Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands

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Understanding spatial ecology is fundamental to effectively managing large, wide-ranging carnivores such as the leopard (*Panthera pardus*). While numerous studies have been conducted on leopards within protected areas, more information regarding leopard ecology is needed outside such areas for effective conservation. This study examined the spatial ecology of leopards living on commercial Namibian farmlands, and assessed information from other studies to investigate which factors appeared to influence leopard range size and density. Home range sizes were particularly large in Namibia, with high range overlap, and neither sex exhibited exclusive home range use. There were no significant differences in range size between males and females, or between wet and dry seasons for either sex. Rainfall did not directly affect range size, but exerted an influence via prey biomass. Leopard density was positively correlated with prey biomass and negatively related to range size. Leopards showed marked variation in range size and land tenure systems between studies, reflecting their remarkable ecological flexibility. Nevertheless, large home range sizes and low population densities mean that leopards require large, contiguous tracts of suitable habitat, and that more conservation efforts must be extended beyond protected areas to ensure the long-term viability of leopard populations in such areas.

Key words: carnivore conservation, home ranges, leopard, Namibia, *Panthera pardus,* spatial ecology.

INTRODUCTION

Leopards (*Panthera pardus*) are the most widely distributed wild cats, and occupy a broad variety of habitats, from rainforests to deserts and from the fringes of urban areas to remote mountain ranges (Nowell & Jackson 1996; Kitchener 1991). In Africa, leopards inhabit over 40 countries, ranging from Senegal to South Africa (Nowell & Jackson 1996), with the sub-Saharan population size estimated at 714 000 (Martin & de Meulenaer 1988). Although this is widely considered to be an over-estimate (Nowell & Jackson 1996), the leopard is not currently considered endangered in sub-Saharan Africa. However, regional populations are increasingly threatened by habitat fragmentation and degradation, as well as persecution by local people to protect livestock (Nowell & Jackson 1996; Myers 1986).

The spatial ecology of leopards has primarily been reported within protected areas (Bailey 1993; Eisenberg & Lockhart 1972; Hamilton 1976; McDougal 1988; Bothma *et al.*1997), with fewer studies of their ecology on private land (Mizutani

1999; Mizutani & Jewell 1998). It was estimated in 1986, however, that only 13% of the leopard's potential range was within protected areas (Martin & de Meulenaer 1988; MacKinnon & MacKinnon 1986). Therefore, developing suitable management strategies outside protected areas could be a key factor in the future conservation of leopards, and more detailed knowledge is required of their ecology in such areas.

In Namibia, the majority of large predators, such as lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) have been extirpated from the farmlands to reduce livestock depredation, leaving leopards and cheetahs (*Acinonyx jubatus*) as the top predators. Previous studies have found that leopards show some behavioural differences in habitats where they are not competing with larger carnivores (Eisenberg & Lockhart 1972). One of the aims of this study was to investigate whether leopards living on farmland habitat, with reduced intraguild competition and a sedentary prey base, showed similar ecological flexibility in terms of home range size and spatial use. Additionally, we sought to examine which factors may be the key determinants of leopard home range size and

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spatial ecology, by collating information from studies conducted in various parts of the leopard's range, from South Africa to Thailand. Leopards show a remarkable degree of variation in range size between different regions (Mizutani & Jewell 1998; Norton & Henley 1987; Bothma *et al.* 1997) and investigating the underlying factors affecting spatial utilization is fundamental to the understanding of leopard ecology, and therefore for the successful management and conservation of the species across the vastly differing environments that it inhabits.

METHODS

Study area

Radio-tracking was conducted within an 18 000 km^2 area in north-central Namibia. The study area encompassed the Waterberg Plateau (a 100 km-long protected area that rises 1800 m above sea level), commercial and communal livestock farmland, and several fenced game-farms. The study area was semi-arid and lay between the 400 mm and 500 mm annual rainfall isopleths (Barnard 1998). There was marked seasonality, with most rainfall occurring between November and April, and an average of 472 mm (±156.3 mm) rainfall annually. The topography of the farmland was generally flat and there were no permanent river systems on the farms, although most farms had a number of man-made semi-permanent water reservoirs. The study area was situated in the thornbush savanna vegetation zone as defined by Geiss (1971). Vegetation was typical of xeromorphic thornbush savanna, with dominant woody plant genera consisting of *Acacia, Dichrostachys, Grewia, Terminalia,* and *Boscia.*

Radio-telemetry

Between 1996 and 2000, we examined, radio-collared and released 11 leopards within the study area. Capture cages used to live-trap the study animals measured 2 × 0.75 m, with trap release doors at each end and a trigger plate in the middle. No baits were used to attract leopards to the traps: leopard captures occurred opportunistically during trapping for cheetahs in the area. Capture cages were usually placed near trees or on trails thought to be used frequently by cheetahs. The opportunistic nature of leopard capture during the project means that the studied leopards only represent a small subset of those present on the farmland, which has evident limitations for the larger conclusions that can be drawn from these results. Trapped leopards were immobilized in the capture cage using an air-pump dart gun or blowpipe (Telinject, Germany). Anaesthetics were administered intramuscularly in the hindquarters with Telazol (tiletamine-HCl and zolazepam HCl, Warner Lambert, Ann Arbor, Michigan) 100 mg/ml with a normal dose of 4 mg/kg.

Age classification was based on indicators such as weight, tooth wear, gum recession, wear on pads, pelage, scarring, body size, social groupings of animals caught together, and reproductive condition, and were grouped in age classes as described by Bailey (1993). During examination, the animals were marked with a metal ear-tag and fitted with a neoprene radio-telemetry collar with an external antenna (Advanced Telemetry Systems, Minnesota). The collars were fitted with a 'C' cell lithium battery with a life expectancy of over 36 months. Radio-collars used weighed 280 g; equivalent to less than 1% of body mass for radio-collared leopards of both sexes, well below the 3% limit recommended by Kenward (2001).

Following release, radio-collared animals were tracked once a week from a fixed-wing Cessna 172 aeroplane, utilizing a dual antenna procedure common to aerial tracking. Searching was initiated at an altitude of approximately 243 m (800 ft), and once a signal was detected the pilot would drop to an altitude of approximately 50 m (152 ft), and determine the location of the animal by making a series of banking turns. The position of the animal was determined using a portable Global Positioning System (GPS).

Data were plotted and analysed using ArcView GIS (version 3.2, ESRI, Redlands, CA) and the Animal Movement extension (Hooge *et al.* 1999). Latitude and longitude recordings were used to calculate 95% minimum convex polygon (MCP) home ranges (Mohr 1947; White & Garrott 1990), for leopards with ≥30 radio-tracking fixes. Comparisons with home range estimates from other studies were restricted to those that had also used the minimum convex polygon method to estimate range sizes.

Seasonal home ranges were also calculated using the 95% MCP method, for leopards with ≥15 fixes for the season concerned. Using rainfall figures throughout the study period, we defined the wet season as being from 15 September to 14 April, when 93% of the rain fell, and the dry season from 15 April to 14 September, when 7% fell.

Table 1. Body mass, estimated age, duration of tracking, number of fixes, and overall and seasonal home range sizes for the 11 leopards radio-tracked during the course of the study. Estimates of home range size were calculated using the 95% minimum convex polygon (MCP) method.

Radio-collar no.	Sex	ID no.	Mass (kg)	Age at first collaring (months)	No. months tracked	Total no. fixes	Overall 95% MCP home range size (km²)	No. wet season fixes	Wet season 95% MCP home range size (km²)	No. dry season fixes	Dry season 95% MCP home range size (km²)
103	M	2	50.9	60	5	43	125.2	38	137.4	5	–
861	M	3	52.3	60	26	77	311.9	61	283.0	16	160.8
790(520)	M	7	39.5	36	29	100	–	45	–	55	–
661	M	15	37.5	36	6	6	–	6	–	0	–
791	M	27	45.0	40	11	36	250.0	16	209.8	20	181.9
971	M	31	50.0	38	20	20	–	4	–	16	143.6
Mean			*45.9*	*45*	*16*	*47*	*229.0*	*28*	*210.1*	*19*	*162.1*
S.D.			*6.2*	*12*	*10*	*35*	*95.1*	*23*	*72.8*	*19*	*117.7*
174	F	1	32.0	60	14	80	52.4	48	60.3	32	17.4
820	F	4	24.0	24	27	100	393.5	45	222.2	55	293.6
918(561)	F	5	32.0	48	31	109	137.3	53	1099.1	56	54.1
688	F	6	33.5	24	28	79	132.6	33	55.9	46	105.7
986	F	29	30.0	144	6	17	–	12	–	5	–
Mean			*30.3*	*60*	*21*	*77*	*179.0*	*38*	*359.4*	*39*	*117.7*
S.D.			*3.7*	*49*	*11*	*36*	*148.2*	*16*	*499.2*	*21*	*122.7*

S.D. = standard deviation. All home range size estimates and statistical analyses were restricted to leopards with at least 30 fixes overall and 15 fixes for each season. Data from male ID no. 7 were excluded as he made more extensive exploratory movements after collaring which invalidated estimation of home range size.

Statistical analyses were performed using SPSS version 10.0 software (SPSS Inc. Chicago, USA). Means are presented with the standard deviation (±) after the mean. Normality of variables was tested using the Kolmogorov-Smirnov and Shapiro-Wilk tests, and in cases where there was significant deviation from normality, non-parametric tests were used instead of their parametric equivalents. Levene's test was used to determine homogeneity of variance, and all tests were two-tailed unless otherwise stated.

RESULTS

Details of the tracked leopards and estimated home range sizes are shown in Table 1. One of the female leopards (ID no. 5 in Table 1) was trapped with cubs of around six months old, while another (ID no. 1) had cubs four months after she was radio-collared. One of the male leopards tracked (ID no. 7) made very large exploratory movements for a year after he was radio-collared. These movements were attributed to him dispersing in search of a new territory, making it hard to determine an accurate home range figure, so this animal was excluded from analyses of home range size.

Leopard home ranges

There was no difference in home range size between male and female leopards, either overall ($t = 0.51$, d.f. = 5, $P = 0.634$), in the wet season ($t = -0.50$, d.f. = 5, $P = 0.637$) or in the dry season ($t = 0.607$, d.f. = 5, $P = 0.571$). There were no significant differences between wet and dry seasonal home range size for either male ($t = 1.10$, d.f. = 4, $P = 0.334$) or female leopards ($t = 0.94$, d.f. = 6, $P = 0.384$; Table 1).

Overall, leopards showed a mean annual range overlap of $26 \pm 15\%$ with conspecifics. Male leopards overlapped with each other slightly more (averaging $24 \pm 13\%$ range

overlap) than females did (22 ± 12%), but this difference was not statistically significant ($t = -0.38$, d.f. = 17, $P = 0.712$). There was significant variation in the degree of inter- and intrasexual home range overlap, with females overlapping significantly more with males (40.4 ± 12.2%) than with other females, and intersexual overlap accounting for a greater percentage of female than male ranges (male intersexual overlap = 13.9 ± 13.9%; $F = 7.63$, d.f. = 3, $P < 0.001$).

Comparisons with other studies

Data collected during this study were compared to those from studies conducted in a wide variety of habitats (Table 2), and it was evident that the home ranges utilized on the Namibian farmlands were amongst the largest reported in the literature (Table 3). Estimates of adult male home range size calculated using the 95% MCP method were significantly larger in this study than those reported elsewhere ($t = -22.7$, d.f. = 2, $P = 0.002$). Only one other study (study no. 6, Table 3) specified that they used the 95% MCP method to estimate adult female home range size, so the estimates could not be compared statistically, but the adult female range here was almost ten times larger than the other reported figure. This large disparity in range sizes compared to most other studies was despite the fact that estimated prey biomass in this study area did not differ significantly from those in other published reports ($t = 2.22$, d.f. = 5, $P = 0.077$). The similarity in size between male and female home ranges found here contrasted with the majority of reported data, as adult males had significantly larger home ranges than adult females in 69% ($n = 9$) of other studies with data for both sexes (Table 3).

Factors affecting leopard home range size

Data collected from various regions (Table 3) revealed a significant amount of variation between studies regarding estimates of leopard home range size. Estimates were made using a variety of techniques, which probably accounts for a large degree of variation, but even when analyses were restricted to those made using the 95% MCP technique, estimates of home range size differed significantly between studies, both for male (Mann-Whitney $U = 332$, d.f. = 3, $P < 0.001$) and female (Man-Whitney $U = 134$, d.f. = 1, $P < 0.001$) leopards. These studies were performed in a wide diversity of different habitats, with large variation in prey abundance, rainfall, vegetation and leopard density, as well as disparities in other factors such as whether the study was conducted in a protected area and whether larger sympatric carnivores were present in the area (Table 2). Although comparisons are somewhat confounded by methodological variations, even when restricted just to estimates made using the MCP method, we examined these factors to try to ascertain which seemed to have the most bearing on leopard home range size and density in an area. Home range sizes of adult male and female leopards were highly correlated to one another ($r = 0.82$, $n = 9$, $P = 0.006$). Adult male ranges size was negatively related to leopard density ($r = -0.86$, $n = 7$, $P = 0.014$), and the same trend was evident for adult female range size, although that relationship was not statistically significant ($r = -0.76$, $n = 6$, $P = 0.080$).

Prey biomass was negatively correlated with home range size for both adult males ($F = 21.4$, d.f. = 4, $P = 0.010$) and adult females ($F = 8.43$, d.f. = 4, $P = 0.044$, although the relationships showed slightly different distributions (Fig. 1a,b). Prey biomass was positively related to estimated leopard density in a study area ($F = 19.7$, d.f. = 2, $P = 0.047$; Fig. 2).

Despite the fact that increased rainfall was linked to higher prey biomass in an area ($r = 0.787$, $n = 7$, $P = 0.036$), it had no significant impact on range size for either sex (males: $r = -0.01$, $n = 9$, $P = 0.981$; females: $r = 0.47$, $n = 10$, $P = 0.166$) or on leopard density ($r = -0.14$, $n = 6$, $P = 0.798$).

Protection of an area did not seem to have a significant effect on adult male range size ($t = -1.57$, d.f. = 2, $P = 0.252$), adult female range size ($t = -1.34$, d.f. = 3, $P = 0.272$) or prey biomass ($t = 2.06$, d.f. = 4, $P = 0.108$). Leopards occurred at densities almost five times higher within protected areas (mean = 10.5 ± 4.0 leopards/100 km^2) compared to outside protected areas (mean = 2.1 ± 1.6 leopards/100 km^2), but the low sample size ($n = 6$ studies) meant that the difference was just on the border of statistical significance ($t = 2.74$, d.f. = 4, $P = 0.052$). The presence of larger predators in a particular area did not appear to have a significant impact on home range size for either sex (males: $t = -0.26$, d.f. = 9, $P = 0.799$; females: $t = -1.28$, d.f. = 9, $P = 0.234$) or on leopard density ($t = -0.98$, d.f. = 5, $P = 0.373$).

DISCUSSION

Our study area supported a viable population of leopards due to their protection in the neighbour-

Table 2. Habitat characteristics of study areas where research on the spatial ecology of leopards has been published.

Study no.	Study area	Country	Protected area?	Larger predators	Habitat type present	Mean annual rainfall (mm)	Estimated prey	Estimated abundance (kg/km²)	Reference(s)* leopard density/100km²
1	Cedarberg Wilderness Area, Cape Province	South Africa	Yes	No	Mountain fynbos	–	–	6–9	1
2	Huia Kha Kueng Wildlife Sanctuary	Thailand	Yes	Yes	Dry tropical forest	–	–	4	2 (cited in 26)
3	Kaeng Krachan National Park	Thailand	Yes	No	Forested hills	1000	–	–	3
4	Kalahari Gemsbok National Park	South Africa	Yes	Yes	Desert/grassland	<250	–	0.625	4, 5
5	Kaudom Game Reserve and Bushmanland	Namibia	Mixed	Yes	Woodland savanna	450	34.9	1.5	6
6	Lolldaiga Hills Ranch	Kenya	No	Yes	Scattered tree grassland	690	443	–	7
7	Londolozi Game Reserve	South Africa	Yes	Yes	Woodland savanna	–	–	23.8	6, 8
8	Meru National Park	Kenya	Yes	Yes	Thorn bushland plains	<700	–	–	9
9	Nagarahole National Park	India	Yes	Yes	Tropical forest	1250	9856	–	10
10	North-central Namibian farmlands	Namibia	No	No	Thornbush savanna	468	360.6	2.5–3.8	11, 12
11	Nwaswitshaka River, Kruger National Park	South Africa	Yes	Yes	Woodland savanna	665	3851.7	9.5	13
12	Outside Royal Chitwan National Park	Nepal	No	Yes	Farmland/forest	230	–	–	14, 15, 30
13	Rawalpindi District	Pakistan	No	–	Temperate forest/scrub	–	–	1.8	16
14	Rhodes Matopos National Park	Zimbabwe	Yes	–	–	–	–	23.6	17 (cited in 6)
15	Royal Chitwan National Park	Nepal	Yes	Yes	Riverine forest/tall grass	230	2798	–	15, 18, 31
16	Sabie River, Kruger National Park	South Africa	Yes	Yes	Woodland savanna	665	4559.6	16.4	13
17	Sanjay Gandhi National Park	India	Yes	No	Deciduous forest	2600	–	41.7	19
18	Serengeti National Park	Tanzania	Yes	Yes	Plains/woodland	–	–	3.3–4.7	20 (cited in 21)
19	Serengeti National Park	Tanzania	Yes	Yes	Woodland	–	–	10.4	22 (cited in21)
20	Stellenbosch area, Cape Province	South Africa	No	No	Fynbos/plantation	500–3000	–	0.9	23, 24, 25
21	Tai National Park	Ivory Coast	Yes	No	Tropical forest	1700	–	7.1–11.1	26
22	Tsavo West National Park	Kenya	Yes	Yes	Thorn bushland hills	<700	–	10.8	9
23	Waterberg Plateau Park	Namibia	Yes	No	Thornbush savanna	–	–	–	27
24	Wilpattu National Park	Sri Lanka	Yes	No	Forest/scrub	–	476	3.4	28, 29

*: Norton & Henley 1987; 2: Rabinowitz 1989; 3: Grassman 1999; 4: Bothma & Le Riche 1984; 5: Bothma et al. 1997; 6: Stander et al. 1997; 7: Mizutani & Jewell 1998; 8: Le Roux & Skinner 1989; 9: Hamilton 1981; 10: Karanth & Sunquist 2000; 11: this study; 12: Stander & Hanssen 2003; 13: Bailey 1993; 14: Seidensticker et al. 1990; 15: Seidensticker 1976a; 16: Maan & Chaudhry 2000; 17: Smith 1977; 18: Sunquist 1983; 19: Edgaonkar & Chellam 1998; 20: Schaller 1972; 21: Caro 1994; 22: Bertram 1982; 23: Norton & Lawson 1985; 24: Norton 1986; 25: Norton 1990; 26: Jenny 1996; 27: Zeiss 1997; 28: Eisenberg & Lockhart 1972; 29: Muckenhirn & Eisenberg 1971; 30: Bothma & Le Riche 1986; 31: Seidensticker 1976b.

Table 3. Mean home range sizes, degree of range overlap and daily movements reported in studies of leopard spatial ecology.

Study no.	Mean home range size (km²)					Method of home range estimation	Degree of home range overlap (%)				Mean distance moved per day (km)			Reference(s)**
	Adult male	Adult female	Unk. sex	Subadult male	Subadult female		Between males	% F range overlapping with M	% M range overlapping with F	Between females	Adult male	Adult female with cubs	Adult female without cubs	
1	51 (3)	–	–	–	–	95% MCP	10–57	–	–	–	2.6 (3)	–	–	1
2	32 (2)	14.3 (2)	–	–	–	–	–	–	–	–	–	–	–	2 (cited in 26)
3	17.7 (2)	8.8 (1)	–	–	–	MCP	40	31.5	–	–	2.2 (2)	–	1.8 (1)	3
4	2182 (3)	489 (5)	–	–	–	95% kernel	–	–	–	–	14.4 (40)	13.4 (15)	–	4, 5, 30
5	451.2 (6)	188.4 (3)	–	132.4 (3)	143.7 (1)	MCP	46	41.6	25.5	35	12.2	10.5	6.8	6
6	37.1 (2)	16.9 (3)	–	28.4 (2)	12.3 (1)	95% MCP	0–9	2	3	<10%	–	–	–	7
7	–	23–33 (1)	–	–	–	Observations	–	–	–	–	–	–	–	6, 8
8	–	26.7 (1)	–	–	15.3 (1)	–	–	–	–	–	–	1.3 (1)	–	9
9	21.7 (2)	–	–	–	–	95% MCP	–	–	–	–	–	–	–	10
10	229.0 (3)	179.0 (4)	–	–	–	95% MCP	24	40.4	13.9	21.8	2.1 (4)	1.07 (2)	0.96 (2)	11, 12
11	76.2 (2)	14.8 (4)	–	–	–	MCP	19	70.5	–	18.1	2.8*	1.2*	1.9*	13
12	–	9.5 (2)	–	–	–	MCP	–	–	–	–	–	0.84 (1)	1.45 (1)	14, 15
13	–	–	–	–	–	–	–	–	–	–	–	–	–	16
14	–	–	18 (6)	–	–	–	–	–	–	–	–	–	–	17 (cited in 6)
15	–	8 (1)	–	–	–	MCP	–	–	–	–	–	1.45 (1)	0.84 (1)	15, 18, 31
16	27.7 (3)	18.0 (1)	–	–	–	MCP	21.5	87	–	–	2.8*	1.2*	1.9*	13
17	–	–	–	–	–	–	–	–	–	–	–	–	–	19
18	57.5	14.1–50	–	–	–	Sightings	–	–	–	–	–	–	–	20 (cited in 21)
19	–	15.9	–	17.8	–	–	–	–	–	–	–	–	–	22 (cited in 21)
20	388 (1)	487 (1)	–	–	–	MCP	–	–	–	–	–	–	–	23, 24, 25
21	85.6 (1)	25.4 (2)	–	–	–	MCP	30–60	86.5	22.5	17	3.02 (1)	–	1.85 (2)	26
22	30 (7)	13.9 (1)	–	–	–	–	–	–	–	–	2.9 (5)	–	2.0 (1)	9
23	118.7 (2)	63.9 (1)	–	–	10.2 (1)	MCP	–	–	–	–	–	–	–	27
24	9–10	8–10	–	–	–	–	–	–	–	–	–	–	–	28, 29

*Study area in Kruger National Park not specified.

**1: Norton & Henley 1987; 2: Rabinowitz 1989; 3: Grassman 1999; 4: Bothma & Le Riche 1984; 5: Bothma *et al.* 1997; 6: Stander *et al.* 1997; 7: Mizutani & Jewell 1998; 8: Le Roux & Skinner 1989; 9: Hamilton 1981; 10: Karanth & Sunquist 2000; 11: this study; 12: Stander & Hanssen 2003; 13: Bailey 1993; 14: Seidensticker 1976; 15: Seidensticker *et al.* 1990; 16: Maan & Chaudhry 2000; 17: Smith 1977; 18: Sunquist 1983; 19: Edgoankar & Chellam 1998; 20: Schaller 1972; 21: Caro 1994; 22: Bertram 1982; 23: Norton & Lawson 1985; 24: Norton 1986; 25: Norton 1990; 26: Jenny 1996; 27: Zeiss 1997; 28: Eisenberg & Lockhart 1972; 29: Muckenhirn & Eisenberg 1971; 30: Bothma & Le Riche 1986; 31: Seidensticker 1976b.
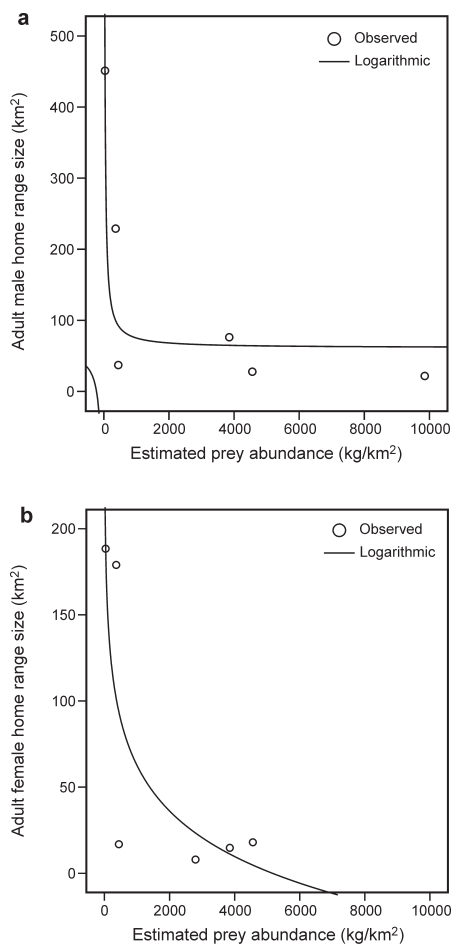
Fig. 1. Relationship between estimated prey abundance (kg/km^2) and mean home range size for (**a**) adult male and (**b**) adult female leopards, using data from published studies shown in Tables 2 and 3. Data included are restricted to those studies that used the minimum convex polygon (MCP) method to estimate range size.
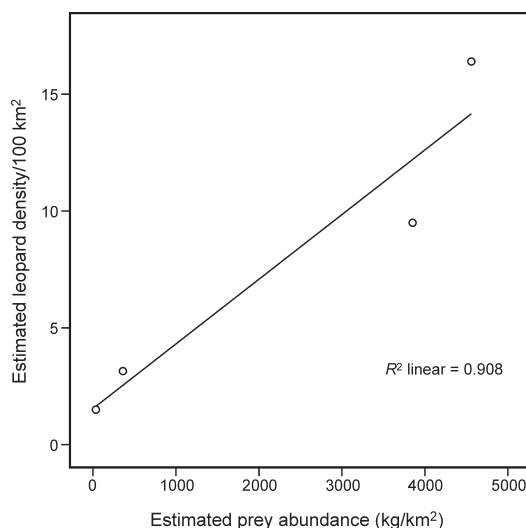

Fig. 2. Relationship between estimates of prey abundance (kg/km^2) and leopard density (leopards/100km^2), using data from published studies shown in Tables 2 and 3. Data were restricted to those studies used for comparative analyses, *i.e.* those that used MCP as their method of home range estimation.

ing Waterberg Plateau Game Park, and the study provides the first data regarding the home ranges of leopards on commercial Namibian farmlands. We found that leopards had larger home ranges in Namibia compared to elsewhere, except for the leopards of the southern Kalahari (Bothma *et al.* 1997), supporting what Stander *et al.* found in 1997. In both Figs 1a and 1b, the largest range estimates are from the two Namibian studies, namely this one and the one by Stander *et al.* (1997), and these clearly drive the resulting trends. Sixteen percent of Namibia is classified as hyper-arid (defined as true desert), 49% is categorized as arid, 32% as semi-arid, and 3% as sub-humid

(Seely *et al.* 1994). In these dry conditions, the expectation would be to have relatively low leopard density and large home ranges for both sexes (Martin & de Meulenaer 1988; Mizutani & Jewell 1998; Bothma & Le Riche 1984). However, we found that rainfall was not directly linked to home range size for either male or female leopards, although it was related to prey abundance, which in turn had an effect on home range size. The lack of a direct relationship between rainfall and either range size or leopard density was surprising, and suggests that there may be a more complex, non-linear relationship between these factors. More complex analyses would be useful for exploring such relationships, but these would require a larger data set: analyses here were restricted by a lack of information on exactly which method was used to estimate range size, and also by a lack of supplemental information such as estimates of range size, rainfall and prey abundance for many studies.

The fact that leopards collared during this study had such large home ranges, despite a relative equality of prey biomass with those reported in other studies, suggests that leopard spatial ecology on Namibian farmlands is affected by other factors besides purely ecological parameters. One important consideration is that the Namibian

leopard population has long suffered substantial persecution and high levels of killing due to conflicts with local land-owners (Zeiss 1997). Previous studies have shown that such perturbation and removals can have considerable impacts on carnivore spatial ecology, including effects such as the expansion of home ranges and increased range overlap (Tuyttens *et al.* 2000). This could be one of the factors influencing the large, overlapping ranges seen in this study, but further detailed investigation into the dynamics of the leopard population is needed to ascertain whether these human-mediated removals are significantly affecting the demography and spatial utilization patterns of leopards in this region.

Investigating effects of prey abundance on home range size for leopards across studies is somewhat confounded by the fact that few authors state whether the estimated prey biomass is restricted to wild prey, or whether they include the potential contribution of domestic stock. We restricted our prey calculations to wild ungulates, but several studies have found that domestic animals make a significant contribution to leopard diet, especially outside protected areas (Edgaonkar & Chellam 1998; Seidensticker *et al.* 1990; Maan & Chaudhry 2000). Additionally, carnivore spatial ecology may be determined primarily by lean season biomass, as this is more of a limiting resource than good season biomass (Van Orsdol *et al.* 1985), yet few studies differentiate between the two. Quantifying and including these factors, as well as conducting further in-depth studies on leopard diet and prey selection, could help develop a more accurate understanding of the determinants of leopard home range size, particularly outside protected areas.

We found no evidence of significant seasonal effects on home range size, which was probably a result of the sedentary prey base on the commercial farmlands that formed our study area. In areas where prey move substantial distances as a result of rainfall patterns, leopards have been shown to undergo seasonal shifts in home range size, expanding as prey species disperse (Grassman 1999; Ilany 1986).

The similarity in size between male and female home ranges on the Namibian farmlands was surprising, as the majority of other studies have found that males have substantially larger home ranges than females (Bothma *et al.* 1997; Bailey 1993; Mizutani & Jewell 1998; Stander *et al.* 1997). It has been hypothesized that polygynous felids,

such as the leopard, should occupy ranges substantially larger than those needed purely to satisfy their food requirements (Bailey 1974), an area known as their metabolic home range size. This can be calculated using the following equation:

$$R_{male} = R_{female} \times \frac{M_{male}^{0.75}}{M_{female}^{0.75}} \, ,$$

where *R* is home range size and *M* is body mass (Sandell 1989). Contrary to Bailey's (1974) findings, male leopards in this study utilized an area that closely approximated their expected metabolic home range size (244 km^2), indicating that in this environment, male leopards did not appear to expand their home range beyond their energetic requirements. This is similar to what was found on ranchland in Kenya (Mizutani & Jewell 1998), where male leopards also had ranges similar to those expected from energetic requirements alone.

Previous studies have found that female leopards tend to configure their home ranges around important resources, such as patches of prey-rich habitat, den sites and possibly water-points, and male ranges typically encompass those of several females (Bailey 1993; Bothma 1997; Mizutani & Jewell 1998; Kruuk 1986). In a harsh environment, such factors may be sparsely distributed enough to necessitate unusually large female ranges, making it impossible for males to cover large enough ranges to overlap those of several females. This may be the case on Namibian farmlands. However other studies of leopard ecology in harsh, arid environments have found that male leopards still manage to maintain significantly larger home ranges than females (Stander *et al.* 1997; Bothma 1997). In this study, however, leopard captures occurred opportunistically during a larger research project on cheetah ecology, rather than during a dedicated effort at saturation trapping, making it hard to draw firm conclusions regarding these spatial arrangements – it is possible that the males were encompassing the ranges of several females that were not tracked, and that these females were overlapping substantially with the radio-collared females.

Similarly, the uncertainty regarding numbers of leopards in the area that were never caught means that the degree of range overlap calculated during this study is a minimum value for both sexes, and the actual value may be considerably higher. Even given this fact, both inter- and intra-sexual range

overlaps found here exceeded 10%, the level considered to indicate exclusivity (Sandell 1989). This agrees with the expectation that large home ranges configured around sparse, unpredictably distributed resources should lead to a high degree of range overlap (Sandell 1989).

The large areas utilized here, and the relatively high degree of home range overlap, suggest that leopards do not rely upon direct territorial defence to spatially exclude conspecifics from their home ranges. This does not indicate interspecific tolerance, however: numerous studies have shown that leopards exhibit strong mutual avoidance, and utilize indirect signals such as scent-marking and vocal communication to ensure temporal separation of conspecifics (Schaller 1972; Ewer 1973; Bothma & Le Riche 1984; Hamilton 1981).

Protection of an area appeared not to influence leopard home range size, but there was some indication of higher leopard densities within game parks and reserves compared to elsewhere. As there was no marked difference in prey biomass between protected and unprotected areas, the lower leopard density outside reserves was probably a result of local persecution by landowners, as leopards are commonly considered a threat both to people and their stock (Nowell & Jackson 1996; Esterhuizen & Norton 1985). This highlights the fact that in many areas, large carnivore densities are determined as much by anthropogenic factors, such as local tolerance of their presence, as by ecological factors such as prey abundance and habitat requirements (Woodroffe 2000; Sillero-Zubiri & Laurenson 2001). This is one of the main objections raised to the leopard population estimates made by Martin & de Meulenaer (1988), who assumed that where leopards occur, they should be at the carrying capacity determined by rainfall, without considering factors such as local persecution (Norton 1990). Although leopard density appeared to be indirectly linked to rainfall via the relationship with prey biomass, the overall determinants of leopard density and spatial ecology are likely to be a complex set of factors including an artificial 'carrying capacity' determined by the attitudes of local communities.

The presence of larger carnivores in an area had no detectable effect on either the home range size or the density of leopards in an area. Although reduced intraguild competition might be expected to result in an increased density of subordinate carnivores (Creel *et al.* 2001), the adaptability of leopards, in terms of both diet and behaviour, means that they can compete successfully for resources even in areas where they overlap spatially with larger predators (Karanth & Sunquist 2000) These adaptations include variation in habitat selection, activity patterns, and prey selection, as well as the caching of food in trees to reduce kleptoparasitism (Seidensticker 1976b; Karanth & Sunquist 2000).

Overall, the large variation in home range size and patterns of spatial utilization observed between different studies is testament to the ecological flexibility of leopards, and their ability to adapt to vastly differing challenges, both environmental and anthropogenic, across their range. This ecological and behavioural plasticity is probably the main reason for the leopard's continued persistence in areas where changes in land use, prey base and habitat structure have caused the extirpation of less adaptable carnivores (Woodroffe 2000). Nevertheless, leopards are still of high conservation concern: their dietary flexibility means that they will readily switch to eating livestock or domestic dogs in areas where their natural prey has been depleted, and this trait exacerbates conflict with local people (Edgaonkar & Chellam 1998; Maan & Chaudhry 2000; Seidensticker *et al.* 1990). In many regions, particularly arid areas, leopards live at low densities and have large home ranges, making it more difficult to contain and effectively conserve viable populations within the boundaries of current protected areas. As with many other species of large, wide-ranging carnivores, effective leopard conservation will therefore require substantial efforts on private land as well as within reserves, to ensure that large tracts of contiguous habitat are available to these predators (Woodroffe 2001). Although this strategy is fraught with difficulties (Gittleman *et al.* 2001), dedicated research and conservation initiatives can have a significant impact on the tolerance of large carnivores outside protected areas (Marker *et al.* 2003; Sillero-Zubiri & Laurenson 2001), and this approach will be critical for the long-term conservation of viable leopard populations across much of sub-Saharan Africa.

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