate periods that cats were classified as sub-adult

ID	Sex	2003		2004		2005		2006		Hours
		WET	DRY	WET	DRY	WET	DRY	WET	DRY	
VL01654	♀	■	■	■	■	■	■	■		547.9
VL01656	♀		■	■	■	■	■	■		206.7
VL01658	♀				■	■				72.5
VL01662	♂				■	■	■	■	■	109.1
VL01665	♂						░	■	■	110.8
VL01667	♂							■	■	201
VL01672	♂								■	100.0
VL01673	♂								░	135
Total										1537.9

3.3 Data analysis

Home range area and overlap were determined using the software package *Arcview, Animal Movement* (Hooge & Eichenlaub, 2000). Annual home range sizes were calculated for all eight African wild cats. For home range analyses only data of individuals considered adult resident cats were included. Two of the female cats disappeared during the last season of the study and were excluded for the year 2006 due to insufficient data.

Home ranges were calculated using minimum convex polygons (MCP) (Mohr, 1947) and overlap in home range was determined from 100% MCP estimates. To identify core areas, a 50% Kernel analysis (Worton, 1989) were performed. Minimum convex polygons (MCP) is considered a robust, non-parametric analysis of home-range size where more than 30 independent points are available (Kenward & Hodder, 1996), nonetheless it is sensitive to outliers (Swihart & Slade, 1985a,b; Kenward, 1987; Harris, Cresswell, Forde, Trewhella & Woollard, 1990). Points from continuous observations of habituated individuals are temporally autocorrelated and this may result in an underestimation of home range size (Swihart & Slade, 1985a,b). Since African wild cats do not have a fixed den site but rest in different places each day, the resting positions can be considered biologically independent locations since they are separated by an activity period (Minta, 1992; Creel & Creel, 2002).

There were no significant correlations between the home range size and the number of points collected for male and female cats (Spearman Rank Correlation, male: $r_s = 0.2$, $P =$ NS; female: $r_s = 0.2$, $P =$ NS). For further analysis and comparisons with other studies the annual home ranges from 95% MCP were used.

Non-parametric Mann-Whitney U and Kruskall-Wallis tests (*Statistica 7.1*: Statsoft Inc., 1984-2006) were used to investigate sexual and seasonal differences in home range size and movement patterns. For all home range analyses the individual wild cat was used as the sampling unit. The variation in spatial spray mark patterns were subjected to a nearest neighbour analysis in *Arcview, Animal Movement* (Hooge & Eichenlaub, 2000) and compared to the expected distribution if the locations were randomly distributed and tested by a Chi Square test of statistical significance for bivariate tabular analysis (χ^2) (Siegel, 1956).

4. Results

4.1 Study population

Mean body mass for the three adult females and three adult males when they were radio collared were significantly different at 4.4 ± 0.3 kg and 5.9 ± 0.2 kg respectively (t-test *t-value* = 7.3, d.f. = 4, $P < 0.01$).

4.2 Annual and seasonal home range sizes

The annual home range data are presented in Table 4.2 with the 100% MCP and the 95% MCP estimates. Annual home range estimates (MCP 95%) in adult males ($n = 4$) were 7.7 ± 3.5 km^2 and in adult female cats ($n = 3$) 3.5 ± 1.0 km^2. As predicted the annual home range sizes (95% MCP) of adult male cats were significantly larger than female African wild cats (Mann Whitney U-test, $Z = 2.3$, $P < 0.02$). Adult male African wild cats exhibited annual home ranges of between 1.6 – 2.2 times larger than adult female cats.

Lindstedt *et al*. (1986) suggested that female home ranges are set by their metabolic demands (HR_{female}), therefore male home ranges could be predicted as HR_{female} x M_{male}/M_{female}, where M is defined as average mass. Sandell (1989) used a similar equation to estimate male home ranges (HR_{male}) based on the energy requirements to sustain themselves: $HR_{male} = (HR_{female}) \times (M_{male})^{0.75} / (M_{female})^{0.75}$. The measured annual home ranges (MCP 95%) of male African wild cats were larger (1.6 and 1.8 times) than the predicted home ranges for energy requirements alone using both formulae respectively. However, for females the annual home ranges were 1.6 times smaller than the predicted home ranges.

Seasonal home ranges did not differ significantly in either male (Mann Whitney U-test, $Z = -1.0$, $P = 0.3$) and female cats (Mann Whitney U-test, $Z = -1.3$, $P = 0.2$). The average home ranges for males in the wet season were 4.7 ± 3.0 km^2 and dry season were 7.4 ± 2.6 km^2; for females were: wet season = 3.0 ± 1.7 km^2 and dry season = 4.0 ± 1.1 km^2 (Table 4.2).

4.3 Social organisation and spatial system

An adequate dataset for all three females enabled the calculation of overlapping ranges for females in 2004 (Table 4.3). Individual home ranges varied largely, from 5.7 km^2 to 13 km^2 (average = 9.3 ± 3.7 km^2, $n = 3$ (MCP 100%)). This large variation might be due to low rodent abundances recorded during 2004 (Chapter 2). However, we found no significant differences in home range sizes of 2004 in comparison to the other years. The three females showed an average of 33.4 ± 13.4% overlap (ranges from 20.6% to 47.3%), however, comparing the 50% core area (Kernel analysis), only two females show a slight overlap (Fig. 4.2).

Table 4.2 Mean annual and seasonal home range (km^2) calculations for all African wild cats (AWC) (5♂ and 3♀), showing 100% and 95% Minimum Convex Polygon (MCP) and 50% Kernel analyses. The overall mean and standard deviation (SD) are included

					Annual home ranges			Resting positions		Wet season			Dry season		
AWC ID	Sex	Body mass (kg)	No. of months tracked	No. fixes	100% MCP	95% MCP	Core home range (50% kernel)	No. fixes	100% MCP	No. fixes	100% MCP	95% MCP	No. fixes	100% MCP	95% MCP
VLO1662	♂	6	25	2625	12.31	10.74	0.4	164	10.48	543	8.23	8.04	2082	11.76	10.54
VLO1672	♂	6	6	579	8.67	7.80	0.76	30	7.14	-	-	-	579	5.06	2.79
VLO1667	♂	5.7	12	730	5.45	4.57	0.46	65	4.08	101	2.23	2.17	629	4.72	4.29
VLO1665	♂*	4.2	16	1912	12.71	7.82	1.09	150	10.81	486	11	3.78	1426	9.54	6.96
VLO1673	♂*	4.2	6	111	5.06	2.79	0.16	53	4.21	-	-	-	111	8.67	7.8
VLO1658	♀	4.6	6	516	5.85	4.19	0.24	104	4.37	290	2.38	1.75	226	12.97	3.07
VLO1654	♀	4.5	31	3025	5.23	4.00	0.37	366	3.31	1030	3.23	2.28	1995	4.93	3.77
VLO1656	♀	4	26	1481	7.68	2.4	0.42	187	7.08	377	5.74	4.84	1104	6.14	5.24
Female	Mean	4.37	21	1674	6.25	3.53	0.34	219	10.02	565.67	3.79	2.96	1108.33	8.01	4.03
(n = 3)	SD	0.32	13.23	1265.59	1.27	0.98	0.09	133.9	1.88	404.47	1.74	1.65	884.51	4.34	1.1
Male	Mean	5.48	14.75	1461.5	10.16	7.71	0.68	102.25	10.92	376.67	7.15	4.66	1379	8.67	7.40
(n = 5)	SD	97	7.97	978.19	4.19	3.52	0.32	65.07	7.93	240.43	4.48	3.03	727.64	2.94	2.59

* sub adult cat when caught and body measurements were taken

Table 4.3 Annual Minimum Convex Polygon (MCP) home range areas (km^2) for eight African wild cats (5♂ and 3♀)

ID	Sex	Year	100% MCP	95% MCP	Fixes
VLO1662	♂	2004	17.29	16.38	290
		2005	9.72	7.92	336
		2006	9.92	7.93	1999
VLO1665	♂	2005	10.74	8.18	143
		2006	14.67	7.46	1769
VLO1667	♂	2006	5.45	4.57	730
VLO1672	♂	2006	8.67	7.80	579
VLO1673	♂	2006	5.06	2.79	111
VLO1654	♀	2003	3.54	1.70	547
		2004	5.69	4.86	1188
		2005	8.32	6.00	600
		2006	1.48	1.41	690
VLO1656	♀	2003	4.08	3.57	89
		2004	9.10	7.26	917
		2005	2.52	1.16	423
		2006	0.52	0.47	52
VLO1658	♀	2004	12.97	3.07	226
		2005	2.38	1.73	290

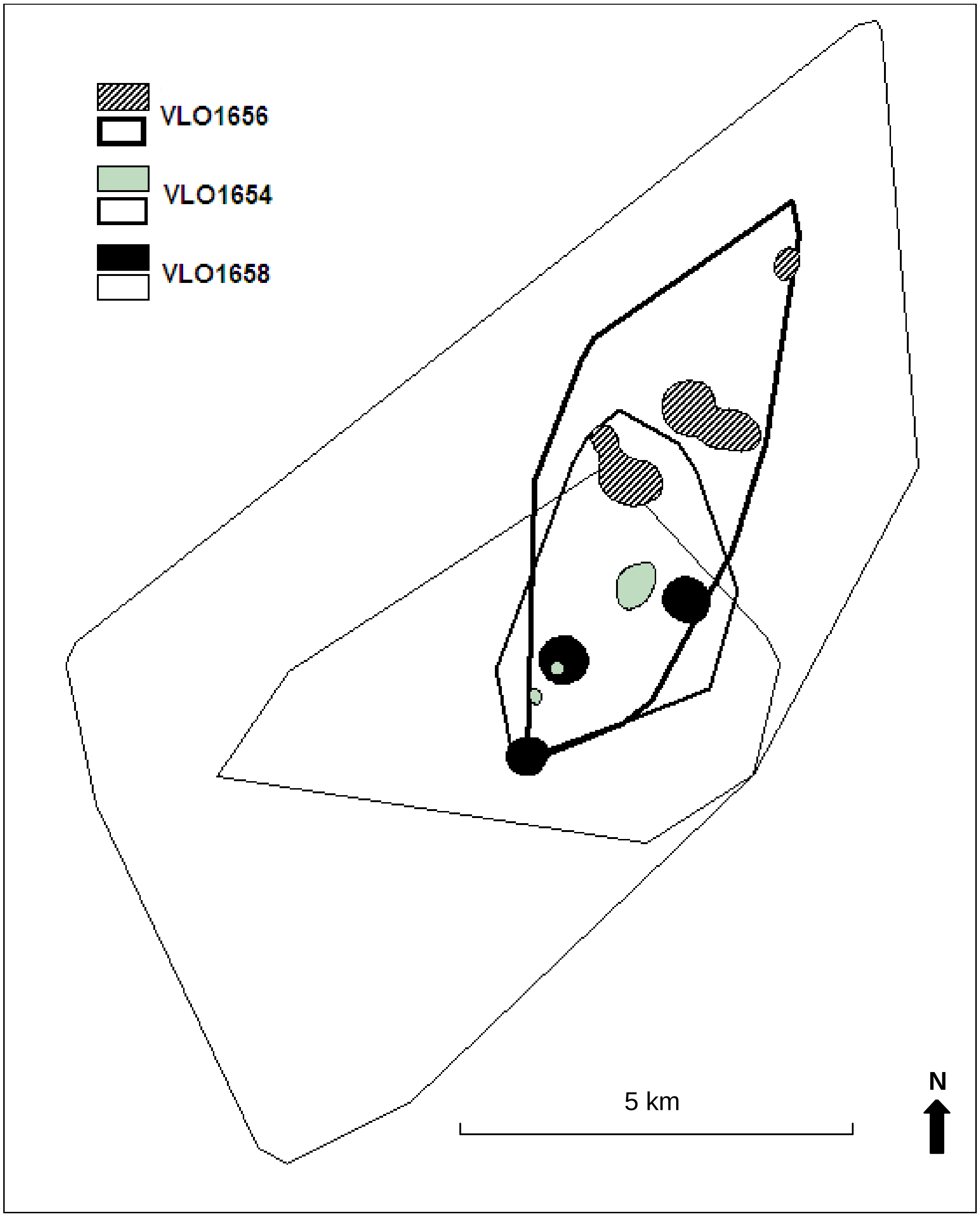

Figure 4.2 Core home range outlines (50% Kernel analyses) and 100% MCPs of three radio collared African wild cat females during 2004 in the Kgalagadi Transfrontier Park. The outline represents the overall study site

Adult male home range overlap was calculated for the year 2006 where home ranges varied from 5.5 to 9.9 km^2 (average = 7.4 ± 2.2 km^2, $n = 4$) Three adult males showed an average of 7.0 ± 6.0% overlap (ranges from 2.0% to 13.7%) and there were no overlap in the 50% core area of a Kernel analysis (Fig. 4.3). The home range of male VLO1672 did not overlap with any other male cats and were excluded in the analysis of home range overlap. The large variation can be explained by the movement patterns of male (VLO1665) that was in the process of establishing his new home range in the year 2006.

Male cat (VLO1665) was a sub-adult cat when caught and moved in a small 2.0 km^2 area where no spray marking activity was evident for the first two months after collaring. Then he started to roam and spray mark over a larger area, including spray marking in the home range of male VLO1662. His movements covered 14.7 km^2 (100% MCP). He became a resident adult male after 5 months with a small annual home range of 5.6 km^2 that did not overlap with his initial area as sub-adult cat, 3.4 km away (straight line measurement from were he was initially caught to the centre of core area of established home range in 2006). The overlap between the roaming cat (VLO1665) and an adult male (VLO1662) decreased from 29.4% to 13.7% when he became resident (Fig. 4.4).

The ranges of resident adult male cats overlapped with up to four different females. The overlapping ranges of three habituated adult females, the location of a den of an uncollared female and two adult males from 2004 to 2005 are presented in Fig. 4.5. During 2004 - 2006 a total of 10 African wild cats were radio collared in the 53 km^2 study area and three non radio collared adult cats were regularly sighted, giving a minimum density estimate of 0.25 cats/km^2.

The patterns of home range use during a single observation period (male: 6.0 ± 3.4 hours and female: 4.7 ± 3.7 hours (range 1 - 14 hours)) are presented in Fig. 4.6 and 4.7 respectively, showing how female cats used a smaller and more concentrated area of their home ranges during an observation period. There was a significant difference between the actual distances moved, measured from GPS recordings, and between the sexes per hour of each observation period (*t*-test: $t = 2.4$, $P = 0.03$) with males: 0.6 ± 0.2 km/h and females: 0.4 ± 0.1 km/h.

4.4 Scent marking behaviour

Females were observed to scent mark in 9.4% of the observation periods of more than 8 hours, either when they had kittens ($n = 5$) or when they were in oestrus, when courting and mating behaviour were observed (*n* = 5). Spraying frequency varied from no spraying to 50 sprays per observation period at a frequency of 3.6 ± 8.7 sprays/km.

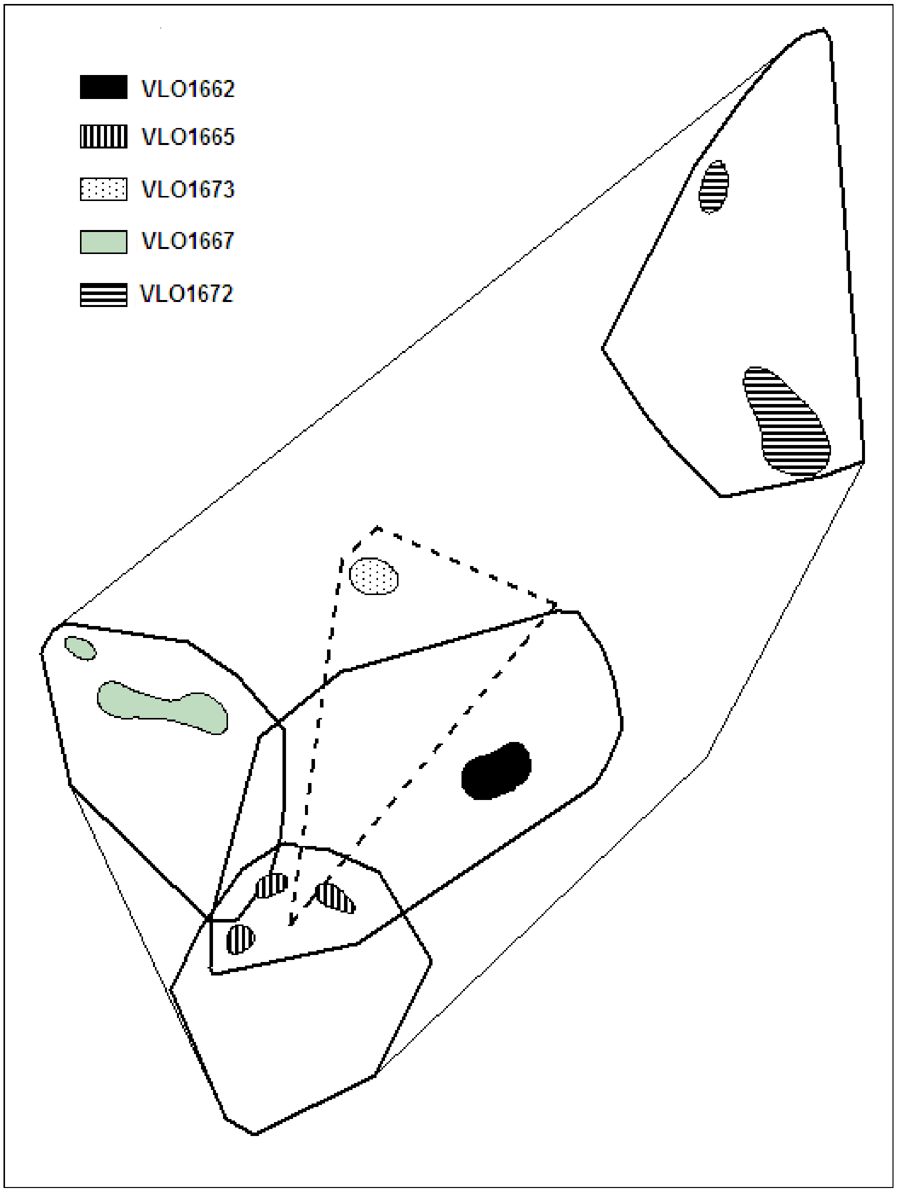

Figure 4.3 Core home range outlines (50% Kernel analyses) and annual 100% MCPs of five radio collared African wild cat males during 2006 in the Kgalagadi Transfrontier Park. The broken line shows the home range of a sub-adult male cat and solid lines represent adult African wild cats. The outline represents the overall study site

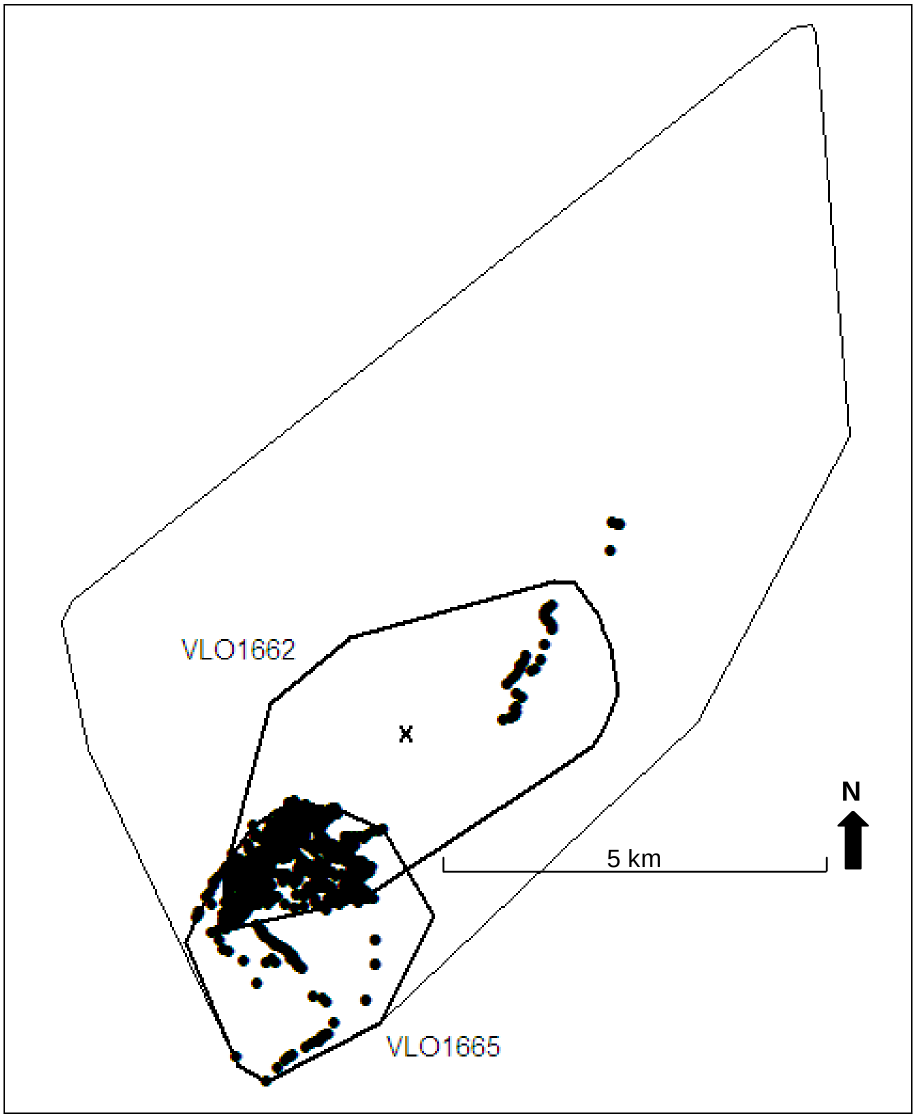

Figure 4.4 Resident home ranges of adult male cats VLO1662 and VLO1665 during 2006. The urine spray marks of VLO1665 as a roaming sub-adult cat from 2005 and 2006 are indicated by (●) and the capture position with a cross (X)

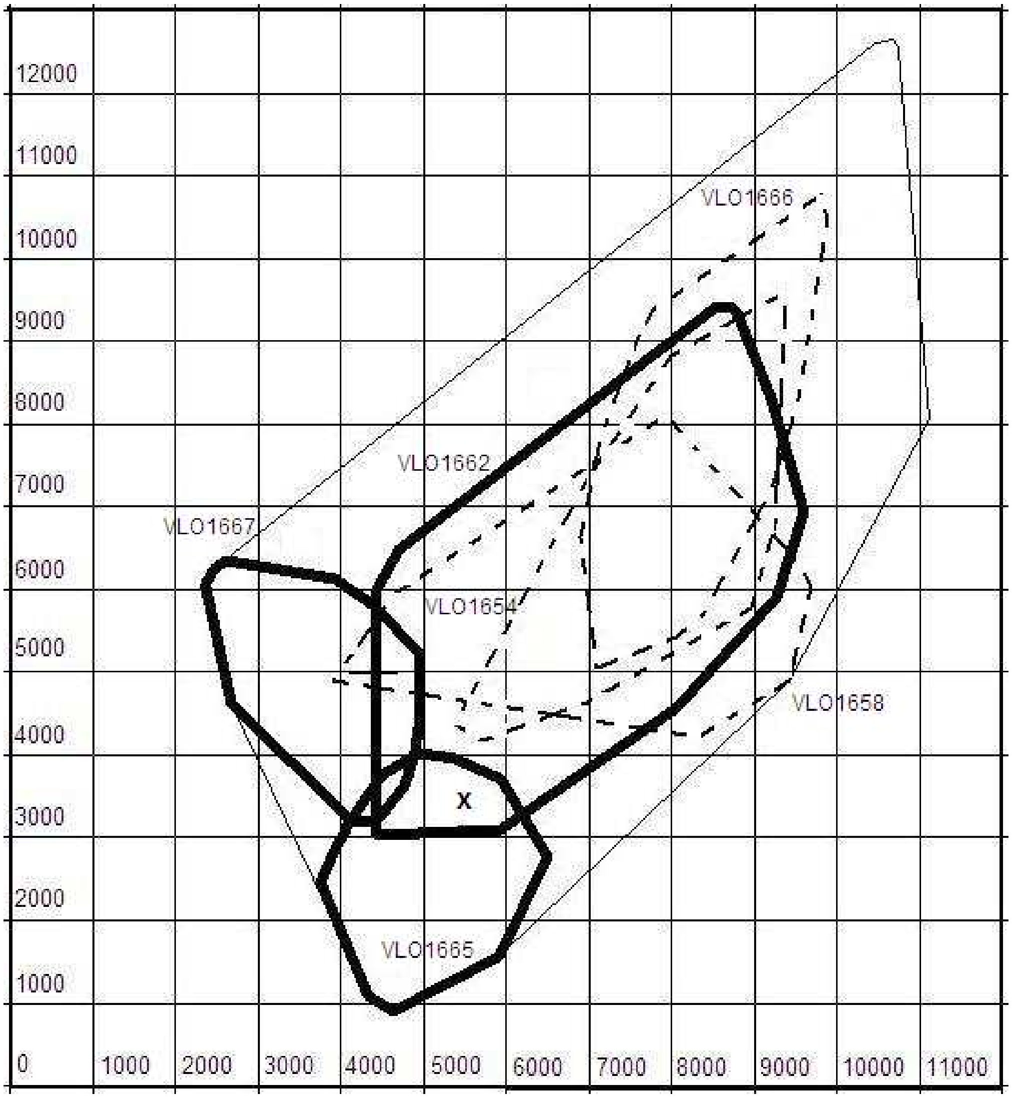

Figure 4.5 100% MCP home ranges calculated for African wild cats tracked during 2004 and 2005 on a 1 km^2 grid. The outline represents the overall study site, with males indicated by the solid lines and females indicated with broken lines. The cross (X) represents the den of an uncollared female in the study site

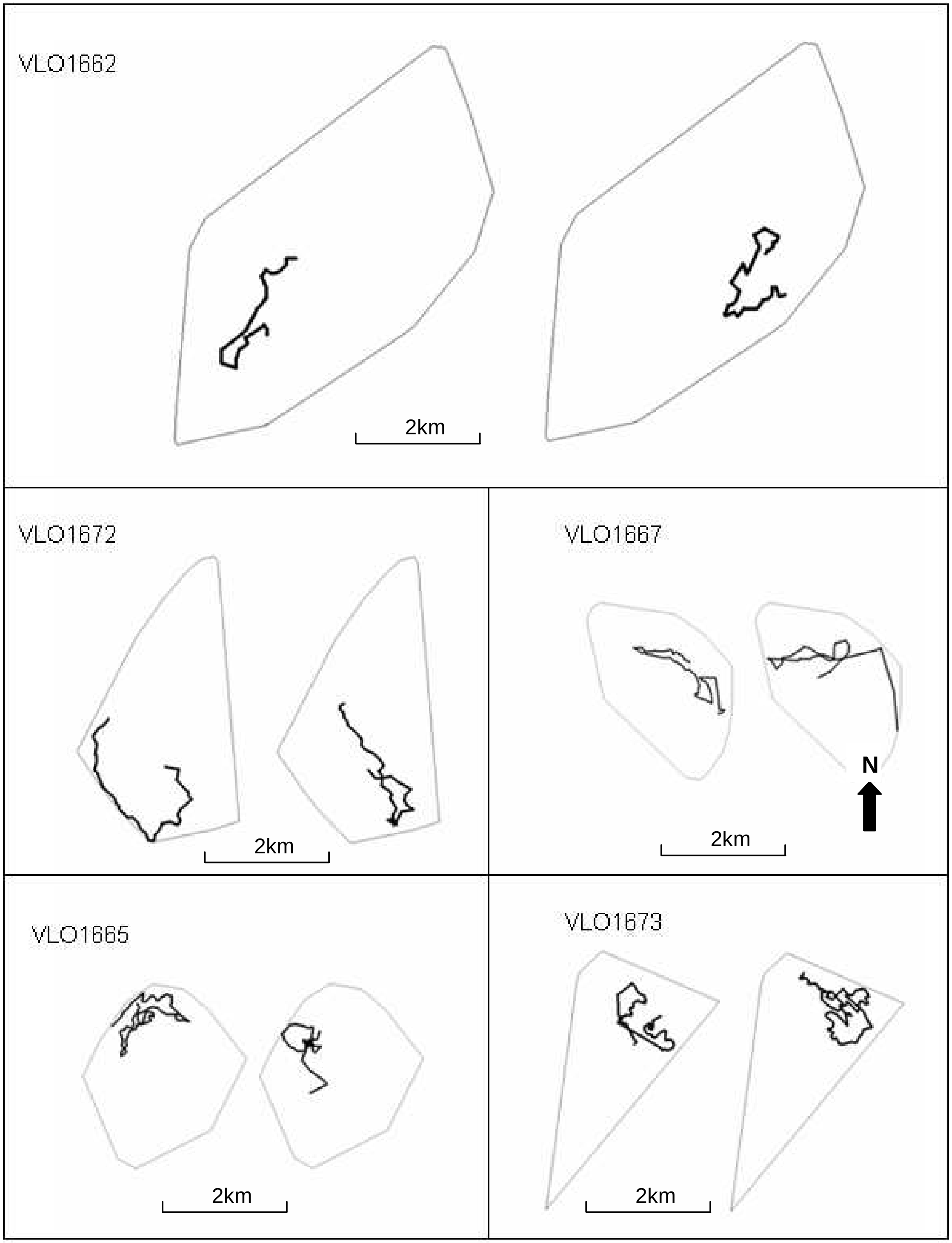

Figure 4.6 Two examples of the daily tracks, of five male African wild cats in relation to their 100% MCP home range boundaries. Tracks were generated from continuous visual observations where GPS points were taken at five minute intervals

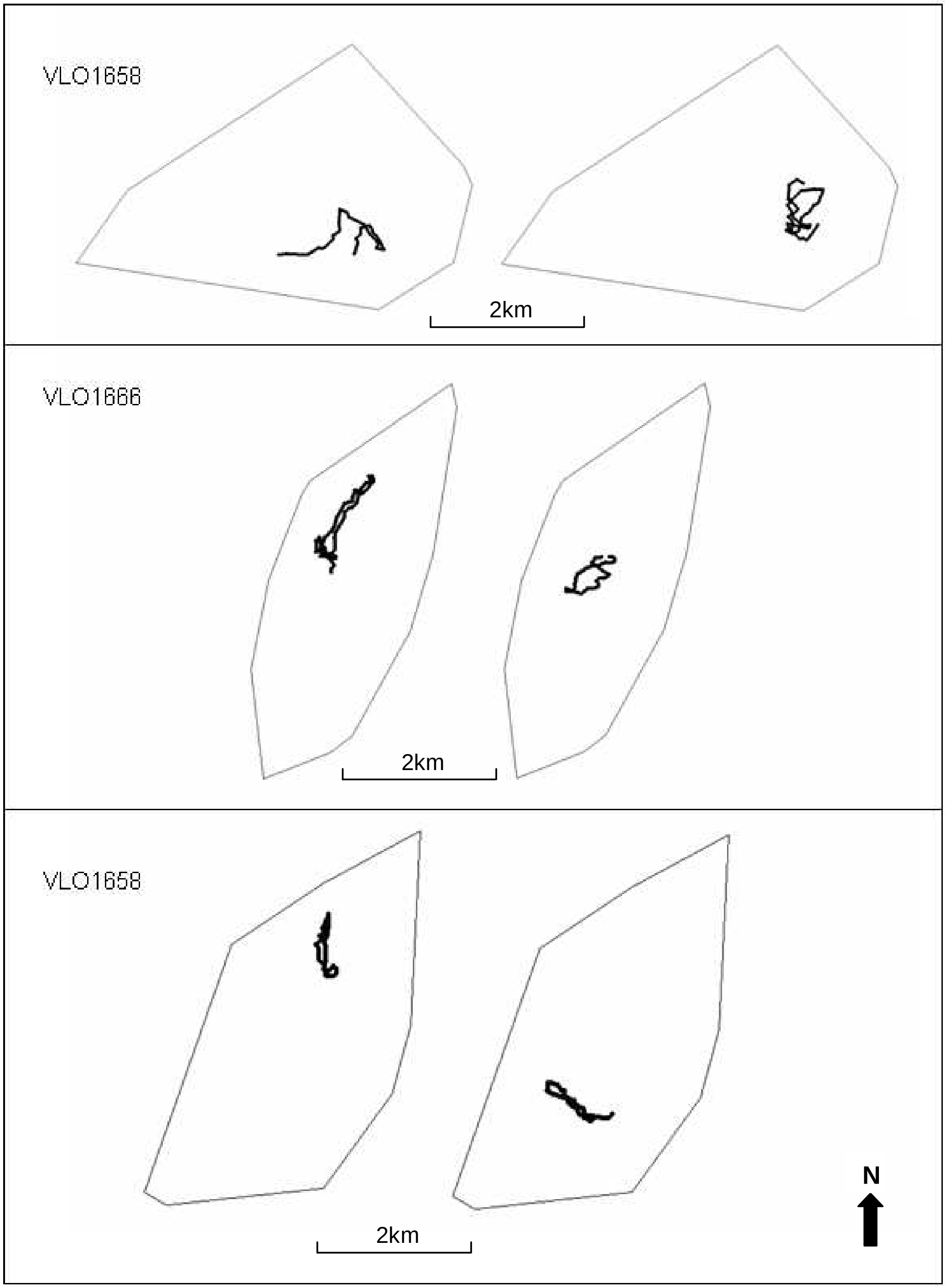

Figure 4.7 Two examples of daily tracks, of three female African wild cats in relation to their 100% MCP home range boundaries. Tracks were generated from continuous visual observations where GPS points were taken at five minute intervals

Cheek rubbing against objects (*n* = 41), claw sharpening (*n* = 25), urine spray marking against objects with raised tail and sometimes quivering of tail (*n* = 2,940) and flehman behaviour after smelling an object (*n* = 17) were all regarded as scent marking behaviour in male cats. They exhibited more spatial and seasonal variation in spray marking than females and spraying ranged from 0 – 193 sprays per observation period of more than 8 hours and an estimated 13.6 ± 23.5 sprays/km travelled. A sub adult male cat increased spray marking activity from no spray markings to 13.9 ± 8.0 sprays/km (range = 1 – 31 sprays/km) over a 5 month period where he became a resident adult cat.

A comparison of the observed and the expected frequencies of spray marking in the core areas of adult African wild cat male cats ($\chi^2 = 35.9$, d.f. = 3, $P < 0.001$) indicate that male cats sprayed to mark their territories and the core areas of their home ranges (Fig. 4.8). A nearest neighbour distance analysis showed that all male spray markings were clumped and not scattered randomly throughout the territories (Table 4.4).

4.5 Breeding system and social interactions in the African wild cat

Overall the rates of intra-specific interactions were very low and African wild cats were mainly solitary except for the short (two to four months) periods when females had kittens or during the brief mating periods, when males trailed receptive females. Table 4.5 gives a description of interactions between cats observed during the study. The most frequently observed encounter entailed African wild cats staring at each other for several minutes from a distance of less than 50m and then walking away without any physical interaction (*n* = 10). Perhaps the most significant observations were the three instances when male cats visited dens with kittens. The males showed no interest in the kittens and seemed more interested in the female cats. Once a female left her kittens (one month old) and followed the male and courting behaviour was observed. It is likely that the male cat was the father of the kittens (Chapter 5) and this would explain the lack of aggressiveness towards the kittens.

No clear seasonality in breeding was evident for African wild cats. Of the 15 litters that were observed during the study 53% were conceived during the hot-dry seasons, 27% during the hot-wet seasons and 20% in the cold-dry seasons. At the beginning of the study (2003) food availability was low and no litters were produced for a 14 month period while observing two radio collared females (Fig. 4.9). However, after an increase in rodent numbers these females produced up to four litters each in a 12 month period (Fig. 4.9). An average of 2.6 ± 1.6 (range 1 – 5) kittens per litter was born and remained with the mother for two to four months.

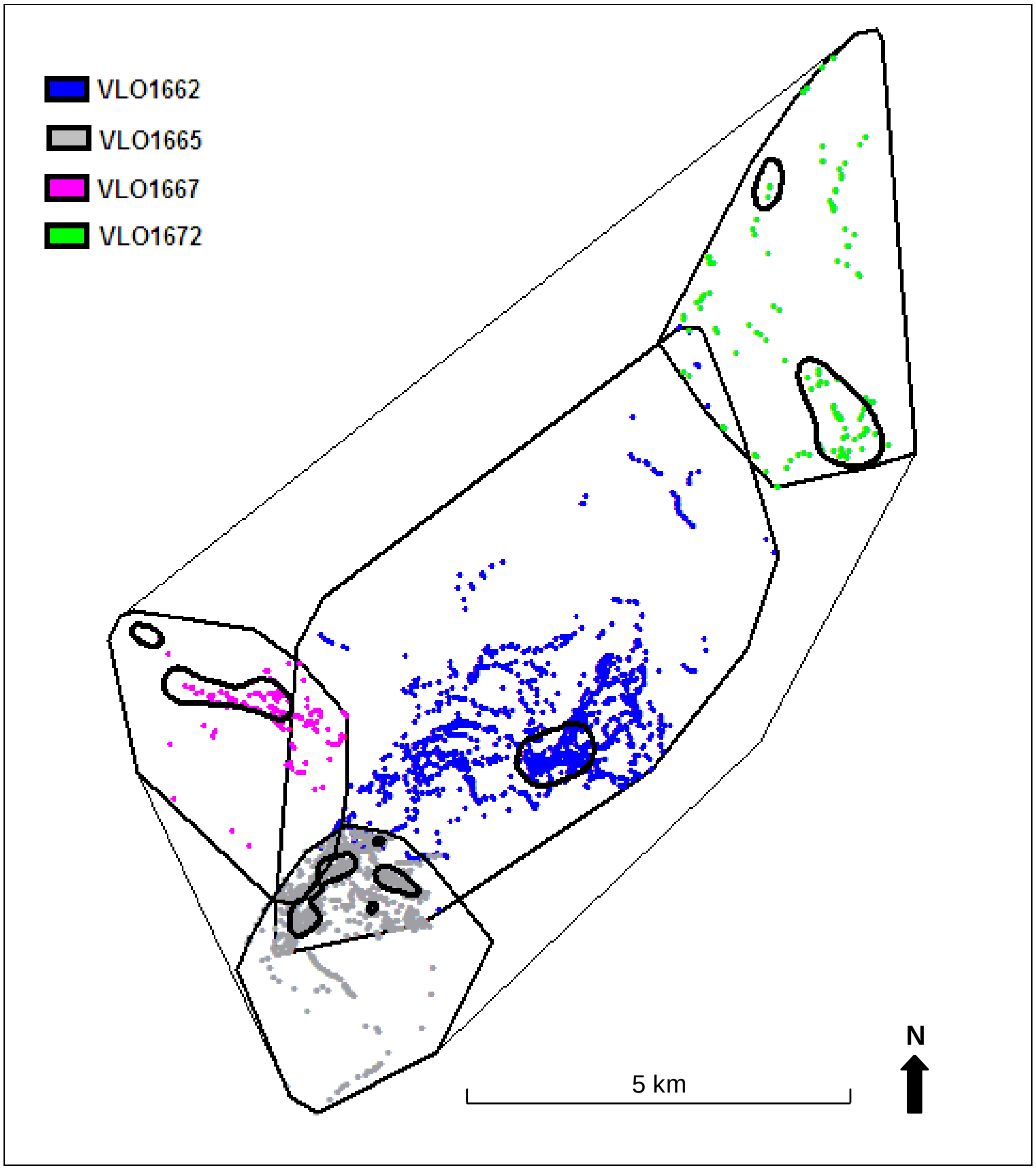

Figure 4.8 Urine spray marking activity of four adult male African wild cats in their 100% MCP home ranges. The 50% core areas in each home range are indicated and the outline represents the study site

Table 4.4 Nearest Neighbour Analysis for four adult male African wild cats to test for spatial randomness of spray marking activity in home ranges and indicating the percentage of spray marking observed in the core areas of their home ranges. R = nearest neighbour index, *n* = spray marking events, *Z* = *Z* score

ID	R	*n*	*Z*	Description	% of observed spray marking in core areas
VLO1662	0.42	1405	-71.71	Tendency towards clumping exists	21%
VLO1665	0.51	1206	-66.44	Tendency towards clumping exists	38%
VLO1667	0.43	151	-23.51	Tendency towards clumping exists	44%
VLO1672	0.45	122	-21.73	Tendency towards clumping exists	35%

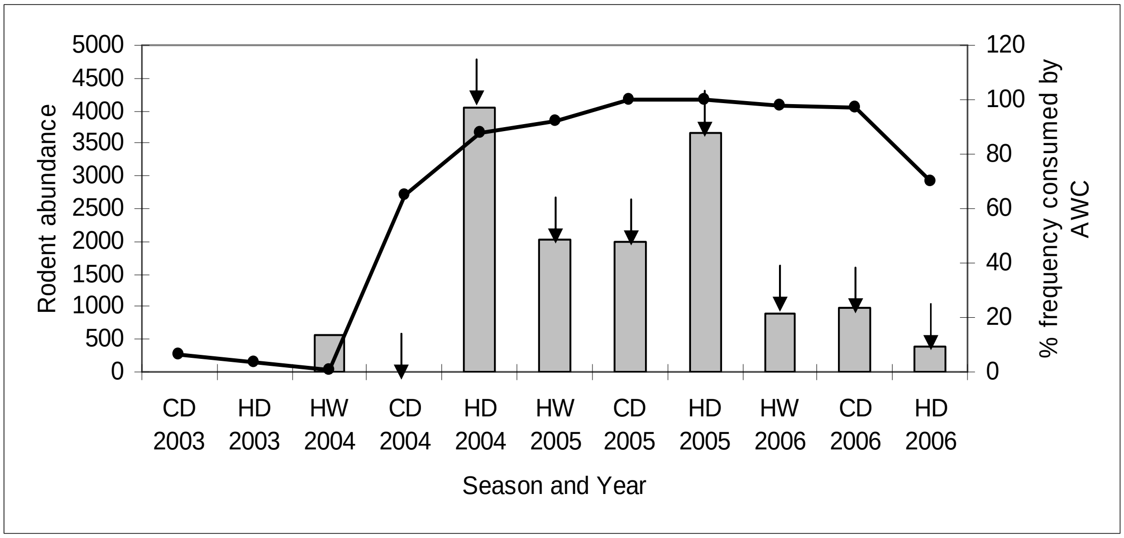

Figure 4.9 Seasonal rodent abundance estimated from rodent trapping (CD = cold-dry season; HD = hot-dry season; and HW = hot-wet season) (Chapter 2) and the percentage frequency with which rodents was consumed by African wild cats (AWC) from 2003 to 2006. Arrows indicate seasons when litters were observed in the study site. During CD 2004 no rodent abundance data were available

Table 4.5 Descriptions of interactions between wild cats from direct observation in the Kalahari from May 2003 to December 2006. The season, the sex of the cats, the duration of the interaction (min), the distance (m) between the cats and any additional information are included. ♀ = female, ♂ = male and U = Unknown sex

Interaction and description	Season	Sex 1	Sex 2	Time (min)	Distance between cats (m)	Additional details
Staring: Two cats stare at each other for several minutes and then continue without any physical interaction	CD 2003	♀	U	2	50	At waterhole, staring and then unknown cat continues walking
	CD 2003	♀	U	5	10	Unknown cat turns away
	HD 2003	♀	♀	2	20	Overlapping area in home ranges, the smaller female turns away
	HD 2003	♀	U	4	20	Both cats continue in different directions without any other interaction
	HD 2003	♀	♀	2	30	Both cats continue in different directions without any other interaction
	CD 2004	♀	U	2	20	Unknown cat turns away
	CD 2004	♀	♀	4	20	Both cats continue in different directions without any other interaction
	CD 2005	♀	U	2	20	Both cats continue in different directions without any other interaction
	HW 2006	♀	U	2	20	Both cats continue in different directions without any other interaction
	CD 2006	♀	♀	2	4	Both cats turn around and ran away
Fighting: Fighting and scratching while caterwauling loudly	CD 2004	♂	♂	10	<1m	Vicious fighting, scratching and rolling in bushes whereafter the cats chased each other over the dunes and disappeared from sight
Following: Two cats follow each other but no spray marking, courting behaviour or interactions were observed	HD 2005	♂	♀	44	20-30	Male follows female
	HW 2006	♂	♀	10	20-30	Male following female
	HW 2006	♀	♂	2	20-30	Female following male
	HW 2006	♀	♂	10	20-30	Male following female
	HW 2006	♂	♂	5	20-30	Adult male following an adult male
Chasing: One cat chases another cat away	HD 2004	♀	♂	1	5	Adult female an adult male stare at each other at waterhole and then female chases male cat away
	HW 2005	♀	♀	30	5	Two adult females stare and then chase each other

	HW 2006	♂	U	20	30-2	Adult male chases sub-adult cat into a tree
	CD 2006	♂	U	1	4	Adult male chases sub-adult cat while caterwauling
	CD 2006	♂	U	10	4	Adult male chases sub-adult cat. Sub-adult cat shows submissive behaviour, turning onto its back with belly exposed, then runs away
	HD 2006	♂	U	1	<1m	Adult male chases sub-adult cat. Sub-adult cat shows submissive behaviour by turns onto its back with belly exposed. Adult cat walks away
Older kittens visit den	HW 2005	♀	U	40	<5m from den	Older kitten visits den with younger siblings, while mother is absent. No aggression or provisioning of food
	HW 2005	♀	U	420	<5m from den	Older kitten hunting with mother while younger siblings remain at den. Both cats return to den whereafter older kitten leaves
	HW 2005	♀	U	30	<1m	Older kitten and mother play while younger siblings remain at den
	CD 2006	♀	U	25	<5m from den	Sub-adult cat approaches den and lies down. Mother hisses softly, no other interactions
	HW 2005	♀	U	30	<5m from den	Older kitten plays with younger siblings while mother remains lying down
Male cat visits den	HD 2004	♂	♀	60	2-20	Male cat moves slowly closer to female with kittens and lies down <5m from female. Female pulls her ears back and hisses but does not chase the male away. Male leaves without any interaction or aggression towards kittens
	HW 2006	♂	♀	20	< 5m from den	Male cat approaches den with kittens while female remains with kittens. No interactions or aggressive behaviour from male
	HW 2005	♂	♀	15	< 5m from den	Male cat approaches den and leaves with female. Courting behaviour follows

Males spent on average 1.7 ± 0.5 days (*n* = 6) with a receptive female while chasing, playing and courting. Mating involves grabbing the female by the scruff of the neck and the female lunging after successful stimulation. Vocalisation was typically felid, with calling observed in both sexes. At first receptive females hiss at males followed by gurgling sounds (Smithers, 1983; Sunquist & Sunquist, 2002). Although males were observed to visit dens they were not observed to assist in the rearing of kittens (Table 4.5).

5. Discussion

Although data on home ranges and spatial organisation in wild cats (*Felis silvestris*) are limited to short term studies, small samples sizes and opportunistic observations (Nowell & Jackson, 1996), home range sizes show large variability (Table 4.6). This could be due to varying densities and distribution of prey (Liberg & Sandell, 1988), caused by the large range of environmental conditions that wild cats occur in (Nowell & Jackson, 1996). The annual home range estimates concluded from our study (female = 3.5 ± 1.0 km^2 and male = 7.7 ± 3.5 km^2) fall within the ranges of previous studies (Table 4.6). An exception is the study by Phelan & Sliwa (2005) on Gordon’s wild cat (*F. s. gordoni*) in the Sharjah desert which reported much larger home range sizes for wild cats than in any other study. Larger home ranges in this desert area may be as a result of lower prey availability, exaggerated by an unusually dry period during their study.

The resource dispersion hypothesis predicts that resources have a patchy distribution and that the minimum number of patches required to sustain a breeding pair will sometimes support additional individuals (Carr & Macdonald, 1986). Althought this was developed to explain carnivore social behaviour and the presence of group living it may also explain patterns in spacing behaviour of solitary carnivores (Carr & Macdonald, 1986). The hypothesis does not consider resource predictability which might be important factor affecting animal spatial organisation (Maher & Lott, 2000).The Kalahari is a semi desert habitat exhibiting variable prey densities and at the onset of our study a lean period in the Kalahari was identified (Chapter 2). Although we do not have sufficient home range data to test these observations, three of the four cats revealed larger home ranges in 2004 than in the following years. The exception was female, VLO1654 that showed a smaller home range during this period. This female was hunting around the waterhole where she spesialised in catching birds (Chapter 3). As rodent numbers increased she changed her behaviour, increased her home range and switched from hunting birds to rodents. Nonetheless, wild cats that lack a rich food resource, such as associated with a waterhole in their home range could potentially increase their home ranges during dry periods in the Kalahari.

All kittens born and raised in our study site disappeared after four months, however, it was not possible to determine how far they travelled from their natal home range. A single sighting of a radio collared cat 80 kilometres north of our study site is suggestive of large dispersal abilities. Young cats may disperse over vast distances and roam until they find a suitable home range or take up residency (Edwards, De Preu, Shakeshaft, Crealy & Paltridge, 2001).

Male home range sizes may not only be determined by food requirements but also by female distribution (Liberg & Sandell, 1988, Altmann, 1990). Therefore, Sandell (1989) predicted that solitary male carnivores should have home ranges 1.2 ± 0.1 times larger than females. In the African wild cat male annual home ranges were 1.8 times larger than the predicted home range estimates. Since females are not evenly distributed males cover large home ranges to increase their reproductive output. Female home ranges were smaller and suggest that food abundances and habitat requirements are sufficient and readily available. Sandell's (1989) prediction is supported by our study as well as by most other wild cat studies, for example the European wild cat, *F. s. silvestris* (Fuller, Biknevicius & Kat, 1988; Stahl, Artois & Aubert, 1988; Biro *et al*., 2004; Phelan & Sliwa, 2005), feral domestic cats, *F. s. catus* (Barratt, 1997; Daniels, Beaumont, Johnson, Balharry, Macdonald & Barratt, 2001; Edwards *et al*., 2001; Molsher *et al*., 2005), bobcat, *L. rufus* (Bailey, 1974; Chamberlain, Leopold & Conner, 2003; Cochrane, Kirby, Jones, Conner & Warren, 2006), black-footed cat, *F. nigripes* (Sliwa, 2004), European lynx, *L. lynx* (Mech, 1980; Breitenmoser & Haller, 1993; Herfindal *et al*., 2005), Canadian lynx, *L. canadensis* (Vashon, Meehan, Jakubas, Organ, Vashon, McLaughlin, Matula & Crowley, 2007), Geoffrey's cat, *Felis geoffroyi* (Johnson & Franklin, 1991) and ocelot, *Leopardus pardalis* (Ludlow & Sunquist, 1987).

Table 4.6 Home range estimates of male and female wild cats (*Felis silvestris*) and feral domestic cats (*Felis silvestris catus)* indicating the study area, study duration, method of calculation and reference cited. Where possible, averages were calculated from estimates given in the literature

Species	Study site	Sex	Sample size	Study duration	Home range size (km^2)	Method	References
F. s. grampia	Northern Europe	♀	1	Annual	8.16	MCP	Phelan & Sliwa (2005)
F. s. silvestris	Deeside, Scotland	♀ and ♂	2	Monthly	1.75	MCP	Corbett (1979)
F. s. silvestris	Ardnamurchan, Scotland	-	-	29 – 74 days	8-18	MCP	Scott *et al*. (1993)
F. s. silvestris	Switzerland	♂	3	-	37	MCP	Liberek (1996)
F. s. silvestris	Switzerland	♀	2	-	4.1	MCP	Liberek (1996)
F. s. silvestris	France	-	-	Seasonal	1.5 – 5.85	-	Artois (1985)
F. s. silvestris	France	♀	6	-	1.84	100%MCP	Stahl *et al*. (1988)
F. s. silvestris	France	♂	6	-	5.73	100%MCP	Stahl *et al*. (1988)
F. s. silvestris	Hungary	♀ and ♂	5	-	3.89 – 8.72	-	Szemethy *et al*. (1993)
F. s. silvestris	Hungary	♀	2	Annual	5.32	100% MCP	Biró *et al*. (2004)
F. s. silvestris	Hungary	♂	2	Annual	6.56	100% MCP	Biró *et al*. (2004)
F. s. silvestris	Italy	♀	1	Annual	11.15	100% MCP	Genovesi & Boitani (1993)
F. s. silvestris	Portugal	♀	6	Annual	1.81 – 3.67	95% kernel	Sarmento *et al*. (2006)
F. s. lybica	Kenya	♂	1	Monthly	1.60	100% MCP	Fuller *et al*. (1988)
F. s. lybica	Saudi Arabia	-	4	-	11.74	-	Coutenay *et al*. (1996)
F. s. gordoni	Sharjah desert	♀	1	Annual	51.21	95% MCP	Phelan & Sliwa (2005)
F. s. gordoni	Sharjah desert	♂	1	Monthly	28.65	95% MCP	Phelan & Sliwa (2005)
F. s. catus	South-east Australia	♂	-	Annual	6.2	100% MCP	Jones & Coman (1982)
F. s. catus	South-east Australia	♀	-	Annual	1.7	100% MCP	Jones & Coman (1982)
F. s. catus	Scotland	♂	-	Monthly	0.19	MCP	Corbett (1979)
F. s. catus	Scotland	♀	-	Monthly	0.10	MCP	Corbett (1979)
F.s. catus	Scotland	♂	-	Monthly	4.59	100% MCP	Daniels *et al*. (2001)
F. s. catus	Scotland	♀	-	Monthly	1.77	100% MCP	Daniels *et al*. (2001)

Few interactions between African wild cats were observed and were mostly between females with kittens or receptive females with males. Extensive female-female home range overlap indicates that food availability is variable in time and space (Sandell, 1989) and related females clustering together have been described in many carnivores (Smith, McDougal & Sunquist, 1987; Logan & Sweanor, 2001; Janečka, Blankenship, Hirth, Tewes, Kilpatrick & Grassman, 2004; Kitchen, Gese, Waits, Karki & Schauster, 2005). Home range overlap in females is common in solitary carnivores e.g. bobcat, *L. rufus* (Zezulak & Schwab, 1979); ocelot, *L. pardalis* (Ludlow & Sunquist, 1987) and kodkod, *Oncifelis guigna* (Dunstone, Durbin, Wyllie, Freer, Jamett, Mazolli & Rose, 2002). Although female wild cat home ranges overlap extensively, the core areas were mostly exclusive and the females were not related (Chapter 5). Territorial behaviour of females could not be determined by direct observations such as scent marking since scent marking activity appeared to be dependent on the reproductive status of females, however, data from multiple seasons as well as breeding and den sites confirmed the residency of the females in our study site. A single observation where one female chased another may be suggestive of territorial behaviour.

Adult male home range overlap was limited and core areas showed no overlap between male cats. Studies on wild cat species confirm the exclusive use of home ranges by male cats, for example black-footed cats, *F. nigripes* (Sliwa, 2004), Geoffroyi cat, *F. geoffroyi* (Johnson & Franklin, 1991), bobcat, *L. rufus* (Cochrane *et al*., 2006) and European lynx, *L. lynx* (Breitenmoser & Haller, 1993). We suggest that spatial exclusivity is due to the high abundance of prey species (Sandell, 1989). This is in contrast with studies of feral domestic cats where large overlap among home ranges of male cats and smaller overlap between females were found (Corbett, 1979; Jones & Coman, 1982; Fitzgerald & Karl, 1986; Daniels *et al*., 2001; Biró *et al*., 2004). Further evidence for male territoriality are substantiated by aggressive behaviour between male cats and a roaming sub-adult male that became resident, with a concomitant increase in spray marking activity and decrease in home range overlap with the resident male. It appears that a pattern of intrasexual territory is displayed that corresponds with other asocial felids (Ferreras, Beltrán, Aldama & Delibes, 1997; Stander, Haden, Kaqece & Ghau, 1997).

Seasonal prey abundance was highly variable and no clear breeding season was identified, therefore, the lack of seasonal differences in male home range sizes is expected. However, receptive females are unpredictable in time and space, therefore, male cat ranges should overlap with several females (Imms, 1987) or they should move over larger areas, covering greater distances than females to maximise their reproductive output (Sandell, 1989). In the Kalahari home ranges of male African wild cats do overlap with those of several females and they have significantly larger home range sizes than female cats. Distances covered by male African wild cats are larger and they travel faster than female African wild cats (Chapter 3). African wild cats shows several ways of scent marking, however, urine spray marking is the most prominent way of communication. Male cats spray mark frequently to advertise their home ranges and aggressive behaviour between male cats was observed. The overall spatial pattern of urine spray marking in male cats is not randomly distributed and shows an increase in spray marking in the core areas of the cats. Female spray marking is related to their reproductive status (Sliwa, Herbst & Mills in press).

The African wild cat seems to be solitary and no evidence of sociality as reported in feral colonies of domestic cats was observed (Laundré, 1977; Macdonald & Apps, 1978; Dards, 1978; Corbett, 1979; Macdonald, 1983; Fitzgerald & Karl, 1986). However it is interesting to note that older siblings did occasionally visit the mother and younger kittens at den sites, although no provisioning of food by older siblings was observed. Furthermore, on three occasions male cats visited females with kittens without any suggestion of infanticide. These observations could be interpreted as a weak form of sociality in wild cats that could manifest itself more strongly under different ecological conditions.

Conclusion

Prey abundance plays an important role in social and spatial organisation of the African wild cat in the southern Kalahari. Food availability influences the reproductive activity of female cats, therefore no clear breeding season was evident. This explains the lack of variability in seasonal home range sizes of both male and female cats. Food resources in the semi desert area vary in time and space, thus females exhibit large overlap in their home ranges, although core areas were exclusive. Since receptive females seem to be the limiting resource for male cats, overlap between males is restricted to small areas. African wild cats were solitary for the majority of the time and communication between cats were via a range of scent marking behaviours that increase in females to advertise their reproductive status. Males scent marked continuously during the study period probably to mark their home range extent to neighbouring and roaming male cats. This study provides a meaningful contribution to our knowledge of African wild cat ranging behaviour as well as the importance of prey abundances on their reproductive ecology.

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CHAPTER 5

Microsatellites reveal patterns of relatedness in a local African wild cat (*Felis silvestris*) population from the southern Kalahari, with limited evidence of hybridisation with the domestic cat (*F. s. catus*)

1. Abstract

The African wild cat (*Felis silvestris*) has a wide geographic range, stretching throughout most of the African continent, except in the tropical forests and true desert areas. Hybridisation with feral domestic cats is thought to be a threat to the genetic integrity of wild cats throughout their range. Several admixture studies on the European wild cat have been reported, but there is limited information available on the status of the African wild cat. Here we report the genetic variation and admixture analysis of 57 wild living African wild cats and 46 domestic cats using 18 microsatellite loci. Cats were morphologically identified as African wild cats (*F. s. cafra*) and two geographically separated domestic cat populations (*F. s. catus*), independent of any prior genetic information. Significant genetic differentiation between these groups confirms earlier suggestions of the distinctiveness of African wild cats and domestic cats. Bayesian cluster analysis also showed evidence of these two distinct entities and identified four cryptic hybrids among the wild cats. All hybrids were either outside or on the periphery of the Kgalagadi Transfrontier Park, suggesting that the level of introgression is low, yet still of concern for the genetic integrity of the African wild cat. The genetic diversity within our wild cat population was significantly higher than in the domestic cat populations and relatedness values were compared with results from direct observations.

Keywords: Felis silvestris, African wild cat, domestic cat, hybridisation, microsatellites, admixture, Bayesian clustering, relatedness

2. Introduction

The wild cat (*Felis silvestris*) is classified as a polytypic species with three or more distinct subspecies: African or Sardinian wild cat (*F. s. lybica*), European wild cat (*F. s. silvestris*), Asian wild cat (*F. s. ornata*) (Nowell & Jackson, 1996; Sunquist & Sunquist, 2002) and possibly the Chinese sand cat (*F. s. bieti*) (Driscoll, Menotti-Raymond, Roca, Hupe, Johnson, Geffen, Harley, Delibes, Pontier, Kitchener, Yamaguchi, O'Brien & Macdonald, 2007), as well as a domesticated form (*F. s. catus*) (Ragni & Randi, 1986; Randi & Ragni, 1991; Wozencraft, 1993; Johnson & O'Brien, 1997). Wild cats are widely distributed in Europe, Asia and Africa, they are closely related and form the so-called 'domestic lineage' in the genus *Felis* (Sunquist & Sunquist, 2002). The domestic lineage diverged around 6.2 million years ago and resulted in seven species (the black-footed cat: *F. nigripes*, the jungle cat: *F. chaus*, the Chinese desert cat: *F. bieti*, the desert of sand cat: *F. margarita*, the African wild cat: *F. silvestris cafra, the European wild cat: F. s. silvestris* as well as the domestic cat: *F. s. catus*) (Ragni & Randi, 1986; Randi & Ragni, 1991; Masuda, Lopez, Slattery, Yuhki & O'Brien, 1996; Nowell & Jackson, 1996; Johnson, Eizirik, Pecon-Slattery, Murphy, Antunes, Teeling & O'Brien, 2006; Johnson & O'Brien, 1997; Johnson & O'Brien, 2007; Randi, Pierpaoli, Beaumont, Ragni & Sforzi, 2001). The domestication of the wild cat most likely occurred in the Near East and probably in parallel with agricultural village development in the Fertile Crescent (Driscoll *et al*., 2007; Driscoll, Macdonald & O'Brien, 2009) 8,000 to 10,000 years ago (O'Brien & Johnson, 2007). Today about 600 million domestic cats are distributed worldwide; they can interbreed with wild cats and produce fertile offspring, both in the wild and in captivity (O'Brien & Johnson, 2007; Robinson, 1977; Ragni, 1993).

The problematic description and classification of the species together with morphological similarities makes it difficult to distinguish between tabby-like domestic cats, true wild cats and, in particular, their hybrid forms. This leads to increased confusion about the subspecific status of *F. silvestris* populations (Clutton Brock, 1999; Allendorf, Leary, Spruell & Wenburg, 2001; Sunquist & Sunquist, 2002; Driscoll *et al*., 2007). Furthermore, continued co-existence of domestic- and wild cats as well as increased habitat reduction for wild cats, raised the fear that widespread interbreeding would lead to genetic extinction through hybridisation and introgression (Nowell & Jackson, 1996; Rhymer & Simberloff, 1996; Randi, 2003; 2008) of populations in Europe (Suminski, 1962), the Near East (Mendelssohn, 1999) and in South Africa (Smithers, 1983; Stuart & Stuart, 1991).

European studies revealed that wild cats and domestic cats are genetically distinct, with different rates of admixture, from recent and frequently hybridising populations in Scotland and Hungary (Beaumont, Barratt, Gottelli, Kitchener, Daniels, Pritchard & Bruford, 2001; Daniels, Beaumont, Johnson, Balharry, Macdonald & Barratt, 2001; Pierpaoli, Biró, Herrmann, Hupe, Fernandes & Ragni, 2003; Lecis, Pierpaoli, Biró, Szemethy, Ragni, Vercillo & Randi, 2006), to contrasting low genetic introgression in Italy, Germany and Portugal populations (Randi *et al*., 2001; Pierpaoli *et al*., 2003; Randi 2003; Lecis *et al*., 2006; Oliveira, Godinho, Randi & Alves, 2008*b*). In the studies where African wild cat samples were analysed (Randi *et al*., 2001; Driscoll *et al*., 2007), wild cats and domestic cats were classified as genetically distinct from each other. The African wild cat is not a protected species; however, hybridisation with domestic cats is a real concern (Smithers, 1983; Nowell & Jackson, 1996). Although genetic introgression has not been fully studied locally, a recent study by Wiseman, O'Ryan & Harley (2000) suggests that introgression appears to be lower than previously thought and occur mainly from the wild to domestic cats.

Apart from concerns regarding the genetic purity of African wild cat populations, especially in and near urbanised areas, very little is known about the biology of this widespread small predator. The southern Kalahari population was selected as the model study population, not only because the open dune habitat is ideal for radio tracking and observing individual cats, but also the remoteness of the area that has been declared a national park since 1931 made the possibility of identifying a genetically pure African wild cat population likely.

Hybrid zones are regions where two genetically differentiated taxa overlap and admixture events occur and have received substantial attention in recent years (Barton & Hewitt, 1989). Hybridisation occurs more frequently than originally believed (Mallet, 2005; Meyer, 2006) and may be due to human induced, such as between domestic and wild species, or domestic and captive species (Nijman, Otsen, Verkaar, de Ruiter, Hanekamp, Ochieng, Shamshad, Rege, Hanotte, Barwegen, Sulawati & Lenstra, 2003; Lecis *et al*. 2006), or between introduced and native species (Goodman, Barton, Swanson, Abernethy & Pemberton, 1999; Riley, Shaffer, Voss & Fitzpatrick, 2003). Natural hybridisation has been described across the zootaxa, including in insects (Beltran, Jiggins, Bull, Linares, Mallet, McMillan & Bermingham, 2002), fish (Saltzburger, Baric & Sturmbauer, 2002), amphibians (Szymura & Barton, 1991), birds (Grant, Grant, Markert, Keller & Petren, 2005) and carnivores (Lehman, Eisenhawer, Hansen, Mech, Peterson, Gogan & Wayne, 1991). In particular the question of hybridisation in domestic and wild cat populations has been extensively studied (Hubbard, McOrist, Jones, Biod, Scott & Easterbee, 1992; Daniels, Balharry, Hirst, Kitchener & Aspinall, 1998; Randi *et al*., 2001; Beaumont *et al*., 2001; Pierpaoli *et al*., 2003; Lecis *et al*., 2006; Oliveira *et al*., 2008*b*). The methods and procedures to identify cryptic population structure and admixture have advanced from mitochondrial DNA and allozyme analysis (Randi & Ragni, 1991; Hubbard *et al*., 1992) to improved accuracy through the use of microsatellites, especially when combining highly polymorphic markers with recently developed Bayesian clustering models (Lecis *et al*., 2006).

Possible evolutionary outcomes of hybridisation could include (i) that two hybrid taxa may merge, (ii) reproductive barriers may be reinforced between parental taxa, (iii) the transfer of genetic material into both parental taxa (this may facilitate adaptive evolution) (iv) a new species of hybrid origin may evolve or, (v) the hybrid zone may become established without any major impact on the parental taxa (Arnold, 1992; Seehausen, 2004). Therefore the studies of hybrids can give important insights into evolutionary processes and adaptation of species (Pastorini, Zaramody, Curtis, Nievergelt & Mundy, 2009).

Knowledge of relatedness and relationships between individuals is important to describe the behaviour and social structure of a species (Ralls, Pilgrim, White, Paxinos, Schwartz & Fleischer, 2001). Social structures are characterised by territoriality, social behaviour, tolerance, dispersal patterns, mating systems and the relatedness of the individuals (Gompper, Gittleman & Wayne, 1998). The African wild cat is described as a solitary felid (Smithers, 1983; Nowell & Jackson, 1996; Sunquist & Sunquist, 2002). Its social organisation shows large home range overlap between females but little overlap between males, although the home ranges of males typically overlap with several females in their home ranges (Chapter 4).

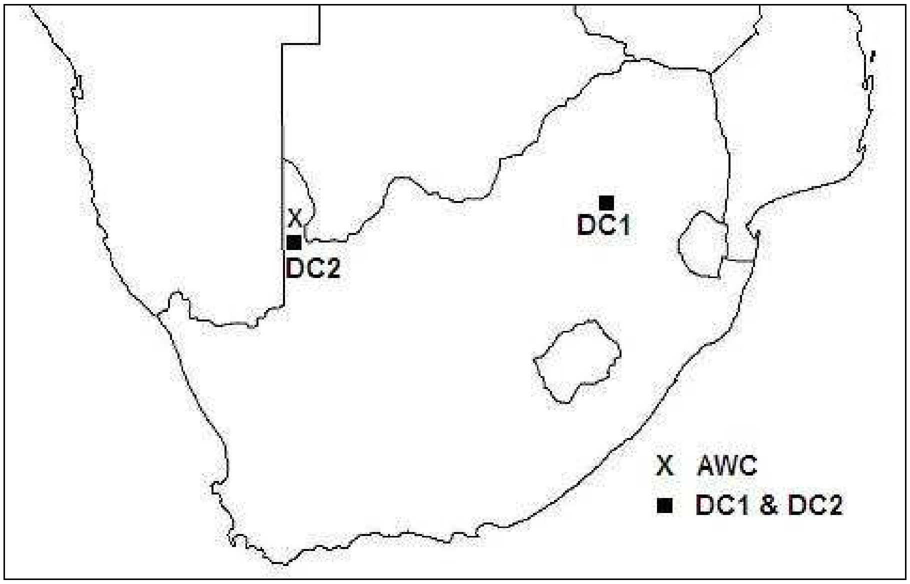
Molecular techniques have been applied widely to investigate social organisation in social carnivores, for example in African lions, *Panthera leo* (Packer, Gilbert, Pusey & O'Brien, 1991); African wild dogs, *Lycaon pictus* (Girman, Mills, Geffen & Wayne, 1997); gray wolves, *Canis lupus* (Smith, Meier, Geffen, Mech, Burch, Adams & Wayne, 1997); swift foxes, *Vulpes velox* (Kitchen, Gese, Waits, Karki & Schauster, 2005); kit foxes, *Vulpes macrotis* (Ralls *et al*., 2001) and raccoons, *Procyon lotor* (Nielsen & Nielsen, 2007) but only very recently in solitary felids e.g. bobcats, *Lynx rufus* (Janečka, Blankenship, Hirth, Tewes, Kilpatrick & Grassman, 2004) and cougars, *Puma concolor* (Biek, Akamine, Schwartz, Ruth, Murphy & Poss, 2006). In our study we used 18 microsatellite loci to analyse: (i) The extent of genetic variation among African wild cats in the southern Kalahari, (ii) the genetic purity of African wild cats, mostly sampled from the KTP, (iii) genetic structure in the wild cat population, and (iv) relatedness between African wild cat individuals of which the spatial organisation were recorded through intense behavioural observations.

3. Materials and Methods

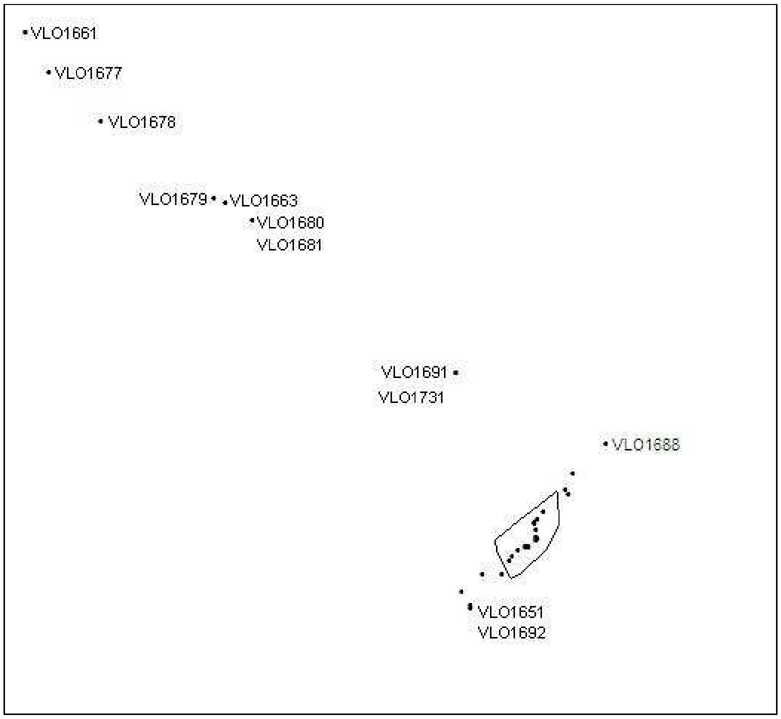
3.1 Sample collection and DNA extraction

We analysed a total of 103 tissue and hair samples, including 57 African wild cats (AWC), 25 Kalahari domestic cat (DC1) and a reference collection of 21 domestic cat (DC2; Veterinary Genetics Laboratory, University of Pretoria; C. Harper pers. comm.) samples (Figure 5.1a). Of the wild cat samples 47 were collected from April 2003 – December 2006 in the KTP (Figure 5.1b and Figure 5.1c), South Africa and Botswana and ten were collected from road kills outside the Transfrontier Park and stored in 95% ethanol. Wild cats were morphologically identified by coat-patterns, long legs and the characteristic reddish tint at the back of their ears (Smithers, 1983). Tissue samples were preserved in 95% ethanol and hair samples in plastic bags. All hair samples consisted of cat whiskers with the root visible at the tip.

(a)


X
DC2
DC1
X AWC
■ DC1 & DC2

(b)


VLO1661
VLO1677
VLO1678
VLO1679
VLO1663
VLO1680
VLO1681
VLO1691
VLO1731
VLO1688
VLO1651
VLO1692

(c)

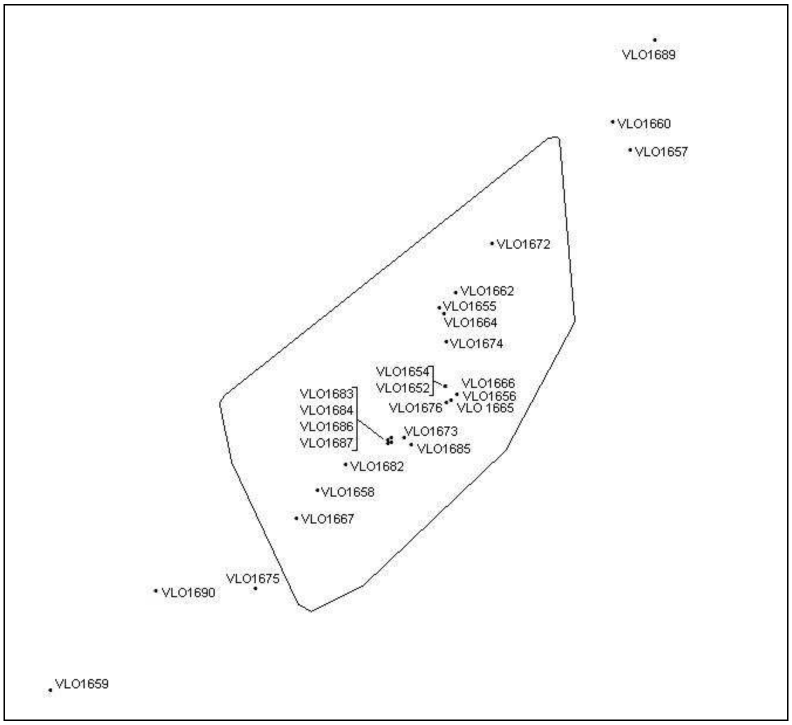


Figure 5.1 (a) Map of South Africa with locations of where all samples were collected, DC = domestic cat populations, AWC = African wild cat population (b and c) the core study site, indicating 38 African wild cats that were sampled and analysed for relatedness and population structure from March 2003 to December 2006

DNA extractions and microsatellite genotyping were conducted at the Veterinary Genetics Laboratory, Faculty of Veterinary Science, University of Pretoria (Onderstepoort). DNA tissue samples were extracted with a Cell Lysis stock solution (10mM Tris–HCl pH 8.0, 50mM NaCl, 10mM EDTA) and Phenol-Chloroform-Isoamylalcohol (Sigma kit) (C. Harper pers. comm.). DNA from hair samples were extracted with 200mM NaOH and 200mM HCl, 100mM Tris–HCl, pH 8.5 (C. Harper pers. comm.). Eighteen microsatellite markers that forms part of an international parentage panel (International Society of Animal Genetics (ISAG)) and developed by the laboratory of Leslie Lyons (University of California Davis) were used for genotyping (Lipinski, Amigues, Blasi, Broad, Cherbonnel, Cho, Corley, Daftari, Delattre, Dileanis, Flynn, Grattapaglia, Guthrie, Harper, Karttunen, Kimura, Lewis, Longeri, Meriaux, Morita, Morrin-O'Donnell, Niini, Pedersen, Perrotta, Polli, Rittler, Schubbert, Strillacci, Van Haeringen, Van Haeringen & Lyons, 2007). These loci were initially chosen based on their variability in various cat breeds, their probability of exclusion in parentage testing of closely related individuals, their robustness in multiplex polymerase chain reaction (PCR) testing and their consistency during testing (Lipinski *et al*., 2007). Table 5.1 provides the initial test panel results from ISAG 2004 discussions (Harper pers. comm.). A comparison with Menotti-Raymond, David, Lyons, Schaffer, Tomlin, Hutton & O'Brien (1999) indicated that although some of these markers map to the same chromosome they are unlinked.

The PCR amplifications were performed in 10µl reaction volume multiplex reactions using AmpliTaq Gold DNA polymerase (Applied Biosystems). PCR conditions were: 95ºC for 5min, followed by 35 cycles of 95ºC for 1 min, 58ºC for 30 s, 72ºC for 30 s, and followed by a final 72ºC for 30min. PCR products along with LIZ 500 size standard were run on a 3130xl Genetic Analyzer (Applied Biosystems) and analysed with STRand Software (version 2.3.94, Board of Regents, University of California, Davis).

Table 5.1 Population data of genetic markers in the domestic cat parentage and identification panel (C. Harper pers. comm.). PIC = polymorphism information content, Chr. = chromosome

Marker	Number (breeds)	Number (all)	Allele range	PIC (breeds)	PIC (all cats)	H (breeds)	H (all cats)	Chr.
FCA005	239	299	130-154	0.7	0.69	0.55	0.56	E1
FCA026	332	407	128-160	0.78	0.79	0.48	0.51	D3
FCA069	307	401	96-116	0.79	0.79	0.53	0.55	B4
FCA075	482	609	104-146	0.75	0.75	0.57	0.59	E2
FCA097	272	355	136-156	0.75	0.77	0.54	0.58	B1
FCA105	362	443	173-205	0.82	0.83	0.51	0.56	A2
FCA149	-	-	-	-	-	-	-	B1
FCA201	358	456	133-161	0.78	0.79	0.58	0.61	B3
FCA220	411	513	210-224	0.43	0.45	0.25	0.26	F2
FCA224	297	382	148-180	0.66	0.63	0.4	0.41	A3
FCA229	374	482	150-176	0.69	0.69	0.51	0.54	A1
FCA240	-	-	-	-	-	-	-	X
FCA293	308	412	179-201	0.8	0.8	0.54	0.54	C1
FCA310	291	394	112-140	0.74	0.74	0.54	0.57	C2
FCA441	399	483	145-173	0.71	0.71	0.56	0.58	D3
FCA453	278	352	184-208	0.67	0.66	0.32	0.36	A1
FCA651	213	306	135-141	0.21	0.23	0.13	0.14	X
FCA678	298	392	216-236	0.7	0.7	0.43	0.45	A1

3.2 Analyses of genetic variation

Allele frequencies, observed (H_O) and expected (H_E) heterozygosity for each locus and for each population were calculated using Genepop 3.4 (Raymond & Rouset, 1995) to determine significant deviations from Hardy-Weinberg Equilibrium (HWE) for all locus-population combinations and to statistically infer Linkage Equilibrium (LE) among loci. Significance levels were adjusted using sequential Bonferroni corrections for multiple comparisons in the same data set (Rice, 1989). We estimated the genetic variation between wild and domestic populations through a hierarchical Analysis of Molecular Variance (AMOVA) with the software GenAlEx (Peakall & Smouse, 2006) using F_{ST} and R_{ST}. The significance of genetic differentiation was tested by random permutation, under the null hypothesis that all individuals belong to a single population. Wilcoxon signed rank tests were used to evaluate the differences in allelic diversity (number of alleles: Na), the allelic richness (effective number of alleles: Ne) and H_E between pairs of geographical groups (Statistica 7.0).

3.3 Population structure and admixture analyses using Bayesian cluster analysis and Principal Component Analysis

Population structure, individual assignments and admixture proportions were estimated through a Bayesian approach implemented in Structure 2.2 (Falush, Stephans & Pritchard, 2007). The number of putative populations, *K*, was determined by comparing the log-likelihood values and *ΔK* (Evanno, Regnout & Goudet, 2005; Waples & Gaggiotti, 2006) over multiple runs (20 iterations each with a 10,000 chain burn-in and 100,000 MCMC chains) for values of *K* ranging from 1 to 8. An admixed model with correlated allele frequencies was used (other model parameters yielded the same results). For assignment of individuals to the inferred clusters, chains of 1 x 10^6, following a burn-in of 100,000, were run three times to ensure convergence. Following Lecis *et al*. (2006) individuals assigned with a probability of membership of $q_i \geq 0.8$ were regarded as belonging to a single cluster, while values of < 0.8 were inferred as an indication of admixture.

Allele frequencies from known or unknown source populations are modelled to assign individuals to one or more populations (Lecis *et al*., 2006), with the assumption that admixture leads to Hardy-Weinberg- and linkage disequilibrium (Pritchard, Stephens & Donnelly, 2000). The programme Structure 2.2 model correlations between loci in an admixed population, to detect more ancient admixture events and identifies population structure where populations are connected by gene flow or has diverged recently (Falush, Stephens & Pritchard, 2003).

A Principal Component Analysis (PCA) was performed using GenAlEx 6 software (Peakall & Smouse, 2006) which is a multivariate technique that plots the major patterns within a multivariate dataset and indicate the relationship between distance matrix elements based on their first two principal coordinates.

3.4 Relatedness estimates within the African wild cat population

Relatedness between individuals in the wild cat population was calculated using the programme GenAlEx (Peakall & Smouse, 2006). The software uses genetic distances from codominant data for a single population. The level of relatedness (*R*) described in Queller & Goodnight (1989) was used: for first order relatives (full sibs and parent-offspring) R-values ~0.5 are expected, second order relatives should on average show values of 0.25, while values below 0.125 indicate unrelated individuals. Individual inbreeding coefficients, kinship and relatedness coefficients were also compared in SPAGeDi version 1.2 (Hardy & Vekemans, 2002). Known relationships, obtained from behavioural observations done on the study population, were used to evaluate these results.

4. Results

4.1 Genetic diversity in wild and domestic cats

We determined individual genotypes for 57 morphologically classified African wild cats, 25 Kalahari domestic cats and the reference collection of 21 domestic cats. All microsatellite loci were polymorphic in both the 57 genotyped wild- and 46 domestic cats with six (FCA453 and FCA651) to 17 (FCA075) alleles per locus (average: 11.61 ± 3.13) (Appendix 4). The number of private alleles (alleles unique to a single population) within the wild cat population was 4.06 ± 0.59, the Kalahari domestic population 0.11 ± 0.08 and the domestic cat reference collection 0.44 ± 0.17. Twelve combinations between pairs of loci disclosed a significant deviation from linkage disequilibrium after Bonferroni correction for 18 independent replications ($P < 0.0028$). The microsatellite loci in this study map on different cat chromosomes (Menotti-Raymond *et al.*, 1999) except as shown in Table 5.2. These loci should be distant enough to allow for independent allele assortment. Pairwise allelic combinations were in linkage equilibrium at all loci over the wild cat genotypes except in one case (significance probability level $p < 0.05$ Bonferroni corrected for 14 comparisons). A significant departure from HWE (Table 5.3) was observed at two wild cat loci: FCA240 (F_{IS} = 0.69, p = 1.00) and FCA651 (F_{IS} 0.77, p = 1.00) and one domestic cat locus FCA240 (Kalahari population F_{IS} = 0.63, p = 1.00 and reference collection F_{IS} = 0.65, p = 1.00). However, both these loci are on the X-chromosome and the large number of male individuals in our study skewed the overall level of homozygosity. Subsequent analyses were conducted with, and excluding, these two loci and the scoring of males as homozygotes at the X-linked loci did not affect the Bayesian clustering or relatedness estimation.

Genetic diversity was significantly higher in the wild cats than in the domestic cats with higher allelic diversity and heterozygosity (Table 5.3). Moreover, Wilcoxon signed rank tests confirmed these results, showing significant differences in H_E (DC1: $Z = 3.2$, $p = 0.001$ and DC2: $Z = 2.9$, $p = 0.004$), Ne (DC1: $Z = 3.3$, $p = 0.001$ and DC2: $Z = 3.1$, $p = 0.002$) and Na (DC1: $Z = 3.7$, $p = 0.0003$ and DC2: $Z = 3.6$, $p = 0.0008$) between the wild and domestic cat populations and no significant differences between the two domestic cat populations. These results encouraged the analysis of wild cats and domestic cats as two distinct genetic entities and the two geographically separated domestic cat populations as one. The $F_{ST} = 0.10$ ($p < 0.01$) over all loci (Table 5.3) and an Analysis of Molecular Variance showed significant differentiation between the wild cat and two domestic cat populations and revealed most of the variance within rather than between the two domestic cat groups (Table 5.4).

Table 5.2 Microsatellite loci that showed linkage disequilibrium and their locations on specific chromosomes

Locus	Locus	Locus	Chromosome	Menotti-Raymond *et al*., (1999)
FCA026	FCA441		D3	Not linked
FCA097	FCA149		B1	Not linked
FCA229	FCA453	FCA678	A1	Not linked
FCA651	FCA240		X	Not linked

Table 5.3 Summary of diversity indices for each locus-population combination, observed (H_O) and expected (H_E) heterozygosities, (Na) number of alleles, (Ne) effective number of alleles, the fixation index (F), the inbreeding coefficient (F_{IS}) and the coefficient of genetic differentiation (F_{ST}) between wild (AWC) and domestic populations (DC)

Loci	African wild cat (AWC) (n = 57)					Kalahari Domestic cats (DC1) (n = 25)					Domestic cat reference collection (DC2) (n = 21)					F_{IS}	F_{ST}
	H_O	H_E	Na	Ne	F	H_O	H_E	Na	Ne	F	H_O	H_E	Na	Ne	F		
FCA005	0.77	0.78	8	4.60	0.01	0.68	0.69	6	3.24	0.02	0.81	0.82	9	5.44	0.01	0.01	0.03
FCA026	0.86	0.88	15	8.01	0.02	0.60	0.62	7	2.60	0.02	0.67	0.79	10	4.74	0.16	0.07	0.08
FCA069	0.84	0.83	12	5.77	-0.02	0.72	0.76	7	4.11	0.05	0.62	0.64	6	2.79	0.04	0.02	0.09
FCA075	0.84	0.87	13	7.97	0.04	0.76	0.75	6	3.93	-0.02	0.71	0.78	9	4.45	0.08	0.03	0.08
FCA097	0.91	0.91	17	11.16	0.00	0.60	0.69	5	3.21	0.13	0.81	0.84	7	6.39	0.04	0.05	0.05
FCA105	0.79	0.86	12	6.90	0.08	0.86	0.84	9	6.17	-0.03	0.62	0.78	7	4.64	0.21	0.08	0.05
FCA149	0.81	0.79	8	4.76	-0.02	0.76	0.66	5	2.96	-0.15	0.76	0.79	6	4.85	0.04	-0.04	0.07
FCA201	0.82	0.87	12	7.51	0.05	0.68	0.68	5	3.15	0.00	0.86	0.82	7	5.44	-0.05	0.00	0.09
FCA220	0.89	0.86	10	6.96	-0.04	0.33	0.62	5	2.62	0.46	0.57	0.73	7	3.64	0.21	0.18	0.10
FCA224	0.93	0.86	13	7.36	-0.07	0.52	0.56	7	2.26	0.07	0.38	0.40	6	1.68	0.06	0.00	0.16
FCA229	0.79	0.81	11	5.37	0.03	0.48	0.58	6	2.39	0.18	0.62	0.60	5	2.48	-0.04	0.05	0.15
FCA240	0.25	0.79	8	4.72	0.69	0.16	0.72	7	3.53	0.78	0.29	0.77	8	4.41	0.63	0.70	0.10
FCA293	0.81	0.86	12	7.18	0.06	0.80	0.76	7	4.24	-0.05	0.71	0.77	8	4.26	0.07	0.03	0.05
FCA310	0.79	0.81	11	5.20	0.02	0.88	0.72	7	3.55	-0.22	0.67	0.76	7	4.14	0.12	-0.02	0.08
FCA441	0.72	0.73	7	3.68	0.01	0.68	0.76	5	4.10	0.10	0.62	0.76	7	4.22	0.19	0.10	0.03
FCA453	0.67	0.61	5	2.57	-0.09	0.52	0.77	6	4.34	0.32	0.43	0.73	5	3.66	0.41	0.23	0.07
FCA651	0.14	0.59	5	2.46	0.76	0.08	0.27	2	1.37	0.70	0.10	0.24	2	1.32	0.61	0.72	0.41
FCA678	0.89	0.86	12	7.20	-0.04	0.41	0.53	5	2.11	0.22	0.62	0.69	4	3.23	0.10	0.07	0.15
Average	0.75	0.81	10.61	6.08	0.08	0.58	0.66	5.94	3.33	0.14	0.60	0.71	6.67	3.99	0.16	0.13	0.10
SD	0.21	0.09	3.24	2.16	0.24	0.23	0.13	1.47	1.09	0.27	0.20	0.15	1.91	1.31	0.20		

Table 5.4 Analysis of MOlecular VAriance (AMOVA) for wild - and domestic cat groups computed using GenAlEx (d.f., degrees of freedom; SS, sum of squares; MS, mean squares; Est. Var., estimated variance)

	Source	d.f.	SS	MS	Est. Var.	%	Stat	Value	Prob
Within all populations	Among Pops	2	46399.681	23199.841	370.201	39%	R_{ST}	0.390	0.010
	Within Pops	203	117339.631	578.028	578.028	61%			
	Total	205	163739.312	23777.868	948.229				
In domestic cats	Among Pops	1	4038.260	4038.260	77.050	13%	R_{ST}	0.129	0.010
	Within Pops	90	46869.709	520.775	520.775	87%			
	Total	91	50907.968	4559.034	597.824				

4.2 Admixture analyses and identification of hybrid individuals

In the Structure simulation that considered all sampled individuals, the highest likelihood and greatest Δ*K* were obtained for *K* = 2 (Fig. 5.2). If the two populations (wild and domestic cats) were admixed, individual admixed samples could be identified by estimating the proportion of membership (*q*) of those individuals. Given two inferred clusters and with the proportion of membership *q* ≥ 0.8, Cluster I grouped all the domestic cats and Cluster II all the wild cats (Fig. 5.3). Four admixed individual cats included a litter of three kittens (VL01732, VL01733 and VL01734) from a known semi tame wild cat mother on the periphery of the park and a wild cat skin sample from another region in the Northern Cape (28º14.181'S, 21º21.068'E) in South Africa (VL01742). All African wild cats collected from inside the Kgalagadi Transfrontier Park were clustered in Cluster II.

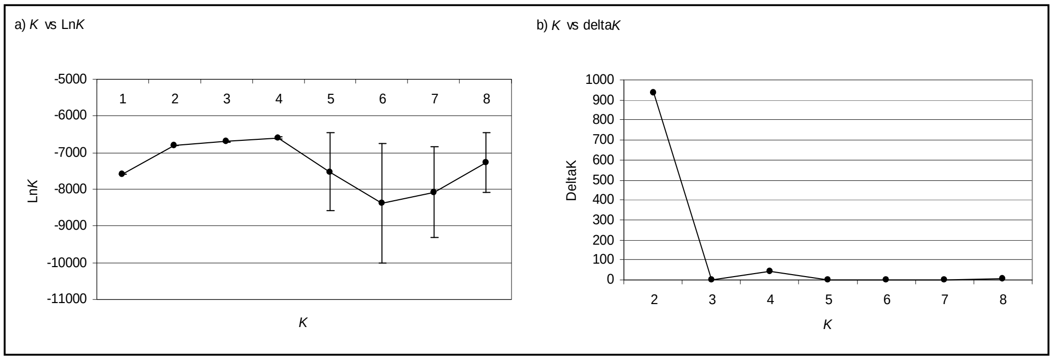


Figure 5.2 a) Probability of the data Ln*K* and, b) Δ*K* against the number of *K* clusters in the wild and domestic cat populations

Figure 5.3 Individual assignment of domestic cats (DC1 and DC2) and wild living African wild cats (AWC) in the southern Kalahari performed using Structure 2.2 with *K* = 2. Each individual is represented as a vertical bar partitioned into K = 2 segments indicating the estimated membership to the two clusters. The horizontal black lines indicate values of individual proportion of membership *q* ≥ 0.80

The results of a Principle Component Analysis plot of all the genotypes are shown in Fig. 5.4. Individual scores were plotted onto two principle axes (PC-I and PC-II), which cumulatively explained 39% of the variance among the samples. This plot showed a clear separation into the different groups, namely wild cats (AWC) and domestic cats (DC). The two geographically separated domestic cat populations (DC1 and DC2) were almost totally overlapping. The four identified hybrids clustered intermediate between the wild and domestic cats (Fig. 5.4).

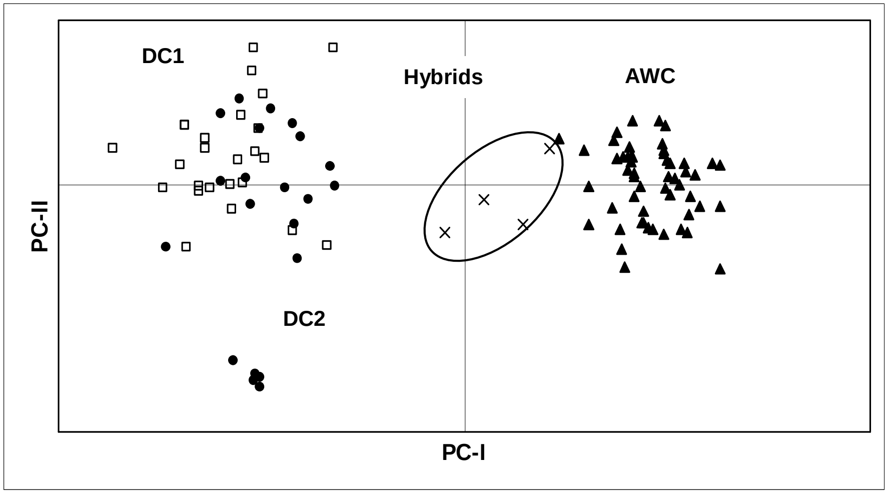


Figure 5.4 PCA of all three populations, African wild cats (AWC, solid triangle ▲), Kalahari domestic cats (DC1, open square □) and reference collection of domestic cats (DC2, solid circles ●). The four hybrids are indicated with crosses

4.3 Genetic diversity within the African wild cat population

The Principle Component Analysis of only wild cats without the hybrids shows seven individuals clustering separately. These seven individuals were shown to be all related to each other (Table 5.5). The ten geographically separated samples cluster all within the larger group of wild cat samples collected in the Kalahari (Fig. 5.5).

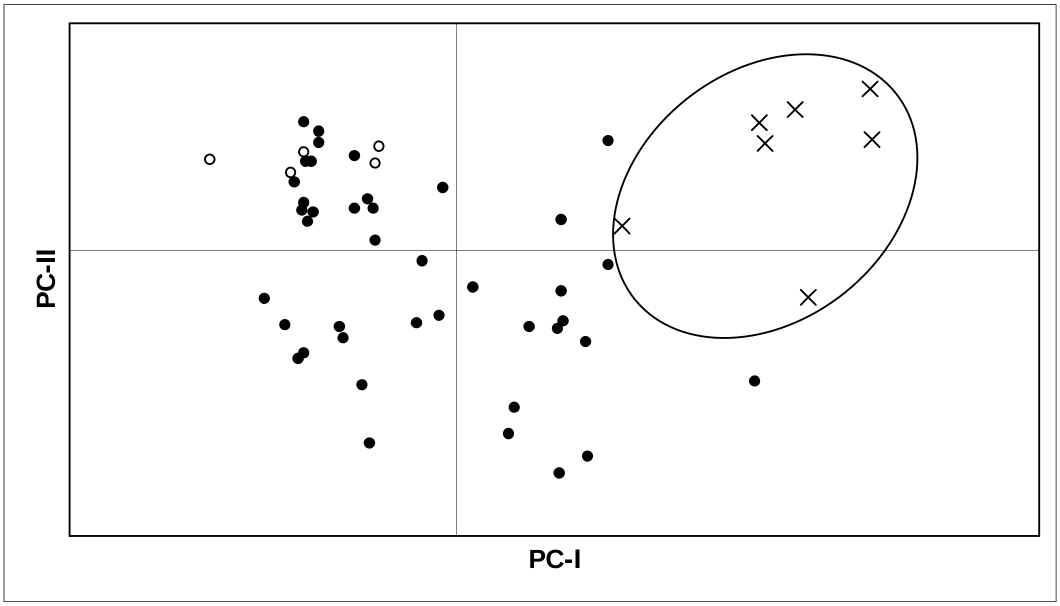


Figure 5.5 PCA of African wild cats without hybrids (solid circles ●), indicating samples collected outside the Transfrontier Park (open circle ○); related individuals from the main study site in the KTP are also indicated (crosses X)

4.4 Relatedness between Kgalagadi Transfrontier Park African wild cats

Given that only a small fraction of the KTP population was sampled, we present preliminary findings on the local population structure of wild cats. The mean relatedness values from Queller and Goodnight (1989) were used to evaluate the relationship between 38 individuals for which spatial information were available (Fig. 5.1b), including the wild cats in the core study site (Fig. 5.1c). Known relationships from behavioural observations and relatedness estimates are tabled in Table 5.5. Relatedness coefficients between adult individuals in the core study site were low (males: R = -0.02 ± 0.123, n = 8; females: R = -0.04 ± 0.113, n = 7; males versus females: R = -0.05 ± 0.138). In order to assess the accuracy of Queller-Goodnight R-values in estimating relatedness between individuals of unknown relationship, we calculated the average *R*-values of known pairs of relationships (Fig. 5.6). The mother-offspring pairs had an average relatedness value (*R*) of 0.47 ± 0.04 and full sibling pairs had an average relatedness (*R*) of 0.42 ± 0.12.

Interestingly, many of the close relationships involved one of the males (VLO1662) that was studied over a three year period (2004-2006, Chapter 4). He is the father of at least five kittens with three different females, of which one (VLO1658) appears to be his mother or sister (*R* = 0.63). On two occasions these cats where observed mating and courting. There was also an observation where the male visited the female while she had kittens. VLO1673, a sub-adult male whom we identified through visual observations as an offspring of female VLO1658 and male VLO1662, were confirmed as such despite allelic mismatches at locus FCA005 and FCA220. This individual showed a very high inbreeding coefficient (0.412). A small kitten VLO1675 caught in the home ranges of the female VLO1654 and male VLO1662 were positively identified as an offspring of these two cats. VLO1662 also sired a litter of three kittens with female VLO1684.

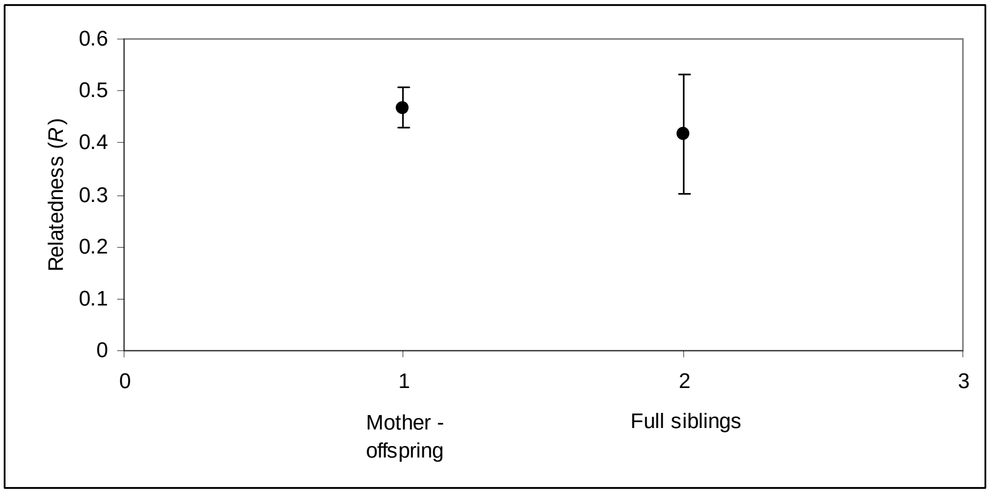


Figure 5.6 Relatedness values for known relationships among African wild cats in the Kalahari study site with the standard deviation included

Table 5.5 Relatedness values (*R*) and the expected relationships according to Queller and Goodnight (1989)

ID	Sex	ID	Sex	*R*	Relationship
VL01662	♂	VL01658	♀	0.63	Full siblings*
VL01662	♂	VL01673	♂	0.58	Parent - Offspring
VL01658	♀	VL01673	♂	0.56	Parent - Offspring
VLO1662	♂	VLO1654	♀	-0.03	Unrelated breeders
VL01662	♂	VL01675	♂	0.38	Parent - Offspring
[#]VL01654	♀	VL01675	♂	0.52	Parent - Offspring*
VLO1662	♂	VLO1684	♀	-0.01	Unrelated breeders
VL01662	♂	VL01683	♂	0.54	Parent - Offspring
VL01662	♂	VL01686	♂	0.53	Parent - Offspring
VL01662	♂	VL01687	♂	0.41	Parent - Offspring
[#]VL01684	♀	VL01683	♂	0.47	Parent - Offspring*
[#]VL01684	♀	VL01687	♂	0.45	Parent - Offspring*
[#]VL01684	♀	VL01686	♂	0.43	Parent - Offspring*
VL01683	♂	VL01686	♂	0.35	Full siblings*
VL01683	♂	VL01687	♂	0.31	Full siblings*
VL01686	♂	VL01687	♂	0.44	Full siblings*
VLO1673	♂	VLO1675	♂	0.07	Half siblings
VL01673	♂	VL01683	♂	0.36	Half siblings*
VL01673	♂	VL01686	♂	0.42	Half siblings*
VL01673	♂	VL01687	♂	0.43	Half siblings*
VL01675	♂	VL01683	♂	0.33	Half siblings
VLO1675	♂	VLO1686	♂	0.10	Half siblings
VLO1675	♂	VLO1687	♂	0.22	Half siblings
VL01658	♀	VLO1675	♂	0.19	Half sibs (aunt)*
VL01658	♀	VL01683	♂	0.38	Half sibs (aunt)*
VL01658	♀	VL01686	♂	0.42	Half sibs (aunt)*
VLO1658	♀	VLO1687	♂	0.09	Half sibs (aunt)*
VL01691	♀	VL01731	♀	0.57	Full siblings*

[#] Known mothers

* Known relationships

5. Discussion

There is considerable controversy over what constitutes a wild cat and whether wild cats can be defined purely by morphological criteria (Daniels *et al*., 1998; Kitchener, 1998). Extensive molecular studies on the European wild cat have been published (Beaumont *et al*., 2001; Randi *et al*., 2001; Lecis *et al*., 2006; Oliveira *et al*., 2008*b*) and the phenomenon where an introduced population hybridise with a native population is not uncommon (Rhymer & Simberloff, 1996). Especially in wild cats it is difficult to estimate degrees of admixture when the gene frequencies in the native population prior to admixture are unknown (Beaumont *et al*., 2001). If an *a priori* known "pure" wild cat population do not exist there will be no reference wild cat population to be used for estimating the rate of crossbreeding between wild and domestic cats (Daniels *et al*., 1998). Domestication produced obvious changes in the domestic cat of which coat coloration is probably the most noticeable one. Coat colouration is controlled by a few genes and wild cats that are homogenous for domestic colour patterns could be classified as domestic on morphological identification alone. Alternatively natural selection against coat colour phenotypes in domestic cats may lead to a selection of wild tabby markings in feral domestic cats (Randi *et al*., 2001). Therefore it is difficult to classify cats purely on a morphological basis as wild and domestic cats (Balharry & Daniels, 1998; Daniels *et al*., 1998). We identified wild cats morphologically by their tabby markings, longer legs and reddish colour behind the ears. We studied their ecology by radio telemetry; however, we compliment our behavioural observations with molecular data from microsatellite analyses.

The genetic variability of African wild cats in the southern Kalahari was examined ($H_E = 0.81$) and although different loci were used the results were comparable to that found in other wild felid studies e.g. cougar, *Puma concolor* $H_E = 0.66$ (Sinclair, Swenson, Wolfe, Choate, Gates & Cranall, 2001); bobcat, *Lynx rufus* $H_E = 0.77$ (Janečka *et al*., 2004); African wild cat, *F. s. lybica* $H_E = 0.80$ (Wiseman *et al*., 2000) and European wild cat, *F. s. silvestris*: Portugal $H_E = 0.76$ (Oliveira *et al*., 2008*b*); Italy $H_E = 0.72$ and Hungary $H_E = 0.81$ (Lecis *et al*., 2006).

Our results confirm that wild and domestic cats are genetically distinct ($F_{ST} = 0.14$, $R_{ST} = 0.39$) and Structure analysis clearly group our wild cat samples separately from the two domestic cat populations, with a clear indication of admixed individuals. Despite the widespread occurrence of domestic cats on the periphery of the KTP, the genetic distinction between wild and domestic cats was high and the existence of private alleles clearly suggest that gene flow between these populations is low and that hybridisation between Kalahari wild cats and domestic cats is limited. The hybrid individuals were offspring from a semi tame wild cat mother, nonetheless, this emphasises that admixture events on the border of the KTP could have serious implications for conservation efforts to protect the African wild cat. Hybridisation in a species can be widespread although it might be locally rare (Oliveira, Godinho, Randi, Ferrand & Alves, 2008*a*). Reports in southern Africa predict that hybridisation is widespread (Smithers, 1983), although at low levels (Wiseman *et al*., 2000). Our data highlights that the general mapping of levels of introgression are important to identify areas, such as the southern Kalahari, as focal areas for efficient conservation management strategies. In future studies, the KTP wild cats can be used as an a priori pure population, but it will be important also to assess natural levels of variation and gene flow among wild cats across their distribution range.

In general adult wild cat ranging patterns showed slight male-male overlap but extensive female-female overlap, although female core areas tend to be exclusive. The home ranges of male wild cats typically overlap with several females (Chapter 4). The grouping of closely related females has been described in many carnivores (Smith, McDougal & Sunquist, 1987; Logan & Sweanor, 2001; Janečka *et al*., 2004; Kitchen *et al*., 2005). However the lack of relatedness among our core study site females might be explained by: (i) a regular local turnover of maternal lineages that would tend to disrupt local clusters of related individuals (Biek *et al*., 2006), (ii) the frequent introductions of new alleles by immigrating males (Goudet, Perrin & Wasser, 2002), or that (iii) female dispersal might be distant enough to prevent spatial clustering of individuals (Biek *et al*., 2006).

Future more intensive sampling will be required to fully characterize local population structure and patterns of relatedness in wild cats. However, observations from our core study site suggest that a dominant male may monopolize paternity.

To conclude, admixture analyses indicate that hybridisation is not frequent in the southern Kalahari. The main threats such as persecution, accidental road killings, habitat loss and fragmentation still persists for the African wild cat in southern Africa. Habitat modification and animal translocation will increase the rate of hybridisation and introgression. The fact that evidence of admixed individuals is already present raises the conservation concerns for the protection of wild cats in southern Africa.

6. References

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CHAPTER 6

Synthesis

The African wild cat, *Felis silvestris cafra*, is one of the most widespread small predators on the African continent (Nowell & Jackson, 1996). However there is a paucity of information on virtually all aspects of its behavioural ecology. Since wild cats are the ancestor of the domestic cat, *Felis s. catus*, and the two species can freely interbreed, one of the biggest threats to wild cats over the globe is hybridisation with the domestic cat. The objective of this study was therefore to describe the feeding ecology, the spatial organisation and the population genetics of African wild cats in the southern Kalahari. This was achieved through radio telemetry and direct observations of habituated individuals that were closely followed and monitored over a period of 46 months. Throughout the study period an assertive effort was made to collect genetic material from wild cats to address the question of hybridisation as well as to supplement our understanding of population structure with molecular techniques. This chapter summarises the key aspects of every chapter and provides an overview of the behavioural ecology and population genetics of the African wild cat in the southern Kalahari.

6.1 What are the feeding habits of the African wild cat and are there sexual and seasonal differences in the diet and foraging behaviour?

African wild cats consume a large spectrum of food and prey resources depending on prey abundance and availability. This study showed that murids formed the bulk of the biomass in the diet, followed by birds and large mammals (> 500 g). Although reptiles and invertebrates were frequently caught they contributed less to the overall biomass of the diet. 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. The lean season (hot-dry) was characterised by a high food-niche breadth and 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 diet composition with males taking more large mammals and females favouring birds and reptiles. In support of the optimal foraging theory our results indicated that African wild cats are adaptable predators that preferred to hunt small rodents, but can change their diet according to seasonal and longer term prey abundances and availability.

6.2 What is the foraging behaviour of the Arican wild cat and does it shows sexual and seasonal differences?

The African wild cat is a successful predator with a hunting style typical of a solitary felid. Three distinct hunting behaviours were identified: (i) a slow winding walk while inspecting holes and scent trails, (ii) sitting and looking around for prey, or (iii) fast walking while spray marking with opportunistic killing of prey, typical of male cats. Both sexes show two daily peaks of activity: in the early morning and the evenings. The timing of the two active periods showed strong seasonal shifts from predominantly nocturnal during the hotter seasons to more diurnal during the colder seasons. A longer period of activity during the day was observed during the cold-dry season with corresponding low food availability, apparently a behavioural response to low prey abundances. In this wilderness area male and female African wild cats differed very little in their activity budgets, with hunting taking up most of their time. African wild cats are solitary and socialising between individuals is minimal. Cats showed gender-specific preferences for specific habitat types, with the number of prey captured corresponding closely to the time spent in each habitat. The major factors influencing the activity patterns and habitat use of the African wild cat are prey abundance and temperature extremes.

6.3 What are the spacial organisation and movement patterns of the African wild cat?

It is generally believed in carnivores that female space use is limited by resource distribution and abundance, whereas males should be strongly influenced by female spatial dyamics. Our results revealed that prey abundance plays an important role in social and spatial organisation of the African wild cat in the southern Kalahari. This also explained the lack of variability in seasonal home range sizes of both male and female cats. Minimum convex polygon (95% MCP) estimates showed male cats had larger annual home ranges (7.7 ± 3.5 km^2) than female cats (3.5 ± 1.0 km^2). Food resources in the semi desert area vary in time and space, thus females exhibited a large overlap in their home ranges, although core areas were exclusive. It seems that female cats avoid each other temporally and spacially, although only one observation of aggressive behaviour were observed it may be through scent marking and therefore female spacing pattern resembles a form of intrasexual territoriality, although ranges are not actively defended.

Since receptive females seemed to be the limiting resource for male cats, overlap between male home ranges was restricted to small areas. Male home ranges are larger than predicted from body size and metabolic considerations alone and adult males appear to be limited by receptive females as has been found in most carnivores.

6.4 What is the scent marking behaviour in African wild cats?

As predicted for a solitary carnivore, in the African wild cat scent marking is an important form of communication. For the majority of the time communication between cats occurred via a range of scent marking behaviours that increased in females to advertise their reproductive status. Males scent marked continuously during the study period to mark their home range extent to neighbouring and roaming male cats, whereas female spray marking appeared to be related to their reproductive status.

6.5 What is the reproductive bahviour of the Afican wild cat?

The African wild cat shows a polygenous mating system as suggested by the spacing patterns, sexual dimorphism and lack of parental care. In contrast to feral domestic cats that shows cooperative care of young in colonies of rich resources, this was not the case in our study, although older siblings did visit dens with smaller kittens. Food availability influenced the reproductive activity of female cats, and during a lean period no kittens were observed or reported in the Kalahari. However, as food abundances increased there was a drastic increase in kittens and two females produced up to four litters in a twelve month period. Therefore no clear breeding season was evident.

6.6 Was the African wild cat genetically distinct from the domestic cat and what were the levels of introgression in the southern Kalahari?

Molecular analyses indicate that African wild cats and domestic cats were genetically distinct. Four cryptic hybrids were identified among the wild cat samples. These hybrids were either outside or on the periphery of the park, indicating that the level of introgression was low, yet still of concern to the genetic integrity of the African wild cat. Preliminary findings on the genetic structure of our wild cat population indicated that related individuals did not cluster together. A more intense sampling of wild cats in a small area over a longer time period will be valuable to address questions of relationships between individuals and reproductive strategies in African wild cats.

6.7 What is the way forward in African wild cat conservation?

Although African wild cats are widely distributed and not protected over most of their range, little information has been available until now about their behaviour in the wild. This study provide detailed observations on feeding habits, foraging behaviour, spatial organisation, reproduction and the genetic status of the African wild cat in the southern Kalahari. These results can, in the absence of other studies, assist in understanding wild cat behaviour across distributional ranges.

Future studies shoud focus on the genetic status of African wild cats in other regions so that more genetically pure populations can be identified and the needed conservation actions implemented. Regions with a high probability of hybridisation should be identified and tested. Hybridisation is a natural process that may be very difficult to prevent, however education and public information on the role of small mesocarnivores and the threat of feral domestic cats to wild cats is important to increase awareness. Therefore reduce the risk of hybridisation events. Monitoring and research, a deeper knowledge of wild cat behaviour, abundance, population dynamics and other aspects of their ecology in other areas is essential.

It is hoped that this study will provide a basis for comparison for future studies on the African wild cat in other habitats and that it provides baseline data that can be used in comparison to other felids. Natural history knowledge of a species behaviour is the key to successful conservation efforts while ignorance of behaviour can lead to conservation failures.

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APPENDIX 1

Techniques used in the study of African wild cat, *Felis silvestris cafra*, in the Kgalagadi Transfrontier Park (South Africa/Botswana)

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Abstract

The techniques used for the capture, marking and habituation of African wild cats (*Felis silvestris cafra*) in the Kalahari are described and evaluated in this paper. African wild cats were captured, with either baited cage traps or chemical immobilisation through darting. Darting proved to be a more efficient and less stressful way of capturing cats. Very high frequency (VHF) radio collars fitted with activity monitors were especially effective in the open habitat of the Kalahari for locating and maintaining contact with cats; they also aided in determining if the cats were active or resting in dense vegetation. The habituation of individual cats to a 4×4 vehicle proved to be time consuming, but it provided a unique opportunity to investigate the feeding ecology and spatial organisation of cats through direct visual observations.

Keywords: Kalahari, capture techniques, chemical immobilisation, habituation

Introduction

The African wild cat (*Felis silvestris cafra*), is widely distributed throughout the African continent and listed by the International Union for Conservation of Nature (IUCN) as least concern (Nowell, 2008). However, status and density estimates of African wild cats are poorly known throughout most of its range. Therefore, the ecological status of wild cat populations is frequently determined from incomplete or unverified data (Nowell & Jackson, 1996). Previous research efforts on African wild cats have focused on scat analyses and opportunistic sightings of cats in their natural environment (Palmer & Fairall, 1988; Smithers, 1971; Smithers & Wilson, 1979; Stuart, 1977; Stuart, 1982). The aim of this study was to gain insight into the population genetics and behavioural ecology of African wild cats in the southern Kalahari. This required the capture of cats for the fitting of radio collars, taking morphometric measurements and obtaining DNA samples. Radio telemetry was crucial for locating individual cats for the collection of data on feeding behaviour, home range and movement patterns. Investigating the foraging and social behaviour relied on the habituation of certain individuals for direct observations.

Steel, wire, mesh and Tomahawk cage traps are widely used in the live trapping of small mammals, for example in the European wild cat and domestic cats (Biró, Szemethy & Heitai, 2005), lynx (Breitnemoser & Haller, 1993), kodkod (Dunstone *et al*. 2002), Blanford's foxes (Geffen *et al*. 1992; Geffen & MacDonald, 1993), leopard cat (Grassman & Tewes, 2005), caracal (Marker & Dickman, 2005; Melville, 2004), black-footed cats (Sliwa, 2004, 2006), dhole (Grassman *et al*. 2005), ferrets (Norbury, Norbury & Heyward, 1998) and civits (Jennings, Seymour & Dunston, 2006).

The successful capture and release of an animal is not only determined by the capture of the animal, but also by how the animals are handled, transported and kept after capture (Ebedes, Du Toit & Van Rooyen, 1996). This paper provides detailed information on the methodology involved in capturing, immobilising and habituating of African wild cats in the southern Kalahari.

Study area

Kgalagadi Transfrontier Park

This study was initiated in March 2003 and continued until December 2006 (46 consecutive months) in the Kgalagadi Transfrontier Park (KTP), which comprises the Kalahari Gemsbok National Park (South Africa) and the adjacent Gemsbok National Park in Botswana. The KTP is a 37,000 km^2 semi-arid wilderness area in the southern Kalahari, described as the western form of the Kalahari Duneveld (Mucina & Rutherford, 2006), consisting of extreme open savannah of *Acacia erioloba*, *Acacia haemotoxylon* and desert grasses. The study was primarily conducted in a 53 km^2 area surrounding the Leeudril waterhole (26º28'17.7" S, 20º36'45.2" E), in the south of the park, and included the Nossob riverbed together with adjacent calcrete ridges, *Rhigozum* veld and dune areas (Fig. 1).

Methods

All capture, darting and handling of African wild cats were approved by the ethics committee, University of Pretoria, (EC 030305-007) and SANParks Animal Use and Care Committee (SANParks AUCC). Approval to conduct research in the Botswana side of the KTP was obtained from the Office of the President: OP 46/1 CVII (48) with a supplementary permit from the Department Wildlife and National Parks (9 July 2006).

1. Capture techniques

1.1 Cage traps/Drop door traps

Cage traps (50cm x 50cm x 150cm) were constructed from welded mesh, with a single sliding door. A stepping plate mechanism towards the rear end of the cage activated the trap door. The size of the cages permitted cats to enter fully before depressing the plate, causing the door to drop. Bait, either locally bought chicken pieces or fresh road kills, suspended from a wire over the plate was used as lure. Additionally, cat urine was collected opportunistically whenever following a focal cat, stored in plastic bags and was added to baited traps as supplementary attractant for other cats (six out of 12 cats were caught with the use of urine as attractant). Cages were sometimes camouflaged by hiding them in vegetation, or covering the sides (only two of the 12 cats were caught when the cages were camouflaged). The stepping plate was covered with soil to give it a more natural feel.

The traps were set late in the afternoons and checked daily, early in the mornings. When a cat was found inside the trap, the far end was covered with a blanket in an attempt to provide a measure of security for the cat. A 40cm × 40cm crush plate, attached to a steel rod, was inserted at the front of the trap and, slowly and gently, the cat was pushed towards the back of the cage. In this way, the cat could be trapped at the far end of the cage, from where it was possible to hand inject it through the wire mesh. Zoletil^{R} (Tiletamine hydrochloride with Benzodiazephine derivative Zolazepam in 1:1 combination), at a dosage of approximately 2.5mg/kg was used for all cats caught by this method.

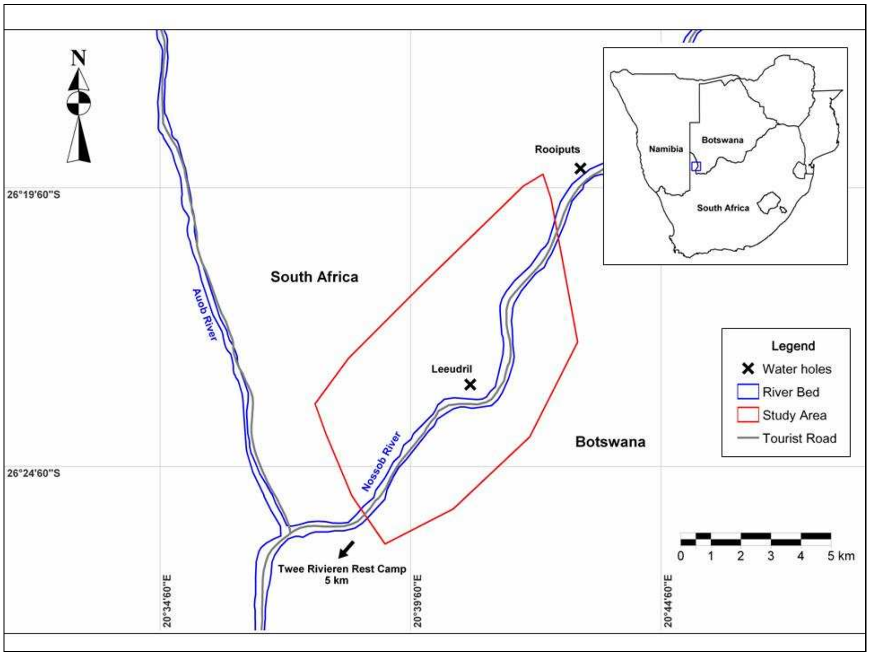

Figure 1 Study site in the KTP, indicating the area, around the Nossob riverbed and Leeudril waterhole where African wild cats, *Felis silvestris cafra*, were radio collared and monitored

Once anaesthetised, cats could be removed from the cages without difficulty, whereupon standard body measurements were taken (Table 1). A small skin sample was collected for molecular analysis and, if relevant, a radio collar was fitted. All procedures were conducted as quickly as possible, and in the immediate vicinity of the trap. On completion of the necessary procedures, the cat was returned to the shaded cage and left to recover from anaesthesia. It was released when it had fully recovered.

1.2 Darting

A CO_2 rifle (Dan-inject JM Standard model) was used to propel a standard dart syringe (10.5mm, 1.5 mL capacity) and fitted with a small rubber stopper to reduce penetration. Owing to the small size of the cats, it was necessary to lower the CO_2 pressure in the rifle as much as possible to reduce the projectile velocity and, in so doing, lessen the impact and therefore the chances of injury to an animal. As a trade-off, the range over which the dart could be propelled had to be reduced. Cats were thus always stalked to within 10m.

Cats caught by darting were immobilised with a combination of drugs and an appropriate antidote as follows (P. Buss and D. Govender, pers. comm.): either Butorphanol (1.38 mg/kg) and Medetomidine (0.4 mg/kg), with the antidote of Antipamezole administered at five times the Medetomidine dose (mg) intramuscularly and Naltrexone administered at 10 times the Butorphanol dose (mg) intramuscularly, or Zoletil (1.58 mg/kg) and Medetomidine (0.07 mg/kg), with the antidote of Antipamezole administered at 6.25–12.5 times the Medetomidine dose (mg) intramuscularly. Zoletil does not have an antidote.

2. Radio collars

African wild cats were fitted with radio collars from Africa Wildlife Tracking CC, weighing 80g – 85g, with external antennae of 20cm and a battery life of up to 18 months. Radio collars were each fitted with an activity monitor to assist in the remote detection of cat activity. Cats were detected with a two or three element handheld Yagi antenna by traversing the home range of the individual study animal and using the dune crests as high vantage points, using a Telonics handheld receiver.

3. Habituation

The open, clear spaces of the Kalahari provide ideal conditions for visual observation of animals (Begg, 2001; Mills, 2003), although the stealthy nature of cats, especially at night, required close proximity to the focal animal at all times. All radio collared cats were habituated to the presence of the research vehicle, allowing the researchers to closely follow individual cats without any obvious influence on their behaviour. This was achieved by

Table 1 Standard body measurements collected from all African wild cats trapped and darted during 2003 – 2006 in the Kgalagadi Transfrontier Park. TL = total length, HB = head body length, T = tail length, E = ear length, hf s/u = hind foot, measured in (cm) and mass (kg). The sex and means of capture are included. Sub adult cats, kittens and cats with insufficient data (*) were not included in the calculation of averages and standard deviation (SD)

ID	Sex	Status	TL	HB	T	Hf s/u	E	Mass (kg)	Capture method
002	♂	Adult	93.5	62.5	31	15.5	7	5	Cage trap
009	♂	Adult	93.4	63	30.4	15.4	7.4	4.9	Cage trap
010	♂	Adult	104	69	35	15.3	7.3	5.9	Road kill
012	♂	Adult	106.6	68	38.6	15.7	6.5	6	Cage trap
014	♂	Adult	97.5	63	34.5	15.2	6.8	5.7	Cage trap
015	♂	Adult	96.3	60.6	35.7	15.5	6.8	4.2	Cage trap
017	♂	Adult	104.8	67	37.8	15.2	6.2	5.7	Cage trap
022	♂	Adult	100.6	63.8	36.8	16	7.5	6	Dart
023	♂	Adult	98.3	63.7	34.6	15.6	7.1	4.1	Dart
024	♂	Adult	98.8	62.8	35.7	16.2	7	6.1	Dart
026	♂	Adult	100.4	66.6	33.8	15.5	8	5.2	Dart
027	♂	Adult	96.8	60.8	36	15.8	7.9	4.4	Dart
031	♂	Adult	102.1	67.6	34.5	16.1	7.1	5	Cage trap
004	♀	Adult	90	59	31	14.5	6.2	4.5	Cage trap
005	♀	Adult	108	67	41	15	7.4	4	Cage trap

006	♀	Adult	98	64	34	14	7.5	4	Cage trap
007	♀	Adult	92.3	60.3	32	14.5	6.6	3.4	Cage trap
008	♀	Adult	96	62	34	15.7	7.7	4.6	Cage trap
028*	♀	Adult	-	-	-	-	-	4.3	Dart
029*	♀	Adult	90.3	58.7	31.6	-	6.8	4.1	Dart
030	♀	Adult	89.6	58.7	30.9	15.7	7.5	3.6	Dart
032	♀	Adult	88.6	57.4	31.2	13.3	6.4	3.7	Dart
034	♀	Adult	89	54	35	15	7.2	3.7	Dart
040	♀	Adult	98.9	61.8	37.1	15.5	7.1	4.4	Dart
001*	♂	Sub adult	78	46	32	15.5	6.8	3.3	Road kill
016*	♂	Sub adult	89	56.5	32.5	14.8	5.6	3.3	Dart
025*	♂	Kitten	84.4	52.9	31.5	14.7	6.5	3.1	Dart
033*	♂	Kitten	82.4	51.4	31	14.2	7.3	2.2	Dart
036*	♂	Kitten	79.6	51.3	28.3	12.8	7.2	2.3	Dart
037*	♂	Kitten	79.6	52.1	27.5	13.5	7	2.6	Dart
039*	♂	Kitten	77.7	48.5	29.2	13.8	6	1.9	Dart
Average	♂	(n = 14)	99.2 ± 4.07	64.4 ± 2.73	34.8 ± 2.29	15.7 ± 0.45	7.2 ± 0.51	5.2 ± 0.68	
Average	♀	(n = 9)	94.3 ± 6.10	60.2 ± 3.67	34.0 ± 3.16	14.8 ± 0.77	7.1 ± 0.53	4.0 ± 0.42	

patiently following cats daily for the first week after initial capture and collaring, at a distance of 50m – 100m, while keeping the engine running. Habituation appeared to be facilitated by keeping the engine running in the beginning and slowly moving closer to the cats. After one week, the following distance was gradually decreased, until the cats could be followed from a distance of 10m – 30m without them looking back at the vehicle. Wild cats were followed on a rotational system, allowing continuous monitoring of a focal animal every night. Cats were located at night by radio tracking, with the initial visual contact being made with a 1,000,000-candle spotlight. Once a cat was located, the headlights of the research vehicle were usually sufficient to follow cats, with the spotlight used only periodically to re-establish contact when lost in patches of denser vegetation, or when cresting sand dunes. Care was taken to keep the spotlight trained behind the cat – to neither influence their hunting success negatively by blinding them, nor positively, by dazzling prey animals.

Results

1. Capture success

1.1 Cage traps

African wild cats were frequently spotted during opportunistic searches and cage traps were placed in close vicinity to these spots. Seven of the ten cats caught in the study site were trapped after being spotted in a specific area. Only three cats were caught by randomly placing the traps in the study site. Trapping success for African wild cats in the Kalahari was 1.4 cats per 100 trap nights. The trapping frequency between wild cats is highly variable and for African wild cats it was estimated at 73 trap nights per new cat, compared to the results of the European wild cat (*Felis s. silvestris*) (Biró *et al*. 2004; Corbett, 1979), at 860 and 299 trap nights per new cat, respectively. Trapping of feral domestic cats (*Felis s. catus*) ranged between 75 and 823 trap nights per new cat (Barratt, 1997; Biró *et al*. 2004; Bromley, 1986; Corbett, 1979; Daniels *et al*. 2001; Molsher, 2001, 2006), for lynx (*Lynx canadensis*) it was 67 trap nights per new cat (Mech, 1980), ocelot (*Leopardus pardalis*) was 116 trap nights per new cat (Dillon & Kelly, 2008) and leopard cat (*Prionailurus bengalensis*) 405 trap nights per new cat (Grassman *et al*. 2005). The main drawback of cage traps appeared to be the reluctance of wild cats to enter, as well as their non-selective nature (Table 1). Loss of bait could possibly have been attributed to the ineffective setting of cages. Bait was stolen on numerous occasions, by smaller mammals such as the yellow mongoose (*Cynictis penicillata*) and rodents; in some instances it was consumed by ants.

Table 2 The percentage capture success expressed as the total of cages (*n* = 1244) used during all the trapping days (*n* = 301) in the KTP

ID	Scientific name	Total	%
Empty cages		870	69.9
Bait stolen from cage		120	9.6
Cape fox	*Vulpes chama*	113	9.1
Black backed jackal	*Canis mesomelas*	38	3.1
African wild cat	*Felis silvestris cafra*	17	1.4
Genet	*Genetta genetta*	2	0.2
Porcupine	*Hysterix africanis*	1	0.1
Spotted hyena	*Crocuta crocuta*	1	0.1
Springhare	*Pedetes capensis*	1	0.1

1.2 Darting

During two darting expeditions, consisting of four nights each (10–14 hours per night), in August 2005 and January 2006, a total of 18 African wild cats were successfully darted, with only one injury reported. Cats were spotted by driving up and down the riverbed, constantly scanning with spotlights in two vehicles and looking for retinal reflections. When cats were spotted, the research vehicle slowly moved in the direction of the cat, maintaining visual contact with the vehicle headlights and a spotlight. Assistants with spotlights in the second vehicle acted as spotters, and when necessary, pedestrian herders directed the cat towards the darting vehicle. The cat was slowly approached until it stopped and a clear shot was possible. Cats were darted from a distance of no more than 10m. Once successfully darted, a cat was followed at a distance of 30m – 40m, with spotlights, until it became fully immobilised. This was important, as a premature approach could have caused the cat to flee, leading to a temporary loss of contact with a highly vulnerable animal. Within 10min – 15min after the drugs were administered, it was possible to walk up to the cat and carefully cover the head and eyes with a blanket. Standard body measurements and genetic samples were taken, and in two cases the cats were fitted with radio collars. Antidotes were very effective and cats regained full motor control within minutes after administering.

African wild cats did not appear to associate the vehicle with the darting procedures, as two cats that were fitted with radio collars were easily habituated to the vehicle afterwards. The majority of cats were darted primarily to collect genetic material for molecular analysis and were not approached again afterwards. Owing to the risk of missing the small target area on the thigh of a cat and potentially injuring it, only qualified, experienced wildlife veterinarians were employed in darting.

African wild cats were immobilised on 31 occasions (13 cats were hand injected and 18 cats were darted). No fatalities were recorded, although the fate of the injured one is not known.

2. Radio collaring

Radio collaring proved to be invaluable for finding and following cats, as they do not return to a fixed den site and are difficult to find at night. The estimated total home range sizes (100% Minimum Convex Polygon) were: adult male = $13.17\text{km}^2 \pm 7.32\text{km}^2$ ($n = 5$) and adult female = $11.75\text{km}^2 \pm 2.01\text{km}^2$ ($n = 3$) (Chapter 4). In total, 12 African wild cats were radio collared. Only one female cat showed a slight irritation to the radio collar, symptomised by localised hair loss ten days after been collared. Symptoms lasted for four weeks, with hair growing back gradually. The cat was monitored daily until all symptoms had disappeared. On two occasions, damaged radio collars were retrieved, (three weeks and two months after being fitted) suggesting that the cats had fallen prey to a larger predator (one unknown and one confirmed from tracks as a caracal, *Caracal caracal*). Two radio-collared cats disappeared (a young female, two months after being fitted and a young male, two days after), either as a result of malfunctioning radio collars or emigration to an area outside the range searched. External antenna of radio collars broke off within 2–6 months, however, this did not seem to make a difference in the detection of cats, because the cats had known home ranges (Chapter 4) and searching for a signal from high dunes was almost always successful.

3. Habituation

On average, the habituation period took 73.8 h ± 63.9 h ($n = 8$), although large individual differences occurred (Table 2). In general, females were easier to habituate (average 36.7 h ± 5.8 h; $n = 3$). Three radio-collared and habituated females had litters during the study period and dens and kittens could be approached without difficulty. Kittens were extremely curious and would investigate the research vehicle of their own accord. Male cats were more difficult to habituate (96 h ± 74 h; $n = 5$), as they move faster and over a much larger area than females, making observations of males more difficult. Habituation was lost quickly and maintaining the maximum degree of habituation required that weekly contact with each cat was maintained.

Habituated African wild cats were visually observed for 1,538 hours (males for 657 hours, females for 881 hours) on a rotational basis. Continued observations of selected individuals provided detailed information on sexual and seasonal differences in diet, foraging behaviour, movement patterns, reproduction and inter-specific interactions.

Discussion

Long-term and intensive field studies on smaller cats are still exceptional and even the common species have not been well studied (Macdonald & Loveridge, in press; Nowell & Jackson, 1996). The reason for this is the relative difficulty associated with studying small felids. Previous research on African wild cats was based on opportunistic sightings, scat and stomach analysis (Palmer & Fairall, 1988; Smithers, 1971; Smithers & Wilson, 1979; Stuart, 1977). Their nocturnal behaviour and general shy and elusive nature, make it practically impossible to study cats in their natural environment without the aid of radio telemetry. Radio telemetry has become more reliable and efficient since the 1980s (Nowell & Jackson, 1996); recently, radio collars have been designed smaller, lighter and reliable enough for the use on smaller cats. However, in spite of the advances in technology, the time required to catch smaller cats for radio collaring purposes poses a challenge. The trapping frequency of African wild cats is comparable with frequencies of the trapping of feral domestic cats (*F. s. catus)* (Barratt, 1997; Molsher, 1999, 2001). This is much lower than the results on European wild cats *(F.s. silvestris*) (Biró *et al*. 2004; Corbett, 1979), which are difficult to catch, the reason possibly being that these populations in Europe have declined, are fragmented and, in many places, are already extinct (Nowell, 2008). For black-footed cats (*Felis nigripes*), the trapping frequency was one cat for 100–200 trap nights (including recaptures) (A. Sliwa, pers. comm.). African wild cats in the Kalahari were regularly spotted during our study period, therefore it is believed that densities are much higher in the Kalahari than in Europe.

The results in this study not only confirm the difficulty of catching African wild cats, but also emphasise the general low success rate of trapping small carnivores in the southern Kalahari. Mainly trap door cages, with various combinations of bait and urine to attract cats were used. Positioning cages in areas of high animal activity should increase the selectivity of the trapping efforts (Boddicker, 1999). Our results suggest that, after an extensive search in the riverbed with a spotlight and placing of traps close to sightings of cats, the success of trapping increased in comparison with randomly placed traps.

The use of a CO_2 Dan inject dart gun proved to be the best method in the capture of free range African wild cats. The time and cost effectiveness of this capture method was enhanced with the use of drugs combined with antidotes. Once all the data and measurements were collected from the cats, they could be revived with the antidote and the darting operation could continue. Special care and qualified personnel (two wildlife veterinarians and four assistants in two vehicles) were needed to assist with darting operations, because the target animal was so small. The cost of qualified veterinarians and personnel needed in a darting operation is high; however, to obtain a representative sample size using only conventional trapping methods might have taken the researcher another few years of intensive fieldwork.

It was relatively easy to habituate African wild cats to a research vehicle (590 hours were needed to habituate eight cats). The Kalahari is the ideal location to study small carnivores, such as African wild cats, because the openness of the environment makes it possible to follow them, even at night (Begg 2001; Mills 2003). Although there were large individual differences between the times needed to habituate individuals (Table 2), it was possible to collect data on feeding, hunting, reproduction and mating behaviour of African wild cats (Herbst & Mills, 2010). To achieve this, radio telemetry was essential and because African wild cats do not travel to the same extent than larger felids, it was feasible to traverse the whole study area in a few hours in search of a signal. This was enhanced by using high dunes as a vantage point.

Conclusion

For dispersed and elusive animals, radio collaring might be the key to obtaining appropriate data (Kenward, 2001). Despite the advances in the use of satellites for radio tracking – platform transmitter terminals and global positioning system collars – they remain relatively expensive in comparison with the VHF transmitters (Kenward, 2001). In this study visual observations of habituated cats fitted with VHF transmitters enabled us to record valuable behavioural information on a nocturnal and secretive animal that more sophisticated and expensive tracking devices could not. This is the first report on the methodology of darting of wildcats (*F. silvestris*), and it proved to be a more efficient and less stressful method than cage trapping of African wild cats in the KTP.

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APPENDIX 2

Prey items captured by African wild cats in the Kgalagadi Transfrontier Park

Prey items captured by African wild cats in the Kgalagadi Transfrontier Park during 2003 to 2006 documented from direct observations. Prey items presented in prey categories and in order of decreasing cumulative mass (measured in grams, g) of prey items consumed by African wild cats. Percentage occurrence is the number of times the food category is present/total number of occurrences of all food items and the percentage of the total biomass consumed from direct observations are included

Species identified	Scientific name	Number caught	Average individual body mass (g)	Mass consumed (g)	Percentage occurrence	Percentage of total biomass consumed
Larger mammals						
Spring hare	*Pedetes capensis*	3	2000	6000		
Hare sp.	*Lepus* sp.	2	2000	4000		
Ground squirrel	*Xerus inauris*	1	625	625		
Sub-total		6	4625	10625	0.24	12.4
Small mammals						
Rodents (unidentified)		1100	50	55000		
Brant’s gerbil	*Tatera brantsii*	50	65	3250		
Brant’s whistling rat	*Parotomys brantsii*	28	80	2240		
Striped mouse	*Rhabdomys pumilio*	19	32	608		
Damaraland mole-rat	*Fukomys damarensis*	3	131	393		
Hairy footed gerbil	*Gerbillurus paeba*	11	26	286		
Short-tailed gerbil	*Desmodillus auricularis*	2	46	92		
Pygmy mouse	*Mus indictus*	6	5	30		
Bushveld elephant shrew	*Elephantulus intufi*	1	42	42		
Sub-total		1220	477	61941	47.79	72.2

Birds						
Lark sp.		50	60	3000		
Namaqua sand grouse	*Pterocles namaqua*	8	300	2400		
Cape turtle dove	*Streptopelia capicola*	9	150	1350		
Spotted thick-knee	*Burhinus capensis*	1	320	320		
Namaqua dove	*Oena capensis*	1	42	42		
Sub-total		69	872	7112	2.70	8.3
Reptiles						
Common barking gecko	*Ptenopus garrulous*	488	5	2440		
Sand snake	*Psammophis* sp.	5	200	1000		
Giant ground gecko	*Chondrodactylus angulifer*	34	23	782		
Ground agama	*Agama aculeate*	13	25	325		
Kalahari tree skink	*Mabuya occidentalis*	5	10	50		
Sub-total		545	263	4597	21.35	5.4
Invertebrates						
Locusts	Order Orthoptera	47	4	188		
Moths	Order Lepidoptera	80	2	160		
Insects (unidentified)		73	2	146		
Formicidae	Order Hymenoptera	5	2	10		
Antlion	Order Neuroptera	3	2	6		
Beetle	Order Coleoptera	2	2	4		
Scorpion	*Opistophthalmus wahlbergii*	5	5	25		
Solifugidae		4	2	8		
Unknown		494	2	988		
Sub-total		713	23	1535	27.93	1.7
Total		**2553**	**6260**	**85810**		

APPENDIX 3

The number of hours of observations on eight African wild cats (male = 5, female = 3) for each hour of the day in each season in the Kgalagadi Transfrontier Park from April 2003 to December 2006. HW = hot-wet, CD = cold-dry and HD = hot-dry

Time of day	Hours ♀			Total	Hours ♂			Total
	HW	CD	HD		HW	CD	HD	
00:00 - 01:00	15.5	13.2	14.2	42.9	6.4	12.3	19.5	38.2
01:00 - 02:00	13.2	7.2	15.5	35.9	3.2	7.3	15.4	25.9
02:00 - 03:00	13.3	6.3	14.3	33.9	2	6.2	10.3	18.5
03:00 - 04:00	9.2	4	13.2	26.4	1	2.5	7.3	10.8
04:00 - 05:00	9.8	3	10.5	23.3	1.3	1.5	6.7	9.5
05:00 - 06:00	7.3	4	5.7	17	1.2	1.8	5.6	8.6
06:00 - 07:00	2	4	5.6	11.6	1.5	2.5	5.2	9.2
07:00 - 08:00	2	8.4	7.2	17.6	1	2	2.2	5.2
08:00 - 09:00	1	10.2	10.8	22	1	2	4.3	7.3
09:00 - 10:00	1	10.3	10.3	21.6	1	2	2.3	5.3
10:00 - 11:00	1	10.4	10.2	21.6	1	2.4	3.5	6.9
11:00 - 12:00	1	8.3	9.8	19.1	1	2.6	3.1	6.7
12:00 - 13:00	1	7.5	5.2	13.7	1	2.5	2.8	6.3
13:00 - 14:00	1	7.2	6.5	14.7	1	3.6	3.5	8.1
14:00 - 15:00	1	8.4	6.3	15.7	1.3	2.2	5.3	8.8
15:00 - 16:00	1	8.1	7.8	16.9	2	9.2	7.5	18.7
16:00 - 17:00	1	15.4	10.2	26.6	4	15.3	11.4	30.7
17:00 - 18:00	6.4	25.1	15.3	46.8	8.4	22.2	18.1	48.7
18:00 - 19:00	27.2	25.5	25.4	78.1	16.3	25.5	27.1	68.9
19:00 - 20:00	25.3	25.6	25.1	76	16.2	24.3	24.4	64.9
20:00 - 21:00	25.1	26.2	25.5	76.8	15.6	27.1	26.2	68.9
21:00 - 22:00	25.2	31.4	25.2	81.8	16.5	26.1	25.3	67.9
22:00 - 23:00	24.6	24.5	28	77.1	15.3	25.5	21.3	62.1
23:00 - 00:00	23.2	18.3	22.5	64	11.1	20.3	19.3	50.7
Total	238.3	312.5	330.3	881.1	130.3	248.9	277.6	656.8

APPENDIX 4

The allelic frequencies at 18 polymorphic microsatellites among African wild cats (AWC), Kalahari domestic cat (KDC) and a reference collection of domestic cats (DCRef)

	Locus:	Pop	N	Allelic frequency																
Allelic size (bp)				134	136	140	142	144	146	148	150	152	154							
	FCA005	AWC	114	0	0	0.009	0.123	0.105	0.219	0.351	0.132	0.053	0.009							
		KDC	50	0	0	0	0.02	0.14	0.02	0.48	0.16	0.18	0							
		DCRef	42	0.071	0.048	0	0.071	0.048	0.095	0.357	0.095	0.119	0.095							
Allelic size (bp)				130	132	134	136	138	140	142	144	146	148	150	152	154	156	162		
	FCA026	AWC	114	0.237	0.061	0.035	0.079	0.009	0.026	0.009	0.009	0.105	0.07	0.088	0.114	0.14	0.009	0.009		
		KDC	50	0.02	0	0	0.1	0	0	0	0.02	0.18	0.06	0.58	0	0	0.04	0		
		DCRef	42	0.024	0.024	0	0	0.024	0	0	0.071	0.095	0.071	0.357	0.071	0.238	0.024	0		
Allelic size (bp)				86	88	90	96	98	102	104	106	108	110	112	114	116				
	FCA069	AWC	114	0.009	0.035	0.07	0.009	0.009	0.035	0.07	0.228	0.211	0.246	0.061	0.018	0				
		KDC	50	0	0	0	0.42	0.02	0	0	0.1	0.08	0.16	0.1	0.12	0				
		DCRef	42	0	0	0	0.143	0	0	0	0	0.095	0.548	0.167	0.024	0.024				
Allelic size (bp)				116	118	120	122	124	126	128	130	132	134	136	138	140	142			
	FCA075	AWC	114	0.018	0.009	0.009	0.044	0.053	0.123	0.132	0.14	0.167	0.184	0.07	0.035	0.018	0			
		KDC	50	0	0.04	0	0	0	0	0	0	0.22	0.38	0.1	0.04	0.22	0			
		DCRef	42	0.024	0.024	0	0	0	0	0.024	0	0.024	0.071	0.071	0.167	0.357	0.238			
Allelic size (bp)				126	130	132	136	138	140	142	144	146	148	150	152	154	156	158	160	162
	FCA097	AWC	114	0.044	0.035	0.026	0.07	0.088	0.026	0.053	0.079	0.175	0.07	0.044	0.061	0.14	0.035	0.018	0.026	0.009
		KDC	50	0	0	0	0	0.06	0	0	0.08	0.34	0.42	0.1	0	0	0	0	0	0
		DCRef	42	0	0	0	0	0.119	0.167	0	0.167	0.167	0.19	0.143	0.048	0	0	0	0	0
Allelic size (bp)				179	181	183	185	187	189	191	193	195	197	199	201	203				
	FCA105	AWC	114	0.061	0.018	0.044	0.193	0.202	0.053	0.184	0.14	0.061	0	0.026	0.009	0.009				
		KDC	50	0	0	0	0	0.114	0.205	0.068	0.227	0.045	0.023	0.205	0.068	0.045				
		DCRef	42	0	0	0	0	0	0.167	0.286	0.286	0.095	0.024	0.119	0.024	0				

Allelic size (bp)				120	122	124	126	128	130	132	134						
	FCA105	AWC	114	0.018	0.061	0.114	0.079	0.307	0.281	0.114	0.026						
		KDC	50	0	0	0.08	0	0.16	0.06	0.52	0.18						
		DCRef	42	0	0.19	0.214	0	0.119	0.095	0.31	0.071						
Allelic size (bp)				137	141	143	145	147	149	151	153	155	157	159	161	163	
	FCA201	AWC	114	0.009	0.044	0	0.018	0.018	0.202	0.14	0.167	0.105	0.132	0.105	0.053	0.009	
		KDC	50	0	0.44	0.06	0	0	0	0.06	0	0.12	0	0.32	0	0	
		DCRef	42	0	0	0.19	0	0.048	0	0.143	0.024	0.167	0.167	0.262	0	0	
Allelic size (bp)				206	208	210	212	214	215	216	217	218	220	222	224	226	
	FCA220	AWC	114	0	0.018	0.009	0.053	0.158	0	0.096	0	0.14	0.219	0.123	0.149	0.035	
		KDC	50	0.104	0	0.021	0	0.063	0	0.542	0	0.271	0	0	0	0	
		DCRef	42	0	0	0.167	0	0.31	0.024	0.381	0.048	0.048	0.024	0	0	0	
Allelic size (bp)				152	156	158	160	164	166	168	170	172	174	176	178	180	182
	FCA224	AWC	114	0	0.098	0.009	0.036	0.018	0.009	0.071	0.018	0.188	0.17	0.188	0.134	0.027	0.036
		KDC	50	0.04	0	0.02	0.64	0	0.02	0	0	0.06	0.08	0.14	0	0	0
		DCRef	42	0.024	0	0	0.762	0	0	0	0	0.095	0.071	0.024	0	0.024	0
Allelic size (bp)				152	154	156	158	160	162	164	166	168	170	172			
	FCA229	AWC	114	0.07	0.018	0.009	0.105	0.219	0.289	0.184	0.053	0.026	0.009	0.018			
		KDC	50	0	0	0	0.04	0.02	0	0	0.22	0.6	0.06	0.06			
		DCRef	42	0	0	0	0	0	0	0.119	0.167	0.595	0.071	0.048			
Allelic size (bp)				154	156	158	160	162	164	166	168	170	172	174			
	FCA240	AWC	114	0.009	0	0	0.289	0.289	0.035	0.07	0.158	0.044	0.105	0			
		KDC	50	0.14	0.28	0.02	0	0	0.08	0	0.04	0	0.42	0.02			
		DCRef	42	0.071	0.167	0.048	0	0	0.095	0	0.048	0.048	0.405	0.119			
Allelic size (bp)					177	179	181	183	185	187	189	191	193	195	197	199	
	FCA293	AWC	114	114	0.035	0.237	0.123	0.096	0.026	0.035	0.175	0.132	0.018	0.079	0.026	0.018	
		KDC	50	50	0	0.22	0	0.04	0.04	0.36	0.2	0.02	0.12	0	0	0	
		DCRef	42	42	0	0.19	0.071	0.024	0.071	0.405	0.024	0.095	0.119	0	0	0	
Allelic size (bp)				116	118	120	122	124	126	128	130	132	134	136	138		
	FCA310	AWC	114	0.009	0.018	0.018	0.096	0.325	0.149	0.167	0.158	0.009	0.009	0.044	0		
		KDC	50	0	0	0.06	0.1	0.32	0.02	0.06	0.04	0	0	0.4	0		
		DCRef	42	0	0	0.238	0.024	0.095	0.143	0	0	0	0.024	0.381	0.095		

Allelic size (bp)				151	153	155	159	163	167	171							
	FCA441	AWC	114	0.053	0.009	0.14	0.386	0.298	0.105	0.009							
		KDC	50	0.18	0	0.24	0.12	0.36	0.1	0							
		DCRef	42	0.024	0.024	0.119	0.31	0.262	0.238	0.024							
Allelic size (bp)				188	192	196	200	204	208								
	FCA453	AWC	114	0.579	0.096	0.079	0.184	0.061	0								
		KDC	50	0.14	0.06	0.3	0.3	0.16	0.04								
		DCRef	42	0.286	0.071	0.381	0.19	0.071	0								
Allelic size (bp)				135	137	149	151	153	155								
	FCA651	AWC	114	0.009	0	0.509	0.368	0.105	0.009								
		KDC	50	0.84	0.16	0	0	0	0								
		DCRef	42	0.857	0.143	0	0	0	0								
Allelic size (bp)				190	192	194	196	198	200	202	204	206	224	226	230	232	234
	FCA678	AWC	114	0.018	0.079	0.035	0.061	0.114	0.272	0.158	0.044	0.088	0.044	0	0	0.053	0.035
		KDC	50	0	0	0	0	0	0.25	0	0.023	0	0.636	0.023	0	0.068	0
		DCRef	42	0	0	0	0	0	0	0	0	0	0.333	0.262	0.048	0.357	0

APPENDIX 5

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Chapter 26

Black-footed cats (*Felis nigripes*) and African wild cats (*Felis silvestris lybica*): a comparison of two small felids from South African arid lands

Alexander Sliwa, Marna Herbst, and Gus Mills

Some of the leading causes for the decline of felid populations are habitat loss, habitat degradation and persecution. Africa's two smallest cat species, the black-footed cat (BFC) (*Felis nigripes*) and the African wild cat (AWC) (*Felis silvestris*) occur in southern Africa's grasslands and semi deserts and are affected by all these causes of decline. Additionally, AWC are threatened by hybridisation with domestic cats (*Felis silvestris catus*) (Smithers 1983; Nowell and Jackson 1996; Macdonald *et al*., Chapter 22, this volume). Our objectives were to: (1) explore the origins of and morphological differences between the two species; (2) compare their life history and ecological parameters; (3) compare ecological factors that impact species abundance and distribution; and (4) identify gaps in research knowledge, particularly with relevance to conservation management of the species. While variation in diet, home range size, resting site use and activity patterns were present between the two species, we could not discern significant differences in these parameters, or in population threats. We propose that collaborative research and concerted action planning will maximise the efficiency of financial resources to develop applied conservation solutions for both species.

26.1 Introduction

The BFC*,* also called the small-spotted cat, is the smallest cat species in Africa and amongst the smallest in the world. Endemic to the arid grassland, dwarf shrub and savannah of the Karoo and Kalahari in the western parts of southern Africa (Fig. 26.1) (Smithers 1983) it has the most restricted distribution of any African cat species (Nowell & Jackson 1996). It shares much of its habitat with the widespread AWC, which ranges throughout most of the African continent (Fig. 26.1; Smithers 1983; Nowell & Jackson 1996). Erratic rainfall affects the food resources in the Kalahari study area of the AWC described here and throughout the distribution range of the BFC (Leistner 1967; Nel *et al*. 1984; van Rooyen 1984).

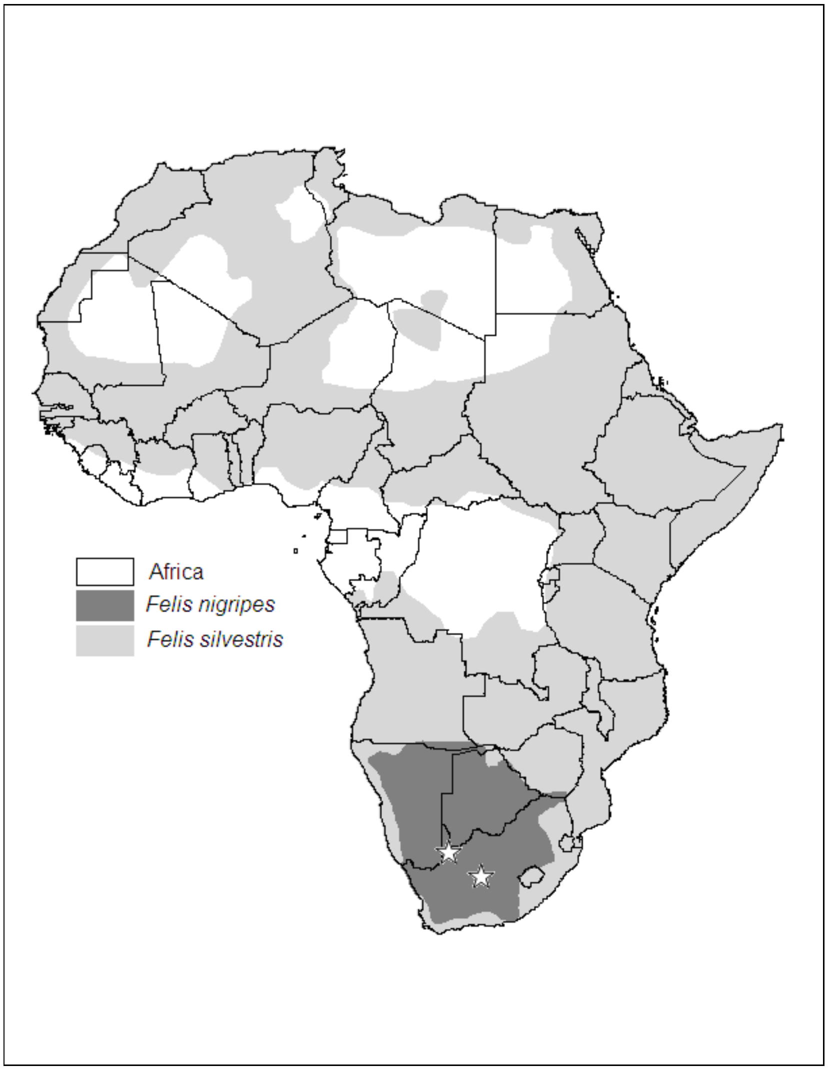

Fig. 26.1 Distribution of the African Wild cat, *Felis silvestris* and Black-footed cat *Felis nigripes* in Africa. The two stars mark the location of the study areas.

Although the species differ markedly both in coat patterns and size (Fig. 26.2) there is considerable confusion by the general public, and thus in their distribution records in southern Africa (A. Sliwa, pers. obs.). However, the contemporary distribution of the two species suggests that the BFC is sensitive to habitat and climatic variables, while the AWC has a very broad ecological niche, inhabiting almost all African habitats, with the exception of the tropical rainforests and true deserts. Within the northern portion of the AWC's distribution, the sand cat (*Felis margarita)* inhabits the driest parts of the Sahara (Sunquist and Sunquist 2002), a small cat similar in several morphological adaptations to the BFC (Huang *et al.* 2002). Reflecting this, AWCs inhabiting truly arid habitats are smaller in stature and mass, i.e. the *gordoni* wildcats of the Eastern Arabian peninsula average only 77-78 % in head-body length (♂♂ 50.3 to 65 cm; ♀♀ 47 to 60 cm) and 51-53% (♂♂ 2.7 kg to 5.1 kg; ♀♀ 2.0 to 3.9 kg) in mass compared to other wildcat subspecies (unpublished data measurements on *F. s. gordoni* by Breeding Centre for Endangered Arabian Wildlife, Sharjah, United Arab Emirates; Phelan and Sliwa 2005; Kalahari *silvestris* – Herbst unpublished data).

Fig. 26.2 (a) African Wild cat female © M. Herbst

Fig. 26.2 (b) Black-footed cat male © A. Sliwa.

All African *Felis* species have been little studied (Nowell and Jackson 1996), thus no clear limitations for their ecological separation have been defined. In this chapter we summarise what is known about the behaviour and ecology BFCs and AWCs from two intensive field studies in South Africa and make suggestions for future research and conservation measures.

26.2 Origin and size

The two cat species belong to the old world domestic cat lineage (Johnson & O'Brien 1997; Werdelin *et al*., Chapter 2, this volume), however, the BFC is thought to have diverged from the other *Felis* species about three million years ago (Johnson *et al.* 2006). The wild cat (*Felis silvestris)* of Europe, Africa, and Asia has been the subject of continuous taxonomic debate. Nowell and Jackson (1996) divided wild cats into four groups: (i) the *silvestris* group comprising the heavily furred forest cats of Europe and the Caucasus; (ii) the *ornata* group including the light-bodied steppe cats of Asia; (iii) the *lybica* group comprising the long legged African wild cats of Africa and the near East; and (iv) the domestic cat, *Felis silvestris catus*. Genetic analysis confirms that these four groups of 'wildcats' are phylogenetically very close to each other (Pocock 1907; Driscoll *et al*. 2007; Macdonald *et al.*, Chapter 22, this volume), and that interbreeding may severely threaten the status of true wild cats. This process is accelerated by habitat loss and increased contact with human settlement and associated domestic cats (Macdonald *et al*. 2004, Yamaguchi *et al*. 2004a, 2004b, Macdonald *et al*., Chapter 22, this volume).

BFCs were shorter (♂♂ = 45 / ♀♀ = 40 cm HB) and smaller in mass (♂♂ = 1.9 / ♀♀ = 1.3 kg) than AWCs (♂♂ = 65 / ♀♀ = 60 cm HB;♂♂ = 5.1 / ♀♀ = 3.9 kg) in the respective study areas close to Kimberley and Twee Rivieren, South Africa (Sliwa 2004; Herbst unpublished data), the difference in body mass being almost threefold. Smaller size allows the BFC to conceal itself better in very short vegetation and find refuge in burrows of fossorial mammals, most commonly those of springhares (*Pedetes capensis*), but also in those of the Cape ground squirrel (*Xerus inauris*), South African porcupine (*Hystrix africaeaustralis*) and aardvark (*Orycteropus afer*). In parts of its distribution the BFC utilises abandoned hollow termitaria (Smithers 1983; Olbricht & Sliwa 1997). In contrast, the Kalahari AWCs spent most of the day resting under dense bushes and vegetation (85%), holes and caves (11%) and open shade (4%) (n = 304; observations of cats resting or sleeping before an activity period; Herbst unpublished data).

26.3 Study areas

The results of the only two in-depth field studies into the behaviour and ecology of these small African cat species provide the basis for comparing them in this chapter. A study of both species in sympatry is still lacking, however the present study areas are only 500 km apart in relatively similar habitat in the Northern Cape Province, Republic of South Africa (Fig. 26.3a, b).

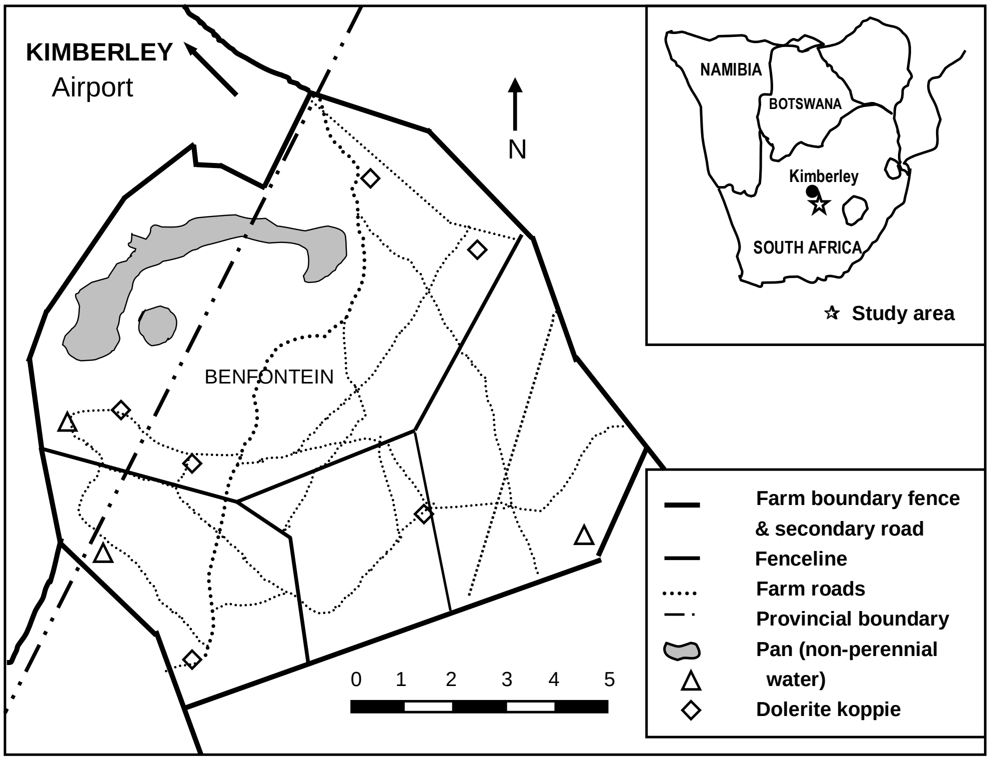

Fig. 26.3 (a) Study area for BFCs, the game farm 'Benfontein', on the border of the Northern Cape and Free State provinces, South Africa. To the northwest of the boundary fence, marked by a thick black line, is Kimberley airport. The pan (solid grey) in the northern part of the study area, the road system, and some special features are shown.

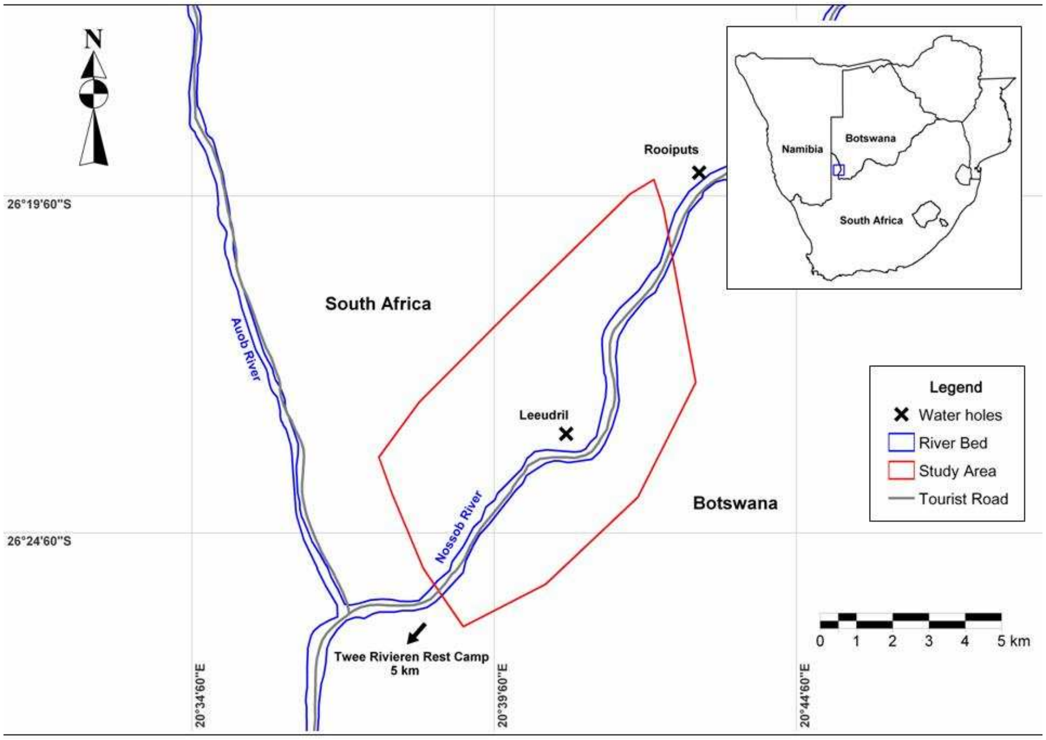

Fig. 26.3 (b) Map of study area for AWCs around the Leeudril waterhole, indicating the riverbed and associated vegetation in the Kgalagadi Transfrontier Park. The Nossob River forms the unfenced border between South Africa and Botswana

The BFC study took place between December 1992 and September 1998 on the 114 km² game farm ‘Benfontein’ (28°50’S; 24°50’E), owned by De Beers Consolidated Mines Ltd., 10 km south-east of Kimberley, (Fig. 26.3a). This area lies at the centre of the known distribution of BFCs (Nowell and Jackson 1996). The study area encompassed 60 km² with a variety of arid vegetation communities (Sliwa 1996, 2004, 2006) including the elements of three major biomes: Kalahari thornveld, pure grassveld, and Nama Karoo, which meet in the Kimberley area (Acocks 1988). An ephemeral pan and its specialised plant communities in the north dominate the farm, but in the south the vegetation changes into grassveld and finally Kalahari thornveld with deeper sandier soils on higher ground. Grass length ranges from ≤ 5 cm close to the pan to > 100 cm in the Kalahari thornveld, where scattered camelthorn trees (*Acacia erioloba*) are interspersed in an open savannah. The climate is ‘semi-arid continental’ (Schulze and McGee 1978), with cool, dry winters (mean T = 8°C in July) and hot summers (23°C in January). Annual rainfall was 431 ± 127 mm for the last 50 years (Weather Bureau, Dept. Environmental Affairs, Pretoria) and occurs mainly in spring and summer. For analysis, the year was divided into three seasons of four months each: winter – May-August; summer – November-February; autumn/spring – March-April and September-

October. Populations of wild bovids, springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcas*) and black wildebeest (*Connochaetes gnou*) are harvested at irregular intervals for sport hunting and are culled for meat, but aside from this, human activity in the study area is minimal. In the southeastern quarter of the farm, varying numbers of cattle (*Bos taurus dom.*) are grazed.

The AWC study was conducted from March 2003 to December 2006 in the Kgalagadi Transfrontier Park (KTP). The main study area was along the southern part of the Nossob riverbed and surrounding dune areas (26°28'17.7"S, 20°36'45.2"E) (Fig. 26.3b). The KTP, incorporating the Kalahari Gemsbok National Park (South Africa) and the neighbouring Gemsbok National Park (Botswana), is a 37 000 km² area in the semi-arid southern Kalahari system, which forms part of the South West Arid biotic zone (Eloff 1984). The KTP is a wilderness area with minimum human impact; only limited tourism activities are present on two main roads in the riverbeds of the park. Herds of springbok, blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*) and gemsbok (*Oryx gazella*) are dominant and large predators such as lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), brown hyaena (*Hyaena brunnea*), and cheetah (*Acinonyx jubatus*), and smaller carnivores such as caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*), Cape fox (*Vulpes chama*), honey badger (*Mellivora capensis*), small-spotted genet (*Genetta genetta*) and various raptor species are common in the KTP.

The vegetation of the Kalahari is described by Acocks (1988) as the western form of the Kalahari thornveld comprising an extremely open scrub savannah. Four main habitat types were identified and described as: (i) the dry riverbed and immediate surroundings; (ii) the adjacent *Rhigozum* veld; (iii) the sandy dune areas; and (iv) the calcrete ridges and limestone plains. For more detailed descriptions of the vegetation see Bothma and De Graaf (1973). The study site is characterised by low, irregular rainfall (Mills and Retief 1984), varying between 200 mm and 250 mm annually. Three seasons are recognised in the KTP: (i) a hot-wet season (HW) ranging from January to April, with mean monthly temperatures equal to or greater than 20ºC, with 70% of the annual rainfall falling during this period; (ii) the cold-dry season (CD) ranging from May to August with mean monthly temperatures below 20ºC and scarce rainfall; and (iii) the hot-dry season (HD) ranging from September to December with monthly temperatures approximately 20ºC and rainfall generally not more than 20% of the annual rainfall (Mills and Retief 1984).

26.4 Methods

BFCs were detected with a spot lamp at night, then were either followed to a hole and dug out by hand, or caught with a net while hiding on the ground. They were also trapped in specially made wire-cage traps, 30 x 30 x 100 cm, baited with dead birds. BFCs were anaesthetised by intra-muscular injection of 20 mg/kg ketamine-hydrochloride and 10 mg/kg acetyl-promazine in order to fit custom-built radio-collars. All radio-transmitters (AVM Instrument Co., Livermore, CA, USA) operated in the 148-150 MHz frequency range. The radio-collars weighed 50 g and had a battery life of 6-8 months. Cats were weighed to the nearest 50 g, measured, and aged based on a combination of tooth wear, body mass, reproductive condition, and subsequent territorial behaviour. A cat was classified as adult when it had permanent dentition with slight discolouring or chipping and adult body size and mass or in females had used nipples. It was classified as subadult if it was independent, had clean white unchipped teeth and, in females, unused nipples with <1 kg body mass. Resident adult males spray marked on a regular basis while non-resident males and subadult males did not. Twenty-one BFCs (six adult males, nine adult females, two subadult females - one became a resident adult, and four subadult males - three of which became resident adults during the study) were captured a total of 50 times. Twenty cats were radio-collared but three collars either stopped transmitting or were dropped after two to six days (Sliwa 2004). The remaining 17 individuals were each radio-tracked discontinuously over a period of 418 ± 355 days (mean ± SD; range: 16-1254 days).

AWCs were either caught in cage traps (10 cats), or immobilised while free-ranging by using a dart gun (18 cats). Cage traps (50cm x 50cm x 150cm) were baited with chicken pieces. A crush plate enabled a hand injection to be administered. AWCs were then immobilised with 25mg/ml Zoletil® (Tiletamine hydrochloride with Benzodiazephine derivative Zolazepam) in order to fit them with radio-collars. Radio-collars weighing 80-85 g from African Wildlife Tracking CC. were used, with a battery life of approximately 18 months. Trapping cats with cage traps did not prove to be very efficient with 1.4% success rate (n = 1244; trap nights = 301). Darting free ranging cats was more effective. It was possible to approach cats with a vehicle at night and temporarily deprive them of sight them with a spotlight. Qualified SANParks wildlife veterinarians used a CO_2 rifle (Dan-inject JM Standard model) with a standard dart syringe (10.5 mm; 1.5 ml capacity) and fitted with a stopper to reduce penetration. Cats were only darted when a clear shot was possible from a distance of 10 meters. Eighteen cats were successfully darted with a combination of drugs (Butorphanol:Medetomidine and Zoletil:Medetomidine) and antagonists (Naltrexone for Butorphanol, and Antipamezole for Medetomidine - Zoletil does not have an antidote) (Herbst *et al.* in prep). In all cases, a small skin sample, taken from a nick in the ear was collected for DNA analysis and, if relevant, a radio-collar was fitted. Eight AWCs, consisting of 3 adult females and 4 adult males and 1 young male were radio-collared.

Cats in both studies were observed directly from a four-wheel-drive vehicle after an initial habituation period of 1-3 weeks. At night, cats were observed with a low-powered handheld spot lamp and focal animals were closely followed at a distance of 10 - 100 m. We kept the beam of the spot lamp slightly behind the cat to avoid illuminating the prey or the cat. When a prey item was caught the observer attempted to identify it to the species level, where possible, and its average mass was taken from the literature and museum mammal collections for later diet analysis (Sliwa 2006, Herbst unpublished data; Tables 26.1, 26.2 and 26.3). Details of the focal cat's behaviour together with the location and length of the dominant vegetation since the last observation were recorded onto an audio recorder whenever the cat changed direction or behaviour, or after 15 minutes. Single fixes were also recorded sporadically. The BFC study included 12 observation periods, each lasting a mean of 50 ± 29 days. A total of 17 450 fixes was obtained while following BFCs over a distance of 2000 km for 3125 hours, including 1600 hours of direct observation (Sliwa 2004). For AWCs, 10 979 fixes and 1538 hours of direct observations were recorded (Herbst unpublished data).

Table 26.1 Non-mammalian prey species (for mammals see Table 26.2) captured by *F. nigripes* on Benfontein Farm, on the border of the Northern Cape and Free State provinces, South Africa; their frequency of consumption, and average mass.

Scientific name	Species identified	No. caught	Average individual body mass (g)	Mass consumed
Invertebrates:				
Solpuga sp.	Solifuge	1	1.0	1
Opisthothalmus glabrifrons	Shiny burrowing scorpion	7	1.0	7
Hodotermes mossambicus	Harvester termite (alates)	~390 (5 x)	0.15	58.5
Planipennia	lacewings, antlions	34	0.5	17
Saltatoria	locusts and grasshoppers	93	1.5	139.5
Lepidoptera	large moths + beetles	26	1.0	26
Total Invertebrates	> 10 Species	~551	~	**249**
Reptiles + Frogs				
Lamprophis fuliginosus	Brown house snake	7	5 - 80	154
Lycophidion capense	Cape wolf snake	1	50	50
Mabuya capensis	Cape skink	1	4	4
Pachydactylus capensis	Cape gecko	3	3	9
Pachydactylus mariquensis	Marico gecko	2	3	6
Pyxicephalus adspersus	Giant bullfrog	1	400	250
Pseudaspis cana	Mole snake (juv.)	1	110	110
Tompterna cryptotis	Tremolo sand frog	1	5	5
Total Reptiles/Amphibians	**8 species**	17		**588**
Birds				
Anthropoides paradisea	Blue crane (chick)	1	130	130
Anthus cinnamomeus	Grassveld pipit	5	25	125
Calandrella cinerea	Redcapped lark	29	26	754
Cercomela sinuate	Sicklewinged chat	1	18.5	18.5
Chersomanes albofasciata	Spike-heeled lark	128	26	3328
Cisticola aridula	Desert cisticola	17	10	170
Columba guinea	Speckled pigeon	1	347	300
Eremopterix verticalis	Greybacked finchlark	4	18	72
Eupodotis afraoides	White-quilled bustard	5	670*	2110
Francolinus levaillantoides	Orange River francolin (scav.)	1	*370*	-
Galerida magnirostris	Thickbilled lark	1	30	30
Malcorus pectoralis	Rufouseared warbler	2	10	20
Mirafra apiata	Clapper lark	51	32	1632
Mirafra sabota	Sabota lark	1	25	25
Mirafra africanoides	Fawncoloured lark	1	20	26
Myrmecocichla formicivora	Southern Anteating chat	9	48	432
Oenanthe pileata	Capped wheatear	1	28	28
Pterocles Namaqua	Namaqua sandgrouse	1	180*	150
Rhinoptilus africanus	Doublebanded courser	8	89	712
Telophorus zeylonus	Bokmakierie	1	65	65
Turnix sylvatica	Kurrichane buttonquail	5	42	210
Unidentified small birds		13	20	260
Eggs of respective:	black bustard, coursers, larks	2+3+6	40, 10, 2.5	125
Nestlings of larks		5	~10	50
Total Birds:	**21 species**	**302**		**10773**

* for calculation - 20% of mass for feathers and bones that were left over

Table 26.2 Mammals consumed by black-footed cats. Average mass of mammals were taken from Skinner & Smithers (1990) and the collection of the McGregor Museum, Kimberley. *Antidorcas*, *Cynictis*, *Lepus*, *Pronolagus*, and *Xerus* were included in Fig. 26.6a as ‘larger mammals’. All the other mammal taxa were pooled into ‘smaller mammals’.

Scientific name	English name	Number consumed	Average mass of one (g)	Mass consumed
Antidorcas marsupialis [1]	Springbok (only scavenged)	1	3000*	1100
Crocidura sp.	Reddish-grey musk shrew	17	9	153
Cynictis penicillata	Yellow mongoose	2	830*	900
Dendromus melanotis	Grey climbing mouse	75	9	675
Desmodillus auricularis	Cape short-tailed gerbil	5	52	260
Gerbillurus paeba	Hairy-footed gerbil	152	26	3952
Lepus capensis [1]	Brown hare	13	1500*	4330
Malacothrix typica	Large-eared mouse	595	16	9520
Mus minutoides	African Pygmy mouse	276	7	1932
Pronolagus rupestris [1]	Smith’s red rock rabbit (juv.)	1	1600*	200
Saccostomus campestris	Pouched mouse	2	46	92
Tatera leucogaster	Bushveld gerbil	87	71	6177
Xerus inauris [1]	Ground squirrel	2	600*	520
Unidentified rodent		16	10	160
Total: Mammals	**14 species**	**1246**		**29971**

Table 26.3 Prey items captured by African wild cats in the Kgalagadi Transfrontier Park during 2003 to 2006 documented from direct observations. Prey items presented in prey categories and in order of decreasing cumulative mass (g) of prey items consumed by African wild cats.

Species identified	Scientific name	Number caught	Average individual body mass (g)	Mass consumed (g)	% occurrence
Larger mammals					
Spring hare	*Pedetes capensis*	3	2000	6000	
Hare sp.	*Lepus* sp.	2	2000	4000	
Ground squirrel	*Xerus inauris*	1	625	625	
Sub-total		6	4625	10625	0.24

Small mammals					
Rodents (unidentified)		1100	50	55000	
Brant's gerbil	*Tatera brantsii*	50	65	3250	
Brant's whistling rat	*Parotomys brantsii*	28	80	2240	
Striped mouse	*Rhabdomys pumilio*	19	32	608	
Damara mole-rat	*Cryptomys damarensis*	3	131	393	
Hairy footed gerbil	*Gerbillurus paeba*	11	26	286	
Short-tailed gerbil	*Desmodillus auricularis*	2	46	92	
Pygmy mouse	*Mus indictus*	6	5	30	
Bushveld elephant shrew	*Elephantulus intufi*	1	42	42	
Sub-total		1220	477	61941	47.79
Birds					
Lark sp.		50	60	3000	
Namaqua sand grouse	*Pterocles namaqua*	8	300	2400	
Cape turtle dove	*Streptopelia capicola*	9	150	1350	
Spotted thick-knee	*Burhinus capensis*	1	320	320	
Namaqua dove	*Oena capensis*	1	42	42	
Sub-total		69	872	7112	2.70
Reptiles					
Common barking gecko	*Ptenopus garrulous*	488	5	2440	
Sand snake	*Psammophis* sp.	5	200	1000	
Giant ground gecko	*Chondrodactylus angulifer*	34	23	782	
Ground agama	*Agama aculeate*	13	25	325	
Kalahari tree skink	*Mabuya occidentalis*	5	10	50	
Sub-total		545	263	4597	21.35
Invertebrates					
Locusts	Order Orthoptera	47	4	188	
Moths	Order Lepidoptera	80	2	160	
Insects (unidentified)		73	2	146	
Formicidae	Order Hymenoptera	5	2	10	
Antlion	Order Neuroptera	3	2	6	
Beetle	Order Coleoptera	2	2	4	
Scorpion	*Opistophthalmus wahlbergii*	5	5	25	
Solifugidae		4	2	8	
Unknown		494	2	988	
Sub-total		713	23	1535	27.93
Total		**2553**	**6260**	**85810**	**100**

26.5 Life history and ecology comparisons

26.5.1 Social organisation and spatial system

Both species are solitary. A maximum of ten adult BFCs were radio-collared simultaneously in summer 1998 in the 60 km² study area, with no further cats sighted, giving an estimated density of 17 adults/100 km² (Sliwa 2004). During 2005-2006 a total of 10 AWCs were radio collared on the 53 km^2 study area and three non radio-collared cats were regularly sighted, giving a minimum estimate of 25 cats/100 km^2. Mean annual home range sizes, using the 100% minimum convex polygon method (MCP) (Mohr 1947), was 20.7 ± 3.1 km² for five male BFCs, and 10 ± 2.5 km² for seven adult females (Sliwa 2004). Mean annual home range (100% MCP) was 9.8 ± 3.4 km² for four male AWCs, and 6.1 ± 1.1 km² for three females. This suggests that despite their smaller size, BFCs have home ranges 64-111% larger than AWCs between the studies, although this difference could have been due to prey resources.

Resident adult male BFCs’ ranges overlapped with up to four different females. Intra-sexual overlap was slight for adult males (2.9%), but considerable for females (40.4%) (Fig 26.5a). Home ranges were relatively stable with mean shifts in range centres from one season to the next of 835 ± 414 m. In addition, the extent of overlap of seasonal ranges of the same individuals was 68 ± 11% (Sliwa 2004). Resident adult male AWCs’ range overlapped with up to four different females. Intra-sexual overlap between adult females was 39.8% but only 5.8% between adult male cats (Fig 26.5b). However, when a subadult male was included in the analysis the overlap increased to 9.7%. The social organisation is thus very similar between the two species and both adhered to the ‘classical’ felid system (Kitchener 1991; Sunquist and Sunquist 2002).

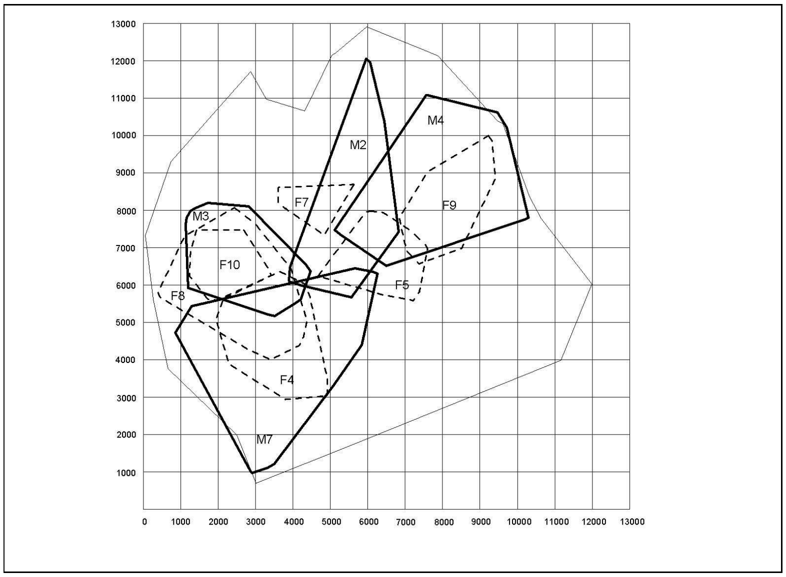

Fig.26.5 (a) 100% MCP home ranges calculated from all records for 10 seasonal ranges of black-footed cats tracked during the summer or non-mating season 1998 (January, February, March) on a 1 km² grid. Outline of the boundary fence of ‘Benfontein’ game farm given. Males = thick solid lines, females = thin broken lines.

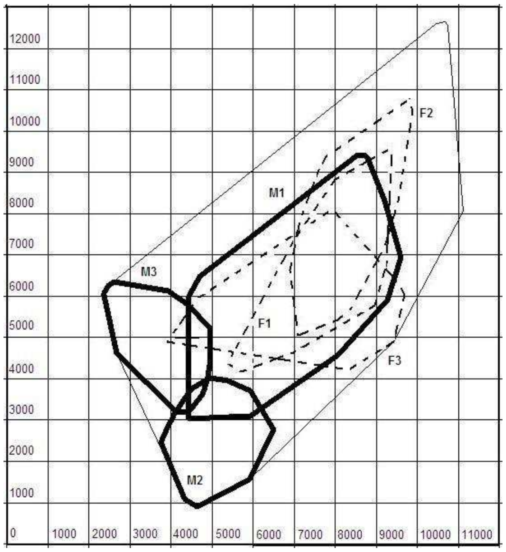

Fig.26.5 (b) 100% MCPs home ranges calculated from all records for 6 seasonal ranges of African wild cats tracked during 2004 and 2005 on a 1 km^2 grid. Outline of overall area of study site given. Males = thick solid lines, females = thin broken lines.

26.5.2 Communication

Female BFC marking frequency varied from no sprays/night to up to 268/night. Males' marking frequencies ranged widely from 0 to 598 sprays/night during the mating season. Adult resident males spray mark regularly (mean = 18 sprays/km) in contrast to non-resident and subadult males who mark only rarely (~1 spray/km) (Sliwa 2004; Sliwa unpublished data). Females left an average of 6.5 ± 10.7 marks/km (range = 0 – 44). Females exhibit urine scent marking patterns depending on their current reproductive state. The highest spray marking frequency (36 sprays/hr) of one female occurred one and a half months before conception of her litter, dropping to a lower frequency (<1 spray/hr) during pregnancy, while being entirely absent when she reared young (Molteno *et al*. 1998). Urine marks were deployed in proportion to intensity of use (Molteno *et al*. 1998). The primary function of urine spraying in females is likely advertisement of reproductive condition and may play an additional role in social spacing (Sunquist 1981).

Female AWCs showed urine spray marking patterns that were related to their current reproductive status. In all cases where females increased spray marking (n = 10) they either had kittens (n = 5) or they were in the presence of a male cat (n = 5). Spraying varied from zero to 50 sprays per observation period (observation period = eight hours or more of continuous following), giving an estimated 3.6 ± 8.7 sprays/km. The primary function of spray marking for females is probably to advertise their reproductive status to male cats, however, unlike with BFCs, spray marking was still performed by females raising young. Male AWCs show much less spatial and seasonal variation in spray marking than females and spraying ranged from 0 – 183 sprays per observation period and an estimated 13.6 ± 23.5 sprays/km moved. BFCs are seasonal breeders while AWCs seem to be more opportunistic with females already coming into oestrous while they are still suckling kittens. Thus the variation in spray marking between the two species might be explained by a difference in the mating system.

Male BFCs have a surprisingly loud call, reminiscent to that of a large domestic tomcat, with calling bouts spaced 10 to 30 minutes apart (n = 19) between July and December, coinciding with the mating seasons. They usually called after sniffing a urine spray mark, often after demonstrating flehmen. Female ‘loud’ calling, similar to that of males, was heard only once, when two competing males moved away from her (Sliwa, unpublished data). The ‘loud’ call probably supplements spray marking, serving both as spacing and attracting mechanisms during the brief female oestrous, lasting for only 36 hours (Leyhausen and Tonkin 1966; Sliwa unpublished data). The tonal frequency is an octave lower than in the larger bodied *Felis* species (Peters *et al*., in press). In addition BFCs utter softer vocalisations while communicating between mother and kittens and during mating between the male and female (Sliwa, unpublished data).

Both male and female AWCs have a loud call which is mostly evident when male cats are calling females and vice versa. The ‘prau’ call described by Dards (1983) and Leyhausen (1979) is a short, relative high-pitched cry, with a rapid rise in frequency and may be repeated. As with BFCs, ‘loud’ calling by the male AWCs usually follows after sniffing a urine spray mark followed by flehmen behaviour. The purpose of these calls is possibly to attract, advertise receptiveness or establish spacing between cats (Kitchener 1991). On two occasions male cats uttered a surprising loud whining-singing sound while courting a female. Females may, in addition, call loudly to kittens after returning from a hunt to locate them in dense vegetation. Upon reunion much softer vocalisations and rubbing between the mother and her kittens occurs. Softer vocalisations were also evident during mating between male and female cats. In summary, both species are not very vocal in general and use vocalisations in a similar context, although only in brief periods throughout the year.

26.5.3 Reproduction and mating behaviour

Wild BFCs mate between late July and March, leaving only four months where no mating occurs. The main mating period starts at the end of winter, in July and August (7 of 11 (64%) matings) resulting in litters born in September/October (Sliwa, unpublished data). One or more males follow the female, who is receptive for only 36 hours (Leyhausen and Tonkin 1966; Sliwa unpublished data) and copulate up to 10 times (Sliwa, unpublished data; n = 3 mating sequences). After a 63-68 day gestation period (Schürer 1988; Olbricht and Sliwa 1997) an average of two kittens (1 – 4) are born inside a springhare burrow or hollow termitarium (Smithers 1983; Olbricht and Sliwa 1997). On the day of parturition, females only leave the maternal den for several hours. However, after four days they will have resumed their normal routine of hunting throughout the night only returning at dawn to suckle the kittens (Olbricht and Sliwa 1997), leaving the kittens for up to 10 continuous hours per night. After their first week, kittens are moved frequently, perhaps to reduce the risk of predation. In their second month they start to eat solid food and are weaned at two months (Olbricht and Sliwa 1995). The mother carries prey back to them, both while at the den and later when kittens are left in patches of long grass waiting for her return. Older kittens are presented with live prey that they learn to hunt and kill, as observed in cheetahs (Caro 1994). Kittens become independent at about five months, when their milk dentition is replaced by permanent dentition. Up to two litters may be raised by a female in a year. One female had litters in February and then eight months later in October 1994 (Olbricht and Sliwa 1997; Molteno *et al.* 1998).

For the AWC no clear seasonality in breeding was evident. However, from all litters (n = 15) observed during the study period, eight were conceived during the hot-dry seasons, four during the hot-wet seasons and three in the cold-dry seasons. At the beginning of the study (2003) food availability was low and no litters were conceived for a 14 month period. However after an increase in rodent numbers each female produced up to four litters in a 12 month period. An average of 3 kittens (1 – 5) per litter was born, with kittens being born in dense vegetation, holes in the ground or small crevices in calcrete ridges. Kittens were moved frequently to new dens. They emerged from the den (n = 5) after 7-10 days, not wandering further than a few metres. The mother spent most of her time at the den and made short hunting trips around the den area. As kittens developed the mother stayed away for extended periods, leaving the kittens in dense vegetation or in close proximity to trees. Initially she hunted for herself and returned to the den to suckle the kittens. However as kittens approached five weeks of age she carried live prey back to the kittens. The kittens played and practised their hunting skills on the stunned prey and either ate it or left the dead prey for the mother, who ate it or covered the remains. Kittens remained with the mother for 2 to 4 months after which they dispersed.

Males spent on average 1.7 ± 0.5 days (n = 6) with a receptive female while chasing, playing and courting. Mating involves grabbing the female by the scruff of neck and the female lunging after successful stimulation (Smithers 1983; Sunquist and Sunquist 2002). Male cats did not assist in the rearing of kittens although they twice visited females with kittens.

26.5.4 Social interactions

For both species of cats very few intra-specific interactions were observed. Adult BFCs of opposite sex met rarely (two incidences) outside the mating season, resulting in a brief nose-to-nose sniff of each other. Agonistic interaction was observed only once between males during the mating season, where the resident cornered and threatened the transient while vocalising, however no physical contact took place. A subadult male encountered an adult female on two occasions, travelled for 300 and 160 m with her while attempting to play. Because a subadult male is unlikely to approach a strange female we tentatively assume this interaction was between a mother and offspring. No such visits were recorded while a female was attending to kittens. A radio-marked subadult male played with another subadult cat on one occasion (Sliwa, unpublished data). In the AWC older kittens did return to the den (n = 3), especially when litters were born shortly after each other, sometimes within a three month period. These older kittens played with the younger siblings (observed in two different litters, in one of which the older kitten returned for three consecutive nights) and joined the mother on hunting forays. On these occasions the mother did not provide prey to the older kitten, who hunted its own prey and the older kitten did not return to the den with the mother. No provisioning of food to younger siblings was observed.

For both species of cats very few intra-specific interactions were observed and AWCs were solitary except for the short periods (2 – 4 months) when females cared for kittens or during the brief mating periods, when males trailed receptive females (1-2 days). Twice male cats visited dens with kittens. The mother remained with the kittens, pulling her ears back and uttering a soft hissing sound after which the male left. Often in encounters (n = 12), AWCs may stare at each other for several minutes at a distance without any interactions after which they walk away from each other. Two males were observed fighting, spitting, scratching and caterwauling after which they ran away from each other. On three occasions the dominant male cat in the study area stalked up to smaller subadult male cats and chased them away.

26.5.5 Inter-specific interactions

On five occasions black-backed jackals circled cornered adult BFCs. Each time the BFC attacked, succeeding in driving the jackal away (Olbricht and Sliwa 1997; A. Sliwa, pers. obs.). However, kittens and inexperienced subadult cats are more likely to be in danger of predation, particularly when two jackals are involved. In the three cases this was observed, both jackals attempted to bite the cat in the back, making it more difficult even for an adult cat to stand its ground, although no incident of killing was directly observed. Black-backed jackals also stole hares (*Lepus* sp) from AWCs on two of the six occasions they were seen to catch one, having being attracted by the noise of the chase through vegetation (as opposed to the sounds of the prey – on only one occasion did a hare cry out loud). Afterwards, the cat successfully took cover in thick vegetation. Although larger mammals such as hares contribute a large amount of food for an AWC, the pirating of kills (kleptoparasitism) by jackals probably contributes to the cats' preference for hunting smaller rodents.

On three occasions in the Kimberley study site, BFCs, on sensing an AWC, squatted low until the AWC passed without detecting them. Recently two radio-marked adult BFCs were reported killed by a caracal and one by black-backed jackal (2007, B. Wilson and J. Kamler, pers. comm.). There were numerous interactions between BFCs with other species resulting in the investigation of the other species or vice versa with no specific outcome, e.g. aardwolf (*Proteles cristatus*), South African hedgehog (*Atelerix frontalis*), springhare, springbok, and even ostrich. Once, a male BFC stole a *Tatera* gerbil kill from a striped polecat (*Ictonyx striatus*), by driving it away. Also a marsh owl (*Asio capensis*) trailed a hunting BFC on three consecutive nights and captured small birds flushed by it (Sliwa 1994).

On five occasions AWCs avoided larger predators (leopards, lions, cheetahs and caracals) by running or hiding from them in dense vegetation. There have been records of caracals and leopards killing and consuming AWCs in the study area (M. Herbst and M.G.L. Mills, pers. obs.). African wild cats chased away Cape foxes and small-spotted genets on rare encounters. A giant eagle owl (*Bubo lacteus*) twice tried to grab a large adult male AWC on his back while the cat was crossing a clearing in the riverbed. The owl was unable to lift the cat and the cat then ran into thick vegetation.

26.5.6 Activity cycle and movement patterns

BFCs were strictly crepuscular and nocturnal, with cats leaving and returning to their dens within 30 minutes of sunset and sunrise (Olbricht and Sliwa 1997). Occasionally, though, during particularly cold and wet conditions they were seen basking close to their den during daylight. Their activity period varied with the length of the night, according to the season, from 10-14 hours. They were active throughout the night, once they left the den at dusk until they returned to a den at dawn, travelling an average of 662 ± 89 m/hour (Fig. 26.4). Part of their activity involved sitting outside rodent burrows, for between 30-120 minutes and (judging by the constant movement of their ears) poising to pounce. On frequent occasions these longer stationary periods resulted in a successful pounce. BFCs used predominately grassy habitats and were never observed to enter rocky or more densely wooded habitats.

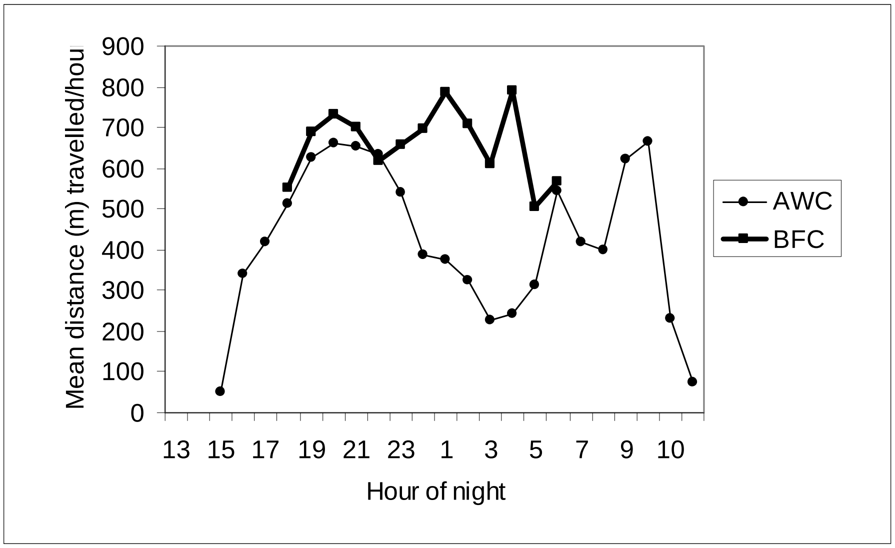

Fig. 26.4 Activity as a function of average distances moved during each hour of the day/night for black-footed cat (BFC; n = 10, 85 nights) and African wild cat (AWC; n = 8, 91 nights).

AWCs were not as nocturnal as generally believed (Smithers 1983; Sunquist and Sunquist 2002) and their activity patterns depend on season and food availability. Typically, they became active as the sun is setting, with a peak activity time between 20:00 and 22:00, followed by a slow decrease in activity in the pre-dawn hours. At dawn there was an increase in activity and they remained active until late in the mornings, especially in winter months (Fig. 26.4). There are periods when cats lie down in front of rodent burrows, waiting for prey to appear. Although the cats may close their eyes, their heads are up and their ears constantly move, remaining alert to the sounds around them (from 344 observations 27% resulted in successful kills, 9% were unsuccessful catching attempts and in 64% no attempts were made). Sometimes the cat would eventually lower the head and spread out laterally, resting and remaining in that position for several hours before continuing to hunt again. In contrast to BFCs, they do not have a shelter to which they return during the day. African wild cats rest in thick vegetation (47%), in the shade of *Rhigozum* bushes (33%) or holes in the ground, trees, small crevices (16%) or just in the open (4%).

Average distances travelled per night by ten BFCs (5♂♂ / 5♀♀) during 85 nights, where they were continuously observed for their entire activity period, was 8.42 ± 2.09 km (4.42-14.61 km). For eight AWCs (5♂♂ / 3♀♀) on 94 nights the distance was 5.1 ± 3.35 km (1.07 - 17.37 km). So BFCs travelled about 65% further per night than AWCs, and this difference could have been influenced by prey abundance.

26.5.7 Diet

During the BFC study, 1725 prey items were consumed by 17 habituated cats (Sliwa 2006). Average prey size was 24.1 g ± 47.4 g (SD). Males fed on significantly larger prey than did females (8 ♂♂ average = 27.9 ± 53.2 g, n = 795 items; 9 ♀♀ = 20.8 ± 41.5 g, n = 930; Mann Whitney U-test: U = 349244, p = 0.042). Fifty-four prey species (Table 26.1 and Table 26.2) were classified by their average mass into different size classes for mammals, birds, amphibians/reptiles, and for invertebrates. Smaller mammals (5–100 g) constituted the most important prey class (54%) followed by birds (26%) and then larger mammals (>100 g; 17%) (Fig. 26.6a). Males and females took prey size classes at significantly different proportions, most notably for small birds (♀♀ = 21% vs ♂♂ = 13%) and larger mammals (♀♀ = 9% vs ♂♂ = 25%) (Sliwa 2006).

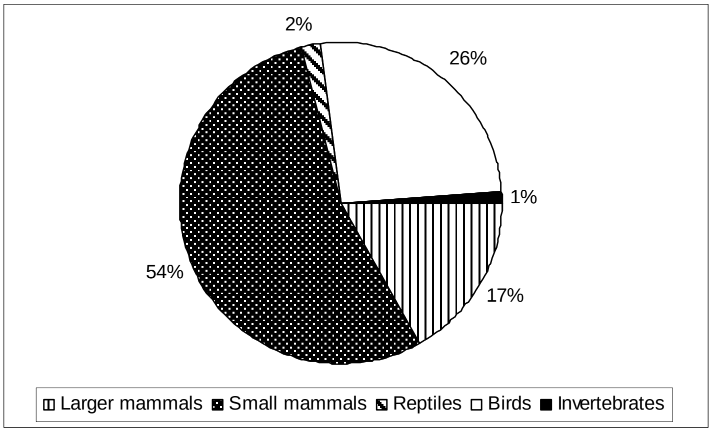

Fig. 26.6 (a) Prey composition from direct observations expressed as percentage of total biomass consumed by black-footed cats, pooled for 5 prey classes and for both sexes combined.

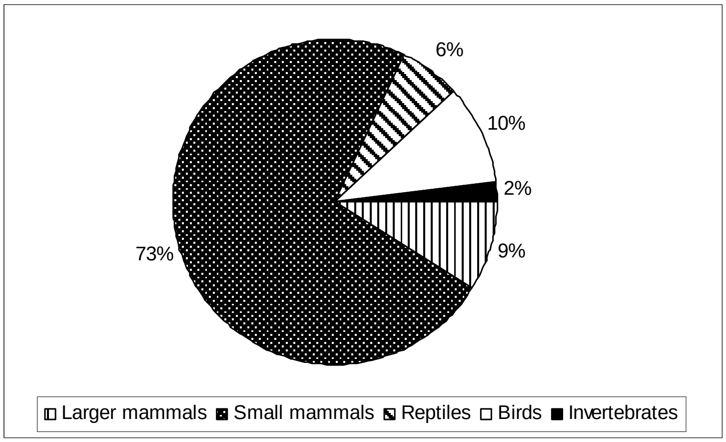

Fig. 26.6 (b) Prey composition from direct observations expressed as percentage of total biomass consumed by African wild cats, pooled for 5 prey classes and for both sexes combined

During the AWC study, 2553 prey items were observed being caught, of which 81% could be identified to one of five food categories (invertebrates, reptiles, birds, small mammals (<500 g), larger mammals (>500 g) and comprising 26 species (Table 26.3). Nineteen percent of the food items were classified as unknown as they were too small and consumed too quickly to be identified, thus data could be biased towards larger food items. From the hot-dry season of 2003 to the cold-dry season 2004 (Sept 2003 – Aug 2004), 97% of these total unknown food items were recorded when rodent numbers were lowest and invertebrate consumption was highest. Excluding unknowns, mammals made up 82% of the cumulative prey biomass consumed (73% small mammals and 9% larger mammals), followed by birds (10%) and reptiles (6%) (Fig. 26.6b). The most frequently captured prey items were small mammals (44%) followed by reptiles (23%). Small mammals almost exclusively consisted of murids with only one recorded insectivore preyed upon (Bushveld elephant shrew, *Elephantulus intufi*). During 1538 hours of observations on eight habituated AWCs, a total of 85.8 kg of prey items were consumed with small mammals contributing to 61.9 kg of the diet. There were no significant difference in the prey size of AWC sexes and both preferred small mammals. AWC females consumed more birds than males (Herbst unpublished data).

For an overall comparison between the diets of the two species, mammals made up 72% of the diet of BFCs compared to 82% of the diet of AWCs, birds made up 26% of the diet of BFCs compared to 10% of AWCs and invertebrates and amphibians/reptiles combined constituted just 2% of the total prey mass consumed by BFCs compared to the 8% for AWCs. With regard to mammals, the most common species taken by BFCs, the 16 g large-eared mouse (*Malacothrix typica*), was considerably smaller than the one most commonly taken by AWCs, the 65 g Brant's gerbil (*Tatera brantsi*). Although the diet composition of both species rank mammals as the preferred prey item, birds seems to be more important in the diet of BFC than in the AWC. However seasonal prey availability is probably the most important determinant in the percentage of consumption of prey species in both BFC and AWC diet.

26.5.8 Seasonal variation in the diet

For the three 4 month seasons of the year recognised in the BFC study, ectothermic prey items were unavailable during winter, when larger birds and mammals (>100 g) were mainly consumed. Small rodents like the large-eared mouse (*Malacothrix typica*, 595 captures) were particularly important (34.5% of all captures, 23% of total prey mass) for females during the spring and early summer when they were suckling kittens. Male BFCs showed less seasonal variation than females in prey size classes consumed (Sliwa 2006). This sex-specific difference in prey size consumption may ultimately help to reduce intra-specific competition. Despite this difference, the largest part of the diet (57%) of both sexes was made up by small sized prey ((♀♀ = 66% vs ♂♂ =4 9) (Sliwa 2006; Fig. 26.7a).

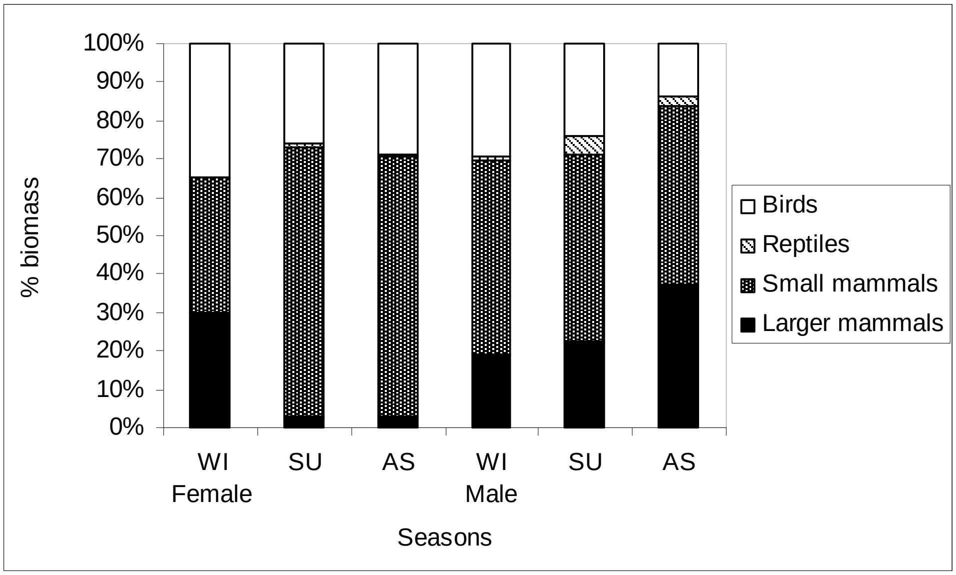

Fig. 26.7 (a) Total prey mass consumed in the four prey categories with percentages larger than 1.5% by male and female black-footed cats across different seasons from visual observations (WI = winter, SU = summer, AS = autumn/spring). Invertebrates were not considered.

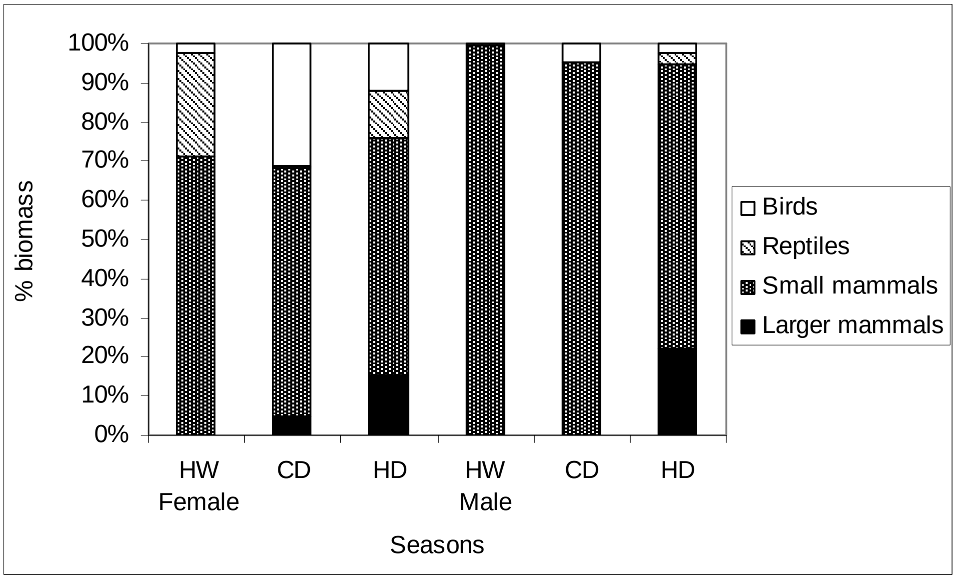

Fig. 26.7 (b) Total prey mass consumed in the four prey categories with percentages larger than 1.5% by male and female African wild cats across different seasons from visual observations (HW = hot-wet, CD = cold-dry, HD = hot-dry). Invertebrates were not considered.

Small mammals and reptiles were the most commonly consumed prey items by AWCs, and combined, these contributed to more than 57% of the prey numbers eaten in each season. Small mammals contributed more than 65% to the cumulative biomass consumed by AWCs over all seasons. During the study, reptiles showed significant seasonal variation, being most common in the hot-wet season (18% of the biomass of the diet of AWC), to less than 1% during the cold months when reptiles are known to hibernate (Branch 1998). The percentage biomass contributed by birds also indicates significant seasonal variation (hot-dry months = 17%, cold-dry months = 1.6%). Because the categories ‘Insects’, ‘Unknown’ and ‘Other’ contributed less than 1.5% to the total prey biomass consumed, these categories were omitted from the analyses. Although the dietary composition for both sexes differed significantly between seasons, small mammals contributed most to the total prey biomass eaten over all seasons (♂♂ = 70% and ♀♀ = 57%) (Fig. 26.7b).

26.5.9 Biomass consumed per distance moved

In order to compare the energy needs for both species we calculated the biomass consumed per night and the distance moved. The average prey mass consumed per night for BFCs was 237 ± 105 g (67 – 611 g) and for AWCs it was 401 ± 358 g (2 - 2250 g). The latter consumed an average of 107.9 ± 133.8 g/km travelled (range 0.94 – 979.9 g) while BFCs consumed only 30.3 ± 17.1 g/km (6.5 – 110.2 g). This translates to an average of 13.7 ± 17.2 (range 1 –

113) prey items captured by AWCs per night compared with 12.4 ± 5.3 (range 2 – 26) captured by BFCs. While the number of prey items caught per night is similar for the species, the difference in biomass consumed per kilometre travelled is 3.5 fold. When this is calculated for the two species per kg body mass, it is 18.9 g/km/kg of cat for BFCs (mean = 1.6 kg body mass for sexes pooled) and 24 g/km/kg for AWCs (mean 4.5 kg), a 38.6 % higher prey mass consumption per km and kg body mass.

During the hot-dry (HD) and hot-wet (HW) seasons, AWCs consumed more biomass per kilometre than during the cold-dry (CD) season (HD = 130.3 ± 177 g/km, HW = 107.8 ± 105.6 g/km, CD = 75.8 ± 48.4 g/km). However during the winter (i.e. CD) months the cats travel further per observation period (eight hours or more of continuous observations) (HD = 4.2 ± 2.5 km, HW = 4.8 ± 4.2 km and CD = 6.5 ± 3.4 km) and they are active over a longer period, including early afternoons and late mornings. BFCs consumed similar biomass per kilometre during all seasons (summer = 31.1 ± 15.7 g/km, winter = 29.5 ± 22.3 g/km, autumn/spring = 30.2 ± 14 g/km). BFCs travelled similar distances in all seasons (summer = 8.9 ± 2.1 km, winter = 8.7 ± 2.3 km, autumn/spring = 7.8 ± 1.8 km).

26.6 Conclusions and recommendations

We compared BFCs with AWCs to see if body size differences might also explain differences in the life history and ecology of these two small felid species (Table 26.4). Observed differences between the species may also reflect the environmental differences of the study areas and also the rainfall patterns of the study periods. Some possible but as yet not fully tested hypotheses are discussed below.

Both cats are mainly nocturnal, however AWCs are more flexible and hunt during daylight. BFCs have a set activity period from dusk till dawn and return to rest mostly within dens during daylight. This may reduce predation risk by diurnal raptors as well as persistent mobbing of BFCs by passerine birds, the latter seen often when they travel at dusk and dawn (Olbricht and Sliwa 1997). Although AWCs in the Kalahari face similar predation risks with even larger predators present, their larger body size may be more advantageous for hunting in daylight hours, possibly being less susceptible to diurnal raptor predation. Alternatively, a more diurnal activity regime might reduce inter-specific competition since the AWC is part of a carnivore guild of various smaller and similar sized carnivores in the Kalahari.

In many predator studies prey abundances and availability have been found to be a crucial factor in facilitating and determining distributions and co-existence (Creel and Creel 1996;

Durant 1998; Karanth and Sunquist 2000). BFCs and AWCs fed mainly on mammalian prey between 5 – 100 g. There was however a difference between the most frequently captured prey species. BFCs hunted mostly large-eared mice (*Malacothrix typica*) (mean = 16 g) (Sliwa 2006), whereas AWCs took Brant's gerbil (*Tatera brantsi*) (65 g). Expressed as prey mass per unit kilogram of cat, BFCs took 10 g of prey and AWCs 14.4 g of prey. Both species consumed a similar number of prey items each night, therefore the fact that the most commonly available rodent eaten by AWCs was larger than that eaten by BFCs resulted in a larger biomass consumed by AWCs. However, when comparing the percentage biomass consumed per unit (kg) body mass of cat, BFCs consumed 14.9% of their body mass per night compared to 8.9% for AWCs. This is probably due to the higher metabolism related to smaller body size in BFCs, and the need to cover longer distances per night to capture enough prey to sustain their energy needs. Despite the strong seasonal variation in biomass consumed per distance moved by AWCs (76-130 g/km), even the lowest prey mass consumed in the cold winter season by AWCs was 2.5 times that consumed by BFCs (30 g/km) (Table 26.4).

The distribution of BFCs may be influenced by the availability and abundance of certain prey species and prey sizes (i.e. the large eared mouse is absent in the Kalahari ecosystem and AWC study site). One could describe the BFC as a habitat specialist that shows a preference for grassland and avoids wooded or rocky areas. It moves further per night, while consuming less biomass per distance than the AWC. This is reflected in the larger annual home ranges and distances travelled per night of BFCs. Alternatively, these differences could have been due to differences in prey abundance between sites.

BFCs consumed more birds (26%) in comparison to AWCs (10%), probably resulting from their smaller size and agility, and being able to conceal themselves better in short vegetation. Thus, a greater abundance of small birds in a habitat may favour BFCs over AWCs. Although we could not compare bird abundance on each site, the body size of a cat may be negatively correlated with hunting success of small birds as demonstrated in the differential hunting success by BFC sexes. However, AWCs may not need to supplement their diet with birds and the larger sized and more abundant rodents might be sufficient for their dietary requirements. During seasons with low rodent numbers in the Kalahari AWCs changed their diet accordingly and took more invertebrates and reptiles during the warmer seasons than BFCs and, to a lesser extent, birds. Seasonal variation in the Kalahari contributed largely to differences in AWC diet and the biomass consumed per night, with less seasonal variation in the BFC study.

Table 26.4 A summary of the ecological and life history traits of African wild cats and Black-footed cats

	Study site	Years data collected	Adult Cats radio collared	Head body size (cm)	Weight (kg)	Resting places	Estimated densities (cats/ 100 km^2)	Home range MCP 100%	Intrasexual overlap	Urine spray marking/ km	Avg litter size (range)	Max litters per year	Activity	Distance travelled per night (km)	Biomass (g) per distance consumed
F. silvestris	Kgalagadi Transfrontier Park, Northern Cape, SA and Botswana	2003-06	♂ = 5 ♀ = 3	♂ = 65 ♀ = 60	♂ = 5.1 ♀ = 3.9	No fixed resting place - dense vegetation or in trees	25	♂ = 9.8 km^2 ♀ = 6.1 km^2	♂ = 5.8% ♀ = 39.8%	♂ = 13.6 ♀ = 3.6	3 (1-5)	4	Mainly nocturnal although active mornings and afternoons	5.1 ± 3.35	401 ± 358/night 108 ± 134/km
F. nigripes	Benfontein, Kimberley, Northern Cape/ Free State, SA	1992-98	♂ = 8 ♀ = 10	♂ = 45 ♀ = 40	♂ = 1.9 ♀ = 1.3	den sites in holes or hollow termitaria	17	♂ = 20.7 km^2 ♀ = 10 km^2	♂ = 2.9% ♀ = 40.4%	♂ = 12.6 ♀ = 6.5	2 (1-4)	2	Nocturnal	8.42 ± 2.09	237 ± 105/night 30 ± 17/km

Source: *Felis nigripes* (Sliwa 1994, 2004, 2006)
Felis silvestris (Herbst unpublished data)

BFCs consumed more birds (26%) in comparison to AWCs (10%), probably resulting from their smaller size and agility, and being able to conceal themselves better in short vegetation. Thus, a greater abundance of small birds in a habitat may favour BFCs over AWCs. Although we could not compare bird abundance on each site, the body size of a cat may be negatively correlated with hunting success of small birds as demonstrated in the differential hunting success by BFC sexes. However, AWCs may not need to supplement their diet with birds and the larger sized and more abundant rodents might be sufficient for their dietary requirements. During seasons with low rodent numbers in the Kalahari AWCs changed their diet accordingly and took more invertebrates and reptiles during the warmer seasons than BFCs and, to a lesser extent, birds. Seasonal variation in the Kalahari contributed largely to differences in AWC diet and the biomass consumed per night, with less seasonal variation in the BFC study.

The AWC was possibly better able to respond reproductively to temporary food restrictions and super abundances than the BFC, although a climatic variation between sites confounds this data. AWCs have larger litter sizes and may raise up to 4 litters per year, while reproduction can fail entirely in years with low prey abundance. Data for comparisons from the BFC is still lacking. AWC mothers take short hunting trips around the den, while female BFCs may need to travel longer distances to capture sufficient prey for their dependent offspring.

26.7 Research gaps in relation to conservation management

Both species were influenced by the presence of competitors and predators. A high density of mesocarnivores like jackals and caracal would both result in harassment, pirating of kills and even intra-guild predation. This has been observed in other predator guilds (Palomares and Caro 1999) specifically between foxes (*Vulpes macrotis, V. velox*, *V. vulpes*) and coyotes (*Canis latrans*) (Moehrenschlager and List 1996) and for large felids between tiger (*Panthera tigris*) and leopard (Seidensticker 1976) and among cheetah, lion and leopard (Caro 1994), but recently also proposed for smaller felid guilds in tropical America comprised of ocelot and oncilla (*Leopardus pardalis*, *L. tigrinus*,) (de Oliveira *et al*., Chapter 27, this volume). In South African farming communities where livestock depredation occurs, densities of jackals and caracals are regulated through predator control. In the protected area of the southern Kalahari there is little interference from human activities and predator numbers are mainly regulated by available food resources (Mills 1990).

Increasing human impact, through population growth and changes in land use patterns (small holdings farming, irrigation, overgrazing), may also affect the two cat species differently. The BFC avoids human contact (Olbricht and Sliwa 1997; Sliwa 2004), while a male AWC radio-monitored in the same study area stayed close to permanent water and human habitation (Sliwa, unpublished data). However, if species like jackals and caracals are removed from small stock farming areas this may be to the advantage of small cats especially the BFC. The AWC seems to have a higher tolerance to human-modified habitats, and may profit from increasing rodent populations associated with farming, however it may also be threatened in its genetic integrity through hybridisation (Nowell & Jackson 1996, Yamaguchi *et al.* 2004b) and disease transfer (Mendelssohn 1989; Macdonald *et al*. 2004) from domestic cats associated with man.

Studies of smaller African felids are in their infancy, especially within their carnivore guild. A number of key questions arise from our comparative research: (1) what are the maximum levels of habitat loss, degradation and fragmentation both species could tolerate? (2) What influences the distribution of the BFC – when does competition pressure from potential predators and competitors become too high, leading to its exclusion from certain areas? (3) Is conservation management for both species similar or mutually exclusive? (4) Could AWCs negatively affect BFC numbers, especially given this behaviour among other felid species?

There is an urgent need for comparative studies of small felids in order to address specific conservation questions. We trust that our studies will both contribute to the basic understanding of BFC and AWC ecology, as well as provide the baseline data for future research and conservation measures for small African felid studies.

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