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CHAPTER 3

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

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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.
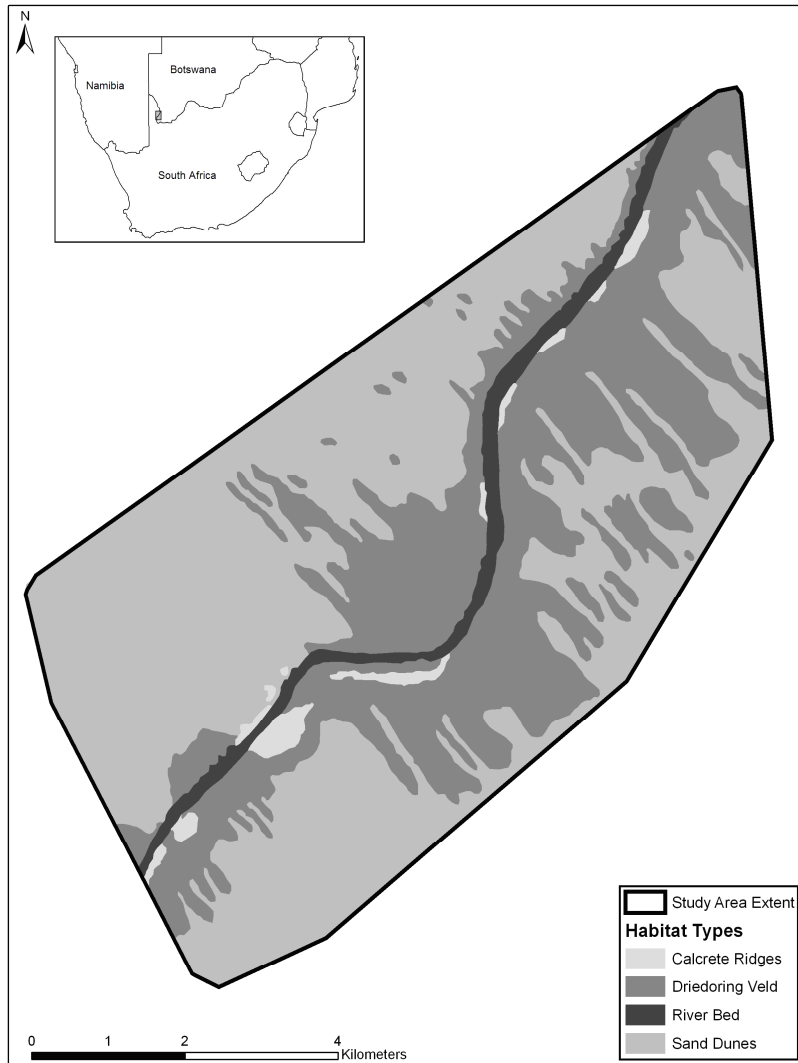

Figure 3.1   Map of the study area in the Kgalagadi Transfrontier Park indicating the different habitat types

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, 26º28'17.7"S, 20º36'45.2"E) for the study period (F ig. 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).
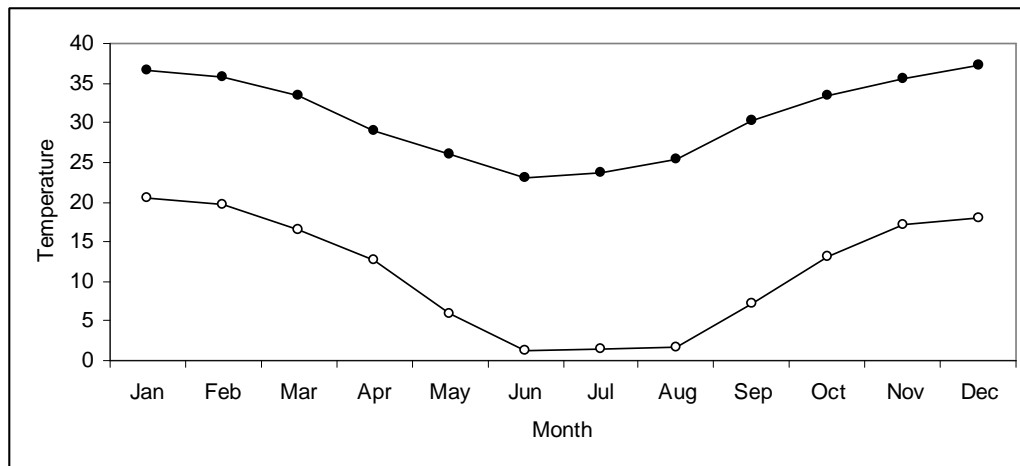

Figure 3.2a   Monthly averages of the minimum (○) and maximum (●) temperatures (ºC) at the Twee Rivieren rest camp for the years 2003 to 2006
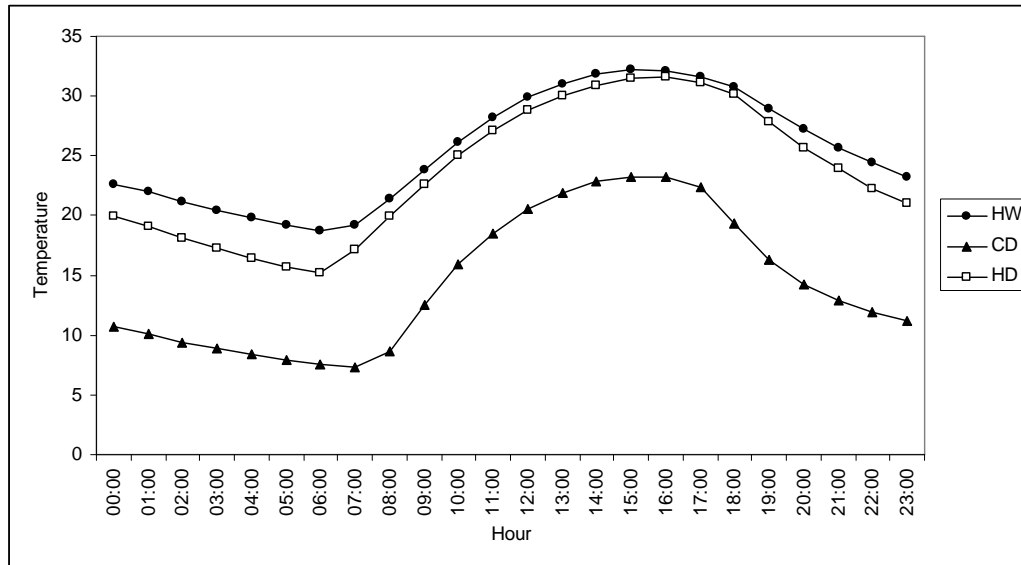
Figure 3.2b   Average hourly changes in temperature in the hot-wet (HW), cold-dry (CD) and hot-dry (HD) seasons calculated from the nearest weather station in Upington

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

| Prey category | Male | | | Female | | | Pooled |
	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).
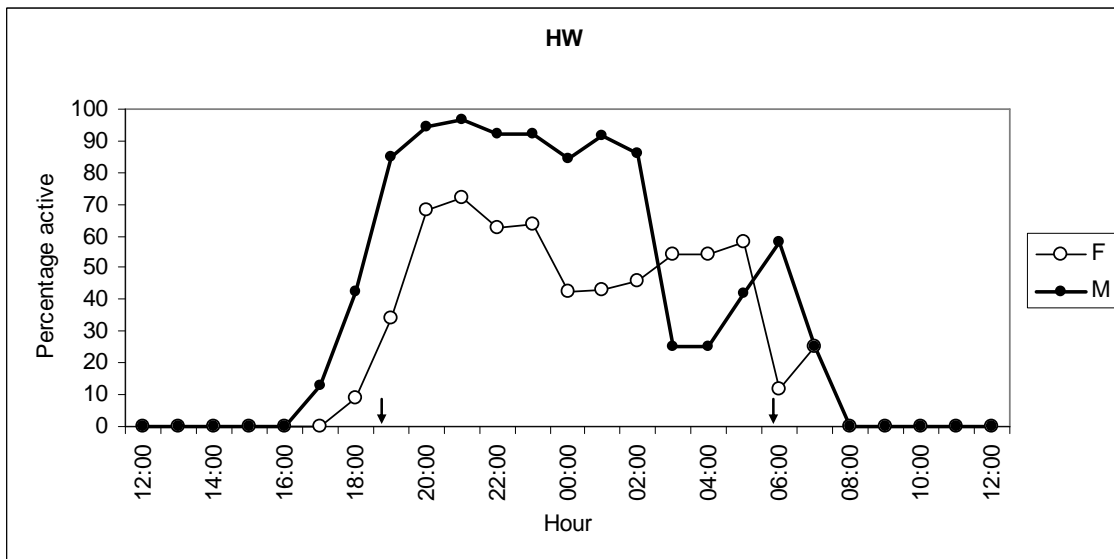
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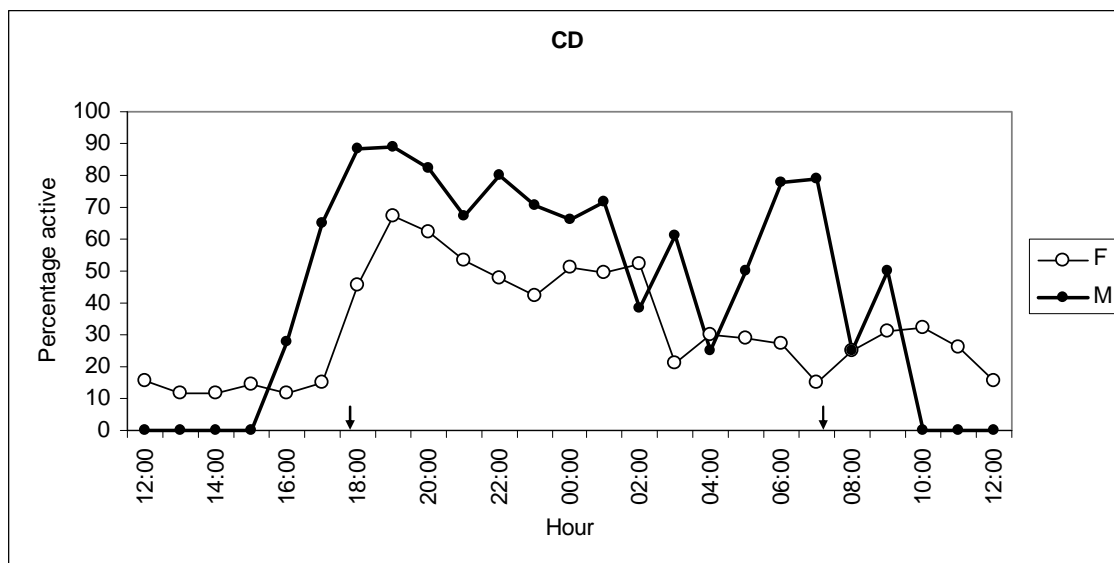
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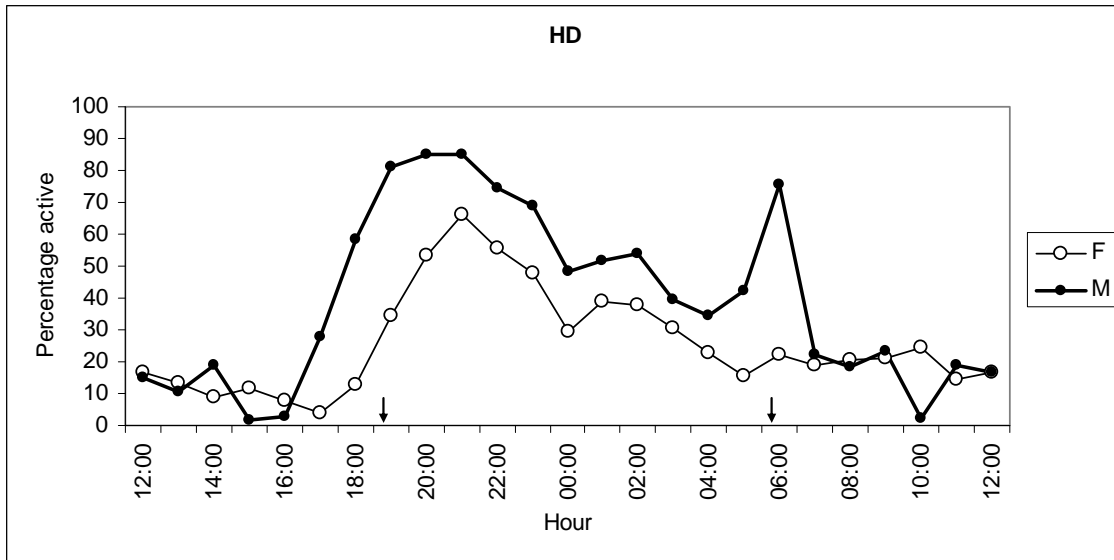
c).

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.
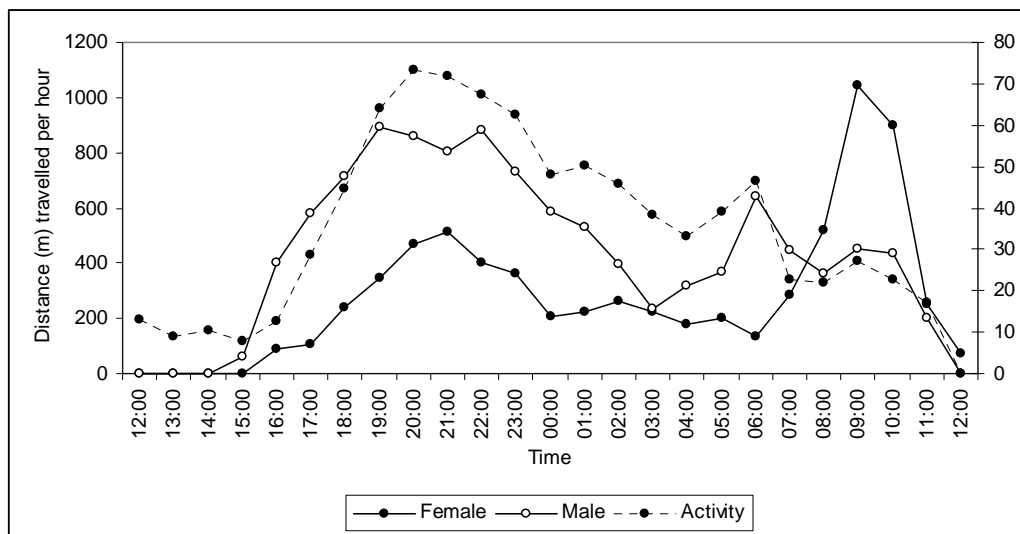

Figure 3.4   The distance travelled (m) and the percentage active per each hour of observation for male and female African wild cats during the study in the KTP. Observation periods = 8 hours or more (males: n = 42 observation periods; females: n = 49 observation periods)

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).
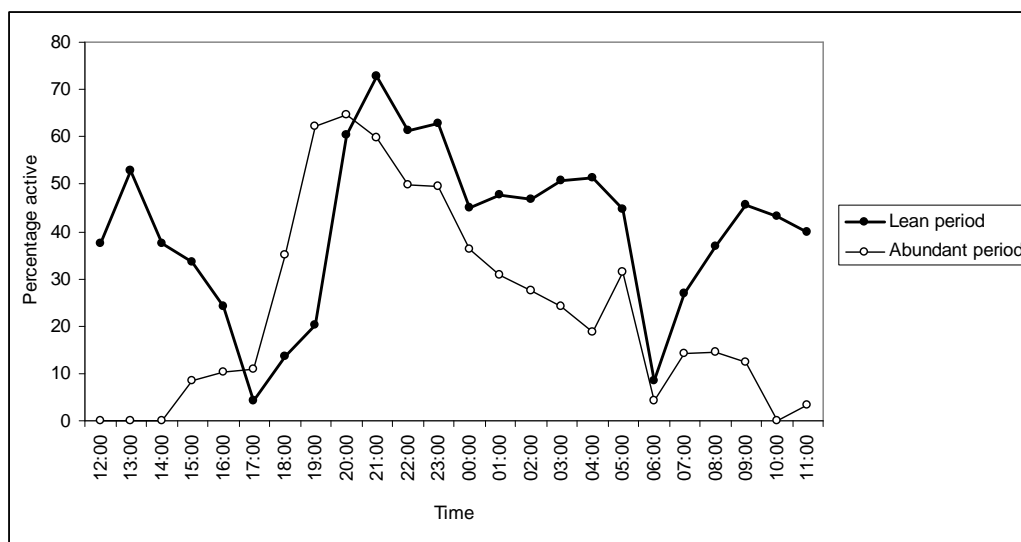

Figure 3.5   Percentage activity of a single African wild cat female over a twenty four hour period, indicating the change from the lean period (●) (cold-dry 2003 to hot-wet 2004) in comparison to the abundant period (○) (cold-dry 2004 to hot-wet 2006)

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

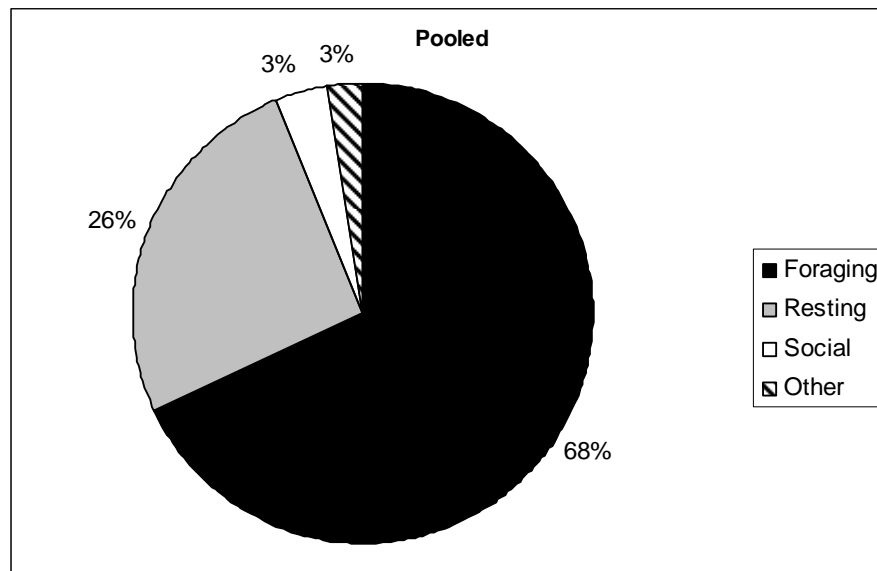| Activity	Male		Female		*t-test*
	Proportion	Percentage	Proportion	Percentage	
Foraging activities		*71*		*65*	NS
Foraging	36.42	69	32.50	60	
Eating	0.98	2	0.63	1	
Sitting	0.21	<1	2.18	4	
Resting activities		*24*		*28*	NS
Resting	8.52	16	11.91	22	
Lying	4.16	8	3.10	6	
Social	*1.52*	*3*	*2.09*	*4*	NS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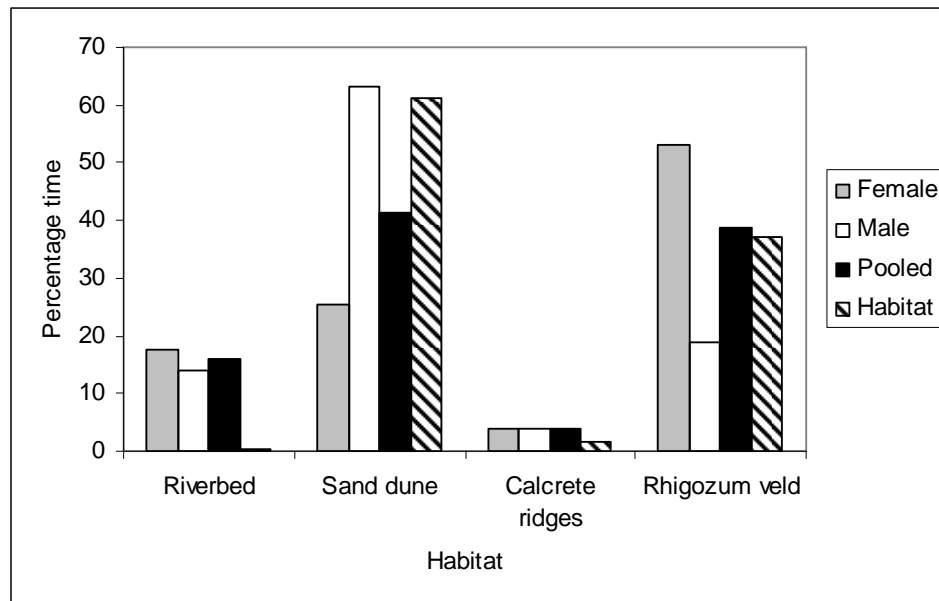

Figure 3.7   The percentage time that males, females and both sexes combined spent active in the different habitats in the KTP. The percentage that each habitat comprised in the study site is included

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)

Prey item	Male				Female			
	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 (χ^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).
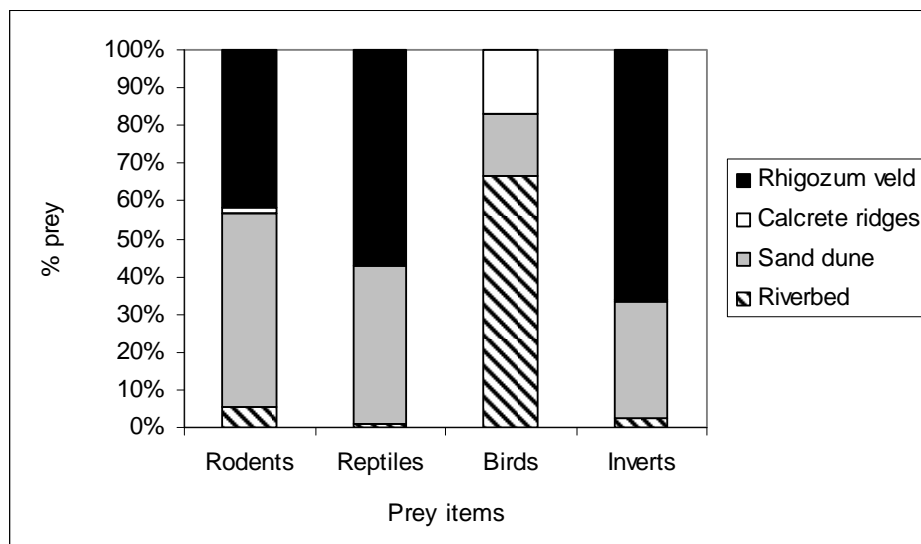

Figure 3.8   The percentage of prey caught in each of the habitats for male and female African wild cats (data pooled)

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,

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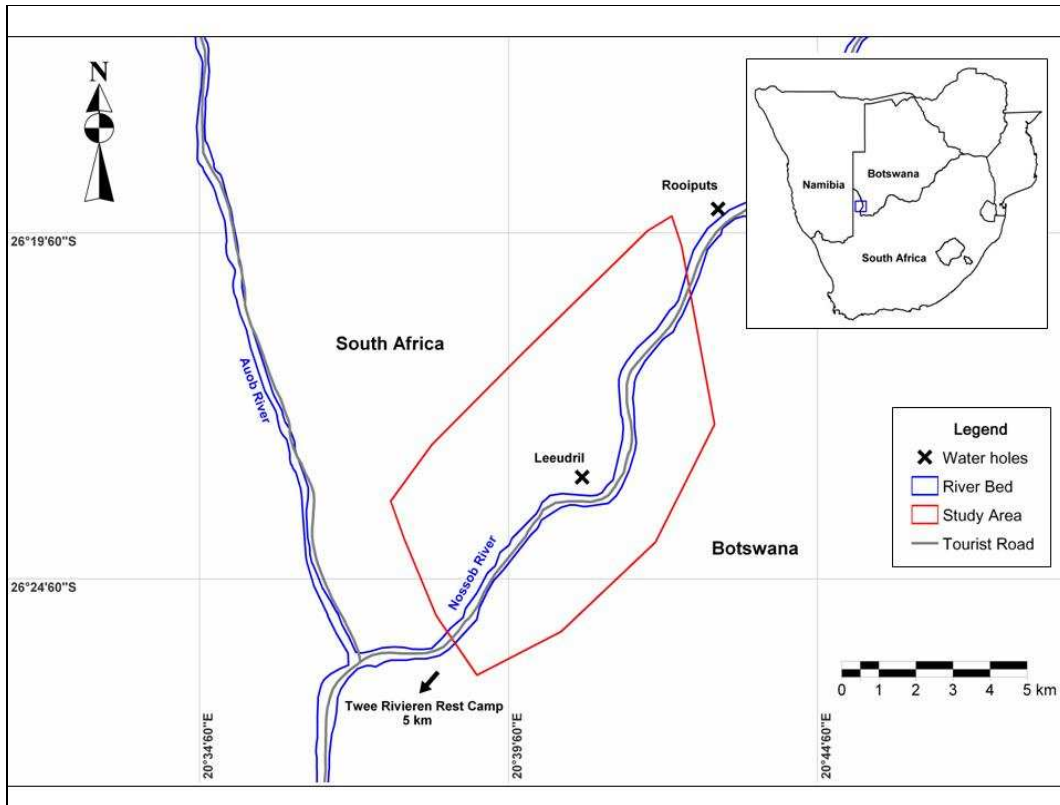
Figure 4.1   Map of the study area in the Kgalagadi Transfrontier Park

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$_{female}$) x (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

AWC ID	Sex	Body mass (kg)	No. of months tracked	No. fixes	Annual home ranges			Resting positions		Wet season			Dry season		
					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
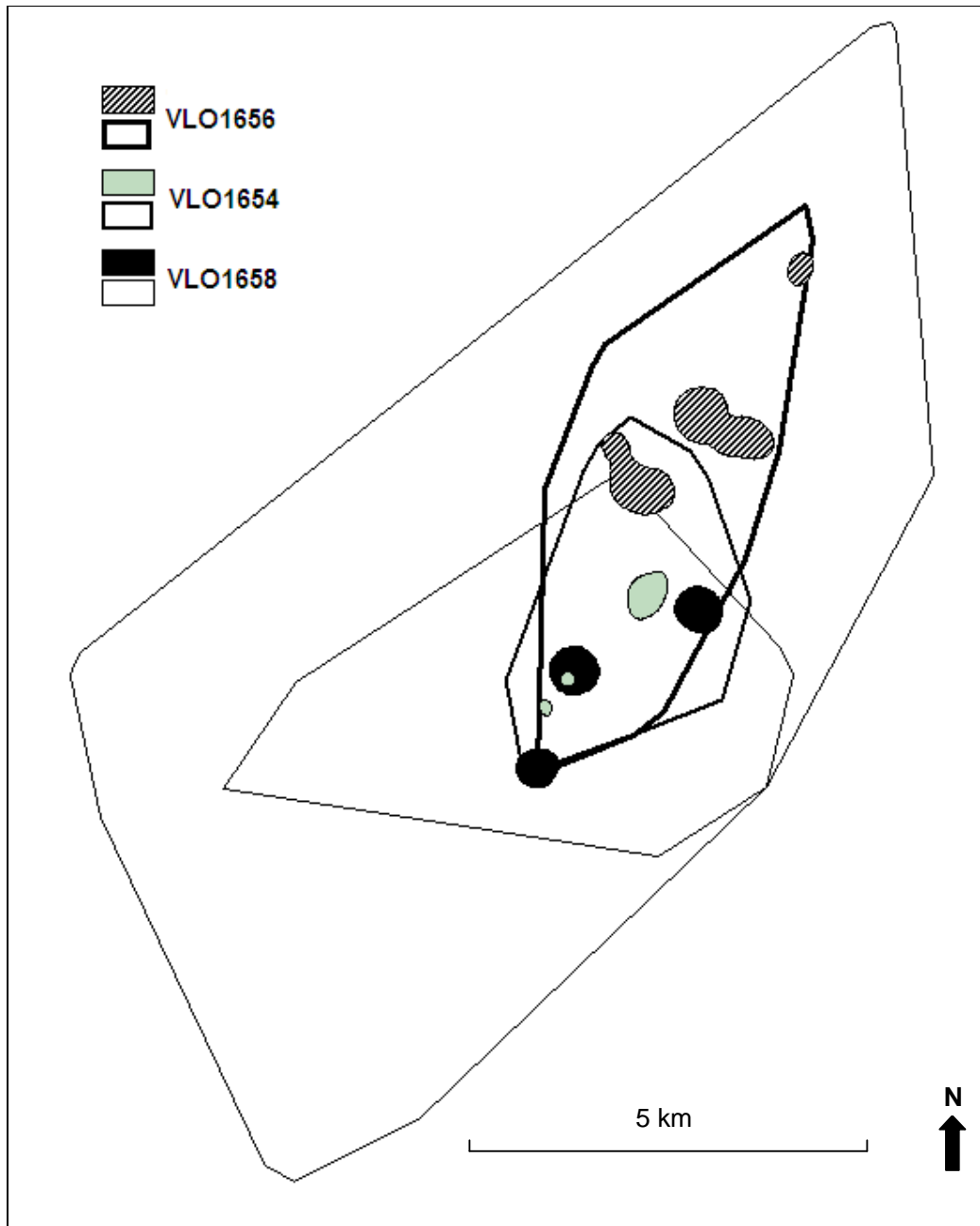
Figure 4.2   Core home range outlines (50% Kernel analyses) and 100% MCPs of three radio collared African wild cat females during 2004 in the Kgalagadi Transfrontier Park. The outline represents the overall study site

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.
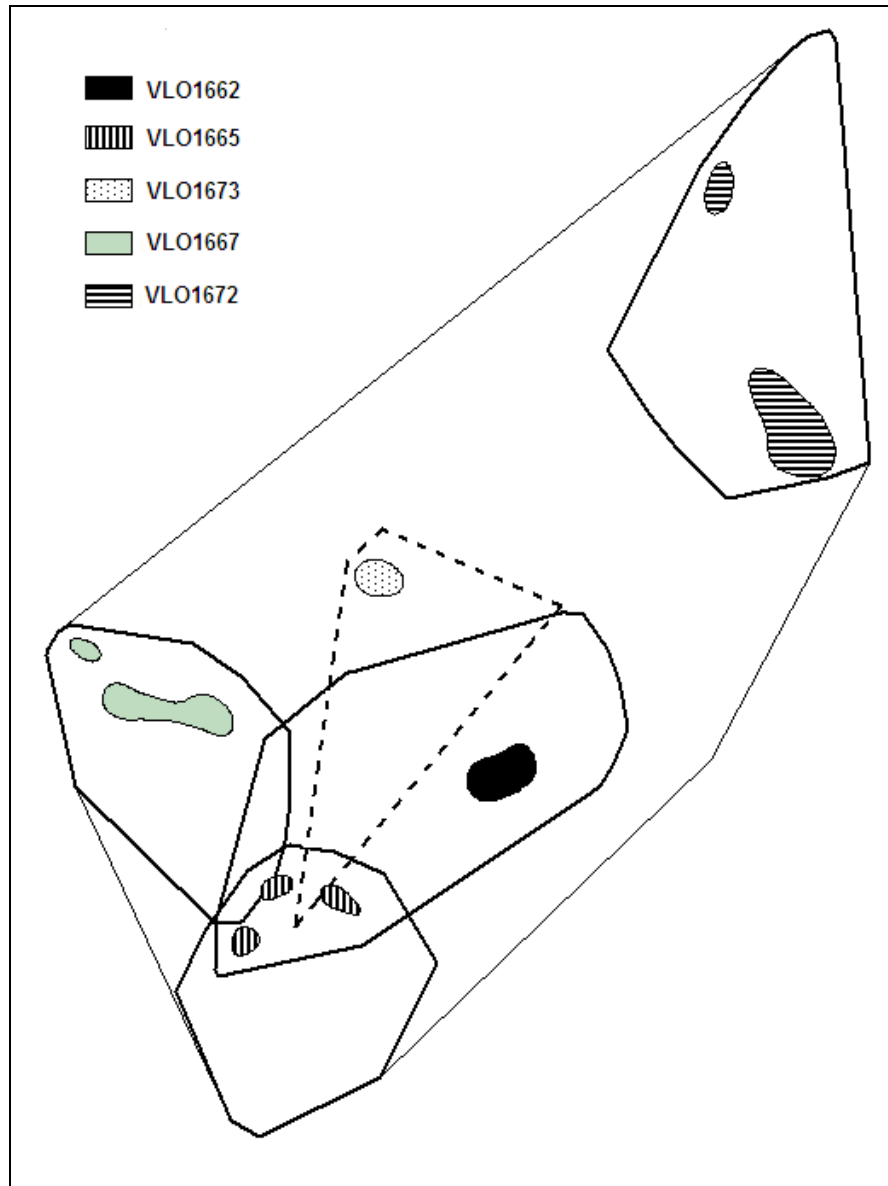

Figure 4.3   Core home range outlines (50% Kernel analyses) and annual 100% MCPs of five radio collared African wild cat males during 2006 in the Kgalagadi Transfrontier Park. The broken line shows the home range of a sub-adult male cat and solid lines represent adult African wild cats. The outline represents the overall study site
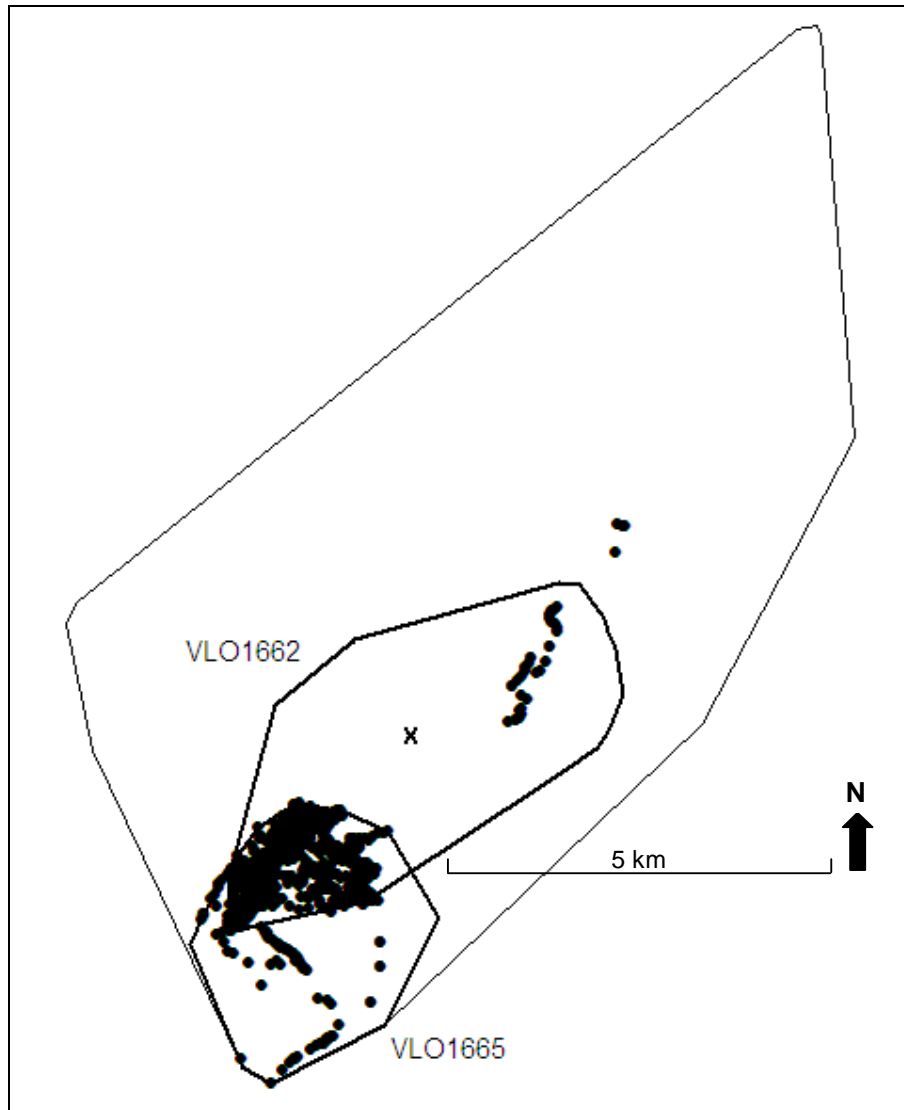
Figure 4.4   Resident home ranges of adult male cats VLO1662 and VLO1665 during 2006. The urine spray marks of VLO1665 as a roaming sub-adult cat from 2005 and 2006 are indicated by (●) and the capture position with a cross (X)
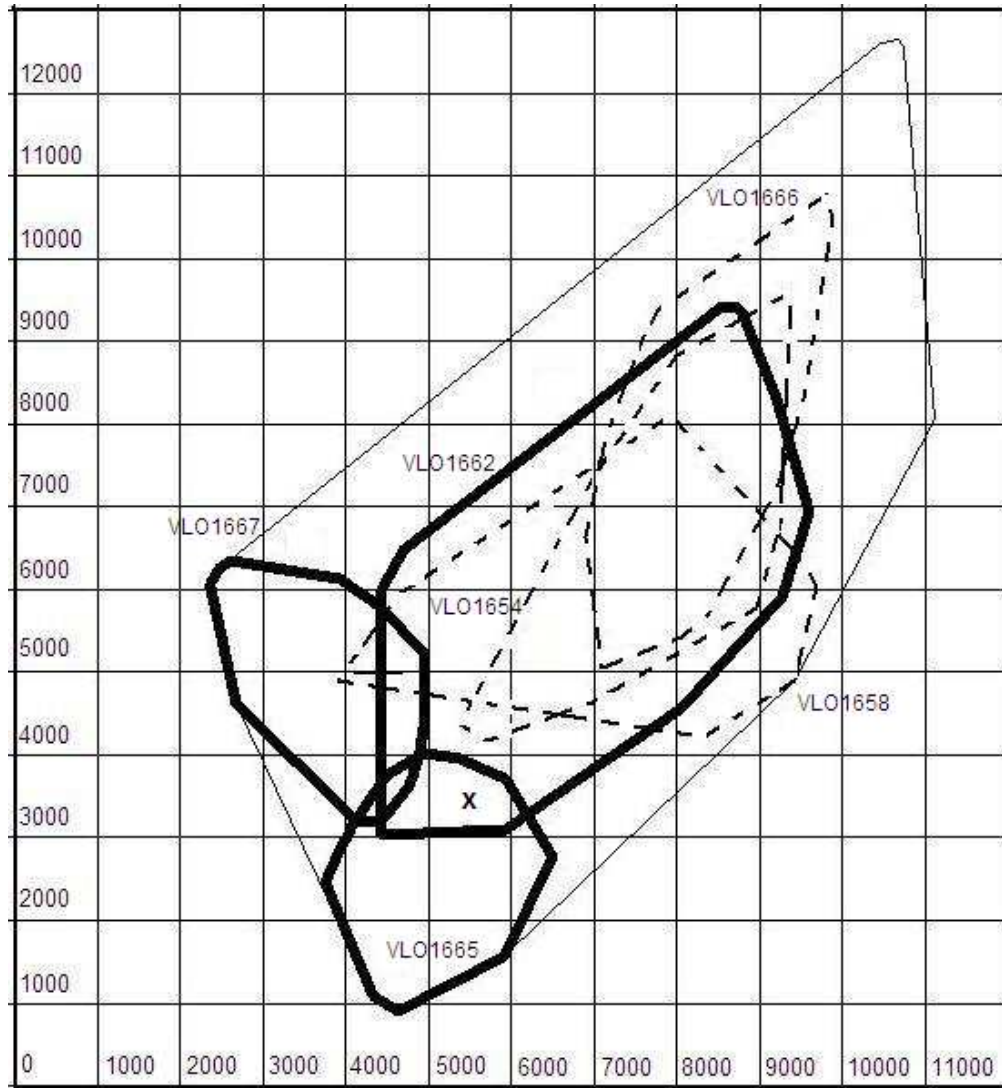
Figure 4.5   100% MCP home ranges calculated for African wild cats tracked during 2004 and 2005 on a 1 km^2 grid. The outline represents the overall study site, with males indicated by the solid lines and females indicated with broken lines. The cross (X) represents the den of an uncollared female in 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
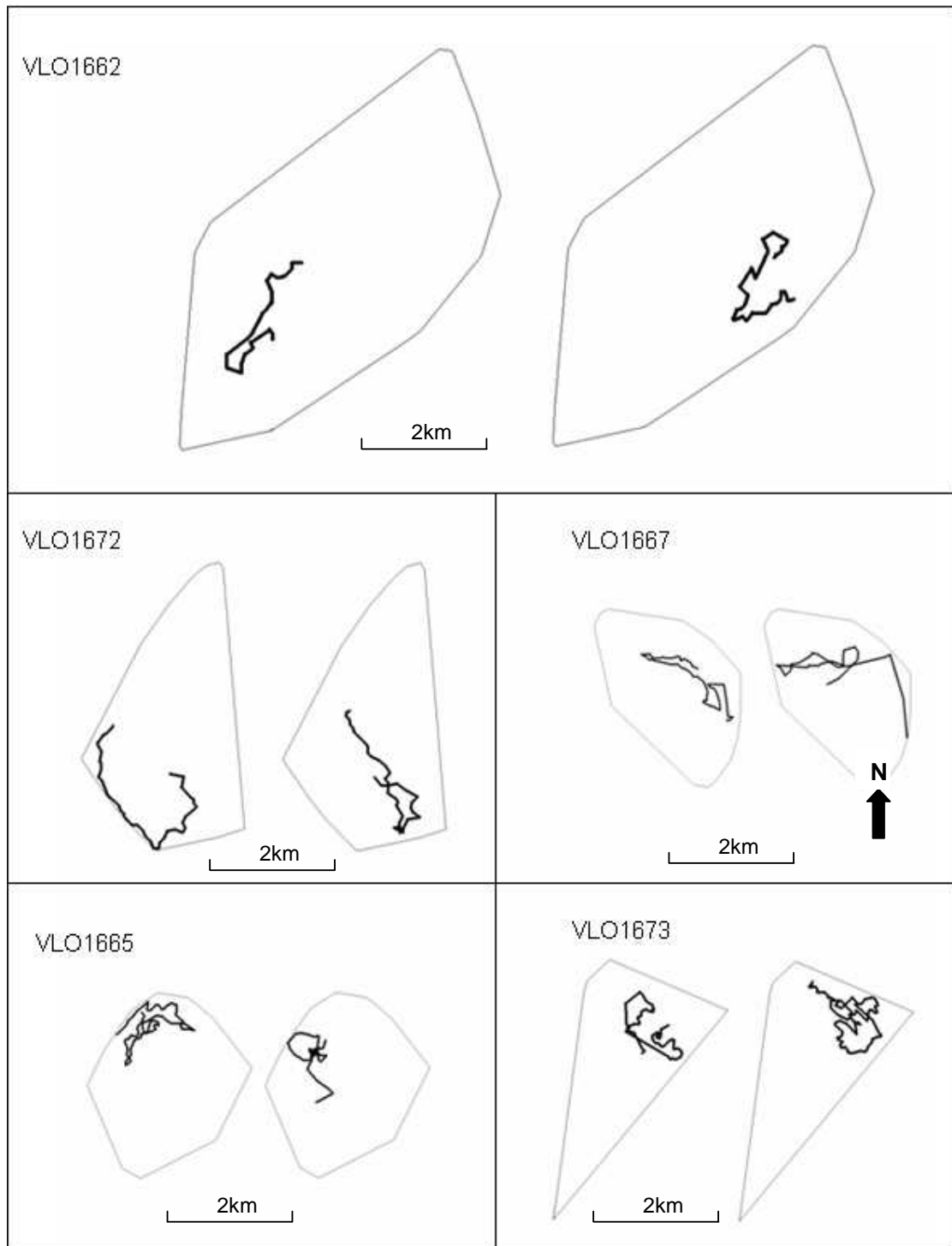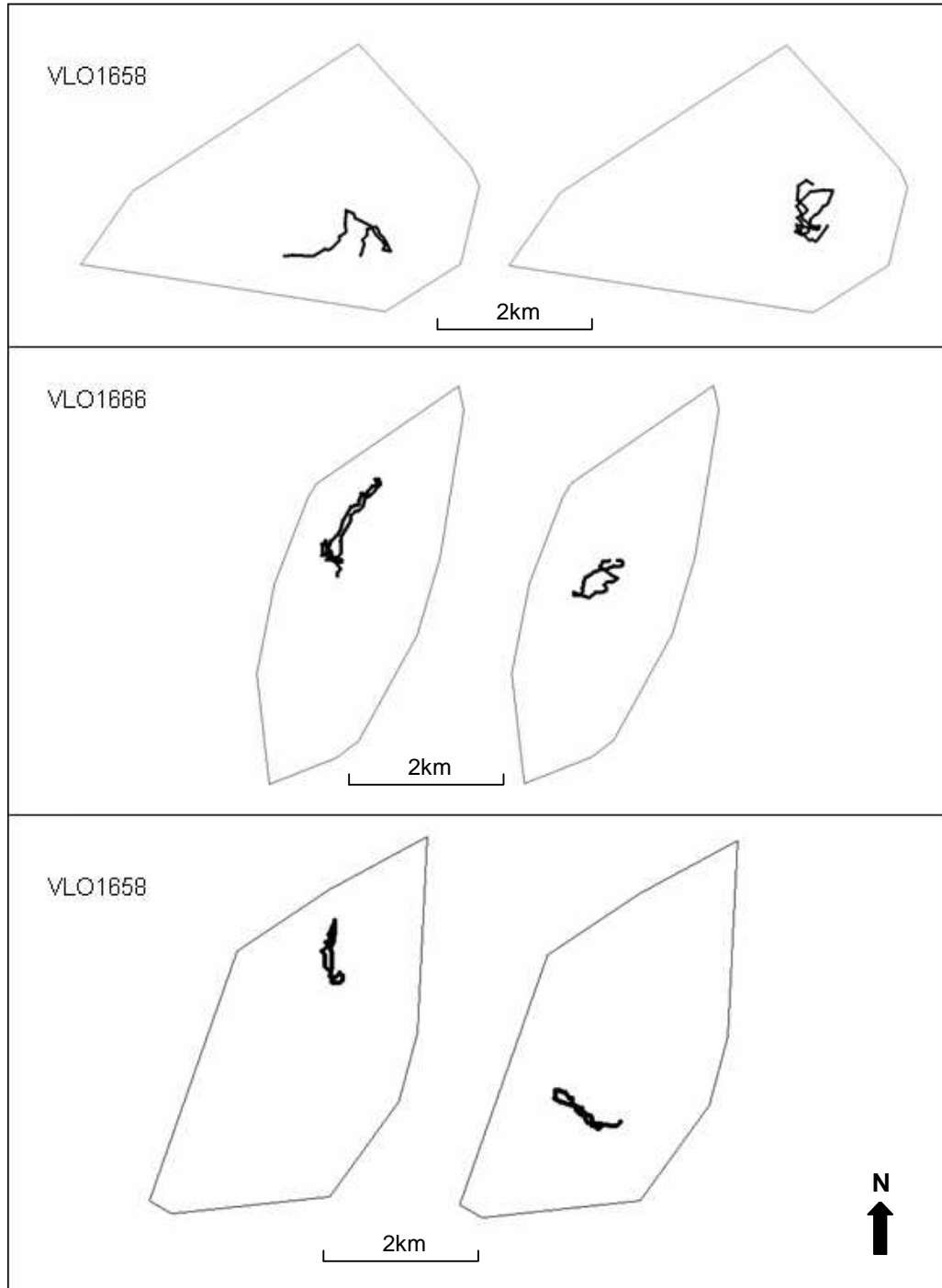
Figure 4.7   Two examples of daily tracks, of three female African wild cats in relation to their 100% MCP home range boundaries. Tracks were generated from continuous visual observations where GPS points were taken at five minute intervals

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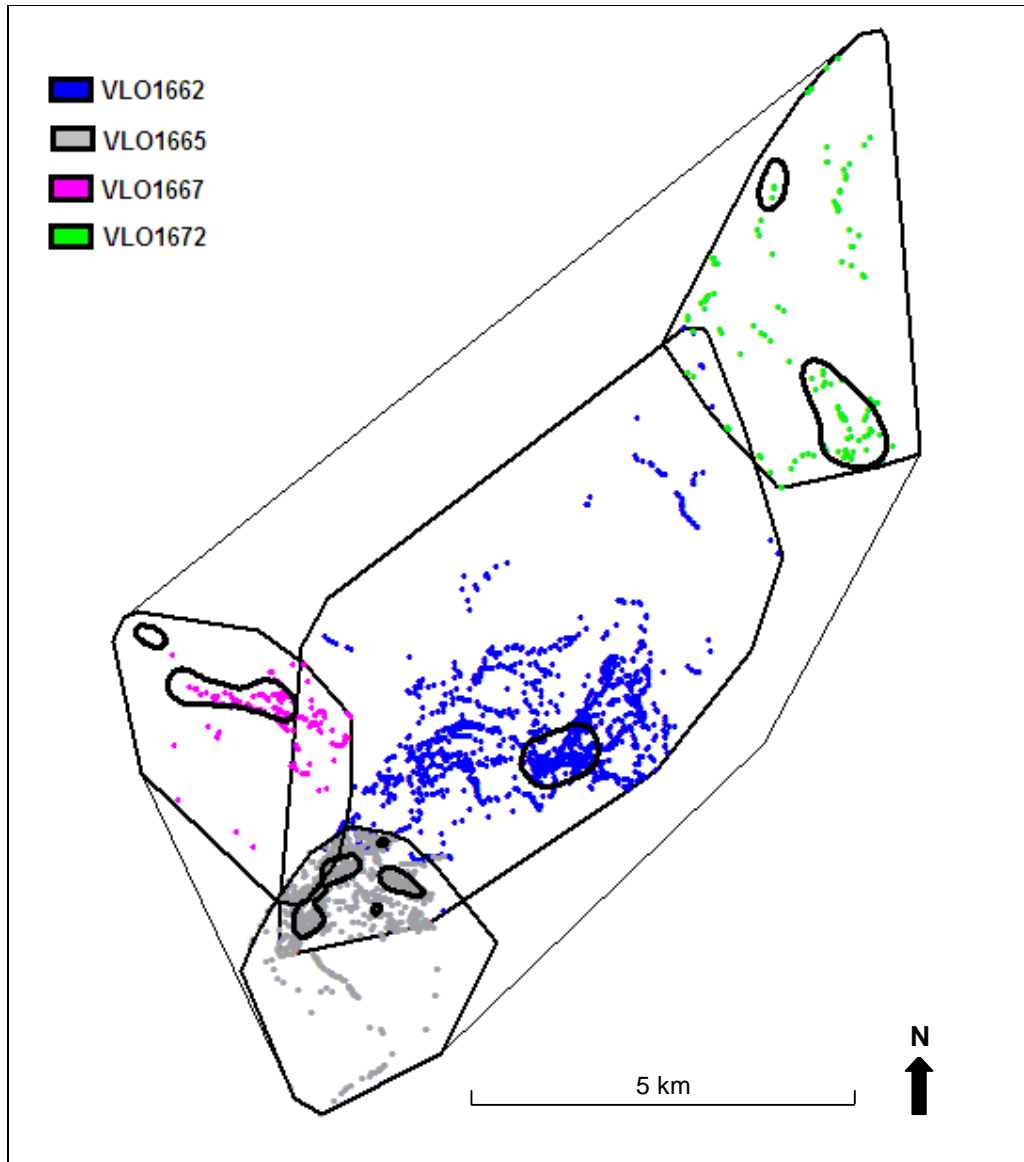
Figure 4.8   Urine spray marking activity of four adult male African wild cats in their 100% MCP home ranges. The 50% core areas in each home range are indicated and the outline represents the study site

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

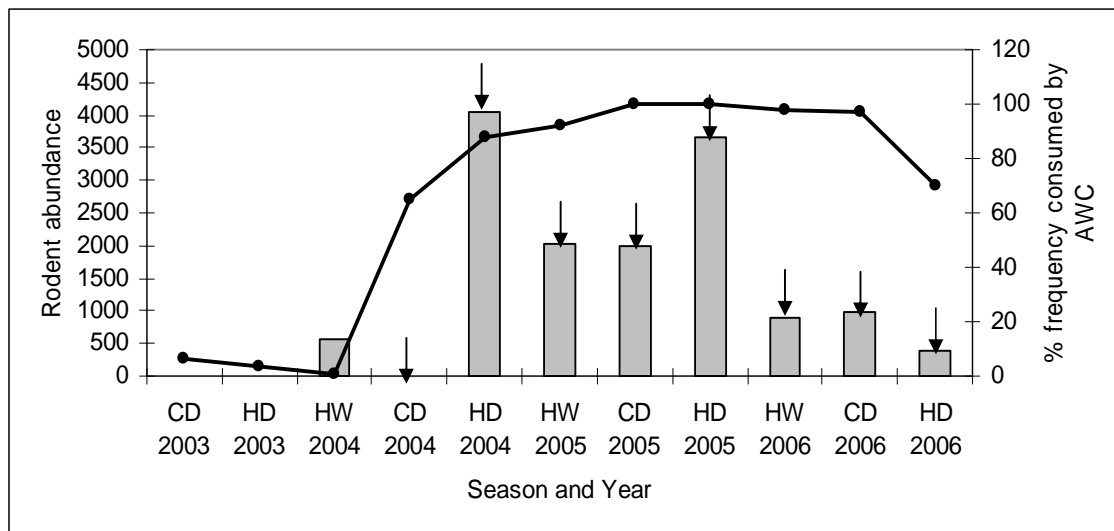| ID	R	n	Z	Description	% of observed spray marking in core areas
VLO1662	0.42	1405	-71.71	Tendency towards clumping exists	21%
VLO1665	0.51	1206	-66.44	Tendency towards clumping exists	38%
VLO1667	0.43	151	-23.51	Tendency towards clumping exists	44%
VLO1672	0.45	122	-21.73	Tendency towards clumping exists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

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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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