Abstract: Knowledge of a species' ranging behaviour is both fundamental to understanding its behavioural ecology and a prerequisite to planning its management. Few data exist on the spatial ecology of cheetahs *Acinonyx jubatus* outside protected areas, but such areas are particularly important to their conservation. Cheetahs on Namibian farmlands occupied exceptionally large home ranges, averaging 1651km2 (1594km2), with no detectable effect of sex, social grouping or seasonality. Despite such large ranges, cheetahs tended to utilize intensively only a small fraction of that area: 50% of the fixes were located within an average of 13.95.3% of the home range. Ranges were not exclusive, overlapping on average by 15.817.0%, with male cheetahs showing more intra-sexual range overlap than did females. Coalitions of males appeared to select for a dense, prey-rich habitat, but this preference was not apparent for other social groupings. Conflict with humans is an important contributor to the species' decline, and these large, overlapping cheetah home ranges result in the movements of each individual cheetah encompassing many farms (21 based on the average home-range size). Consequently, many cheetahs may be exposed to a minority of farmers attempting to kill them, and also that many farmers may see the same cheetahs, thereby gaining an exaggerated impression of their abundance. Conservation priorities for cheetahs outside protected areas are the development of techniques for conflict resolution, as well as the maintenance and restoration of suitable habitat and promotion of land-management practices compatible with the continued existence of large carnivores.

Spatial ecology of cheetahs on north-central Namibian farmlands

L. L. Marker[1,2], A. J. Dickman[1,2,*], M. G. L. Mills[3,†], R. M. Jeo[1,‡] & D. W. Macdonald[2]

1 Cheetah Conservation Fund, Otjiwarongo, Namibia
2 Wildlife Conservation Research Unit, Department of Zoology, Oxford, UK
3 South African National Parks, Endangered Wildlife Trust and Mammal Research Institute, University of Pretoria, Skukuza, South Africa

Correspondence

Laurie L. Marker, Cheetah Conservation Fund, PO Box 1755, Otjiwarongo, Namibia.
Fax: 264 67 306247
Email: cheetah@iway.na

*Current address: Nuffield Building, Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK.
†Current address: Kgalagadi Cheetah Project, P. Bag X5890, Upington 8800, South Africa.
‡Current address: The Nature Conservancy, 4245 North Fairfax Drive, Arlington, VA 22203 USA.

Abstract

Knowledge of a species' ranging behaviour is both fundamental to understanding its behavioural ecology and a prerequisite to planning its management. Few data exist on the spatial ecology of cheetahs *Acinonyx jubatus* outside protected areas, but such areas are particularly important to their conservation. Cheetahs on Namibian farmlands occupied exceptionally large home ranges, averaging $1651 \, km^2$ ($\pm 1594 \, km^2$), with no detectable effect of sex, social grouping or seasonality. Despite such large ranges, cheetahs tended to utilize intensively only a small fraction of that area: 50% of the fixes were located within an average of $13.9 \pm 5.3\%$ of the home range. Ranges were not exclusive, overlapping on average by $15.8 \pm 17.0\%$, with male cheetahs showing more intra-sexual range overlap than did females. Coalitions of males appeared to select for a dense, prey-rich habitat, but this preference was not apparent for other social groupings. Conflict with humans is an important contributor to the species' decline, and these large, overlapping cheetah home ranges result in the movements of each individual cheetah encompassing many farms (21 based on the average home-range size). Consequently, many cheetahs may be exposed to a minority of farmers attempting to kill them, and also that many farmers may see the same cheetahs, thereby gaining an exaggerated impression of their abundance. Conservation priorities for cheetahs outside protected areas are the development of techniques for conflict resolution, as well as the maintenance and restoration of suitable habitat and promotion of land-management practices compatible with the continued existence of large carnivores.

Introduction

Although the creation and maintenance of a connected, representative protected-area network is important for both large carnivore persistence and biodiversity conservation (Margules & Pressey, 2000), the inadequate size of many protected areas means that management of surrounding lands may be equally important for conservation (Newmark, 1996). In Namibia, the majority of wildlife populations exist outside of protected areas (Barnard, 1998), with most of the country's ungulates occurring on commercial farmland (Richardson, 1998). This abundance of prey, coupled with the provision of artificial waterpoints and the widespread extirpation of large competitors, including lions *Panthera leo* and spotted hyaenas *Crocuta crocuta*, make commercial farmland a favourable refuge for cheetahs *Acinonyx jubatus* (Marker-Kraus *et al.*, 1996). Approximately 90% of Namibia's estimated 3000 cheetahs are found on $275\,000 \, km^2$ of farmland in the north-central region of the country (Morsbach, 1987; Marker-Kraus & Kraus, 1990).

This distribution has caused conflict with farmers, who perceive cheetahs as a significant threat to both livestock and ranched wildlife (Marker, Mills & Macdonald, 2003*c*). This conflict led to large numbers of cheetahs being killed or taken into captivity, with an estimated halving of the population size during the 1980s (Morsbach, 1987), and also meant that farmers who captured cheetahs and reported them to the Cheetah Conservation Fund (CCF) were often unwilling to have animals re-released onto their land. Therefore, cheetahs were often moved substantial distances, which could have a marked effect on their spatial ecology in this system. Although conservation efforts seem to have reduced this conflict (Marker *et al.*, 2003*c*), understanding cheetah ecology in this landscape is crucial for developing effective management strategies.

Our goal was to describe cheetah ranging behaviour on Namibian farmlands. Inter-sexual differences in spatial ecology are widely reported (Wilson, 1975; Caro, 1994), and so we examined home-range size in relation to sex, social group composition, age and season. Various aspects
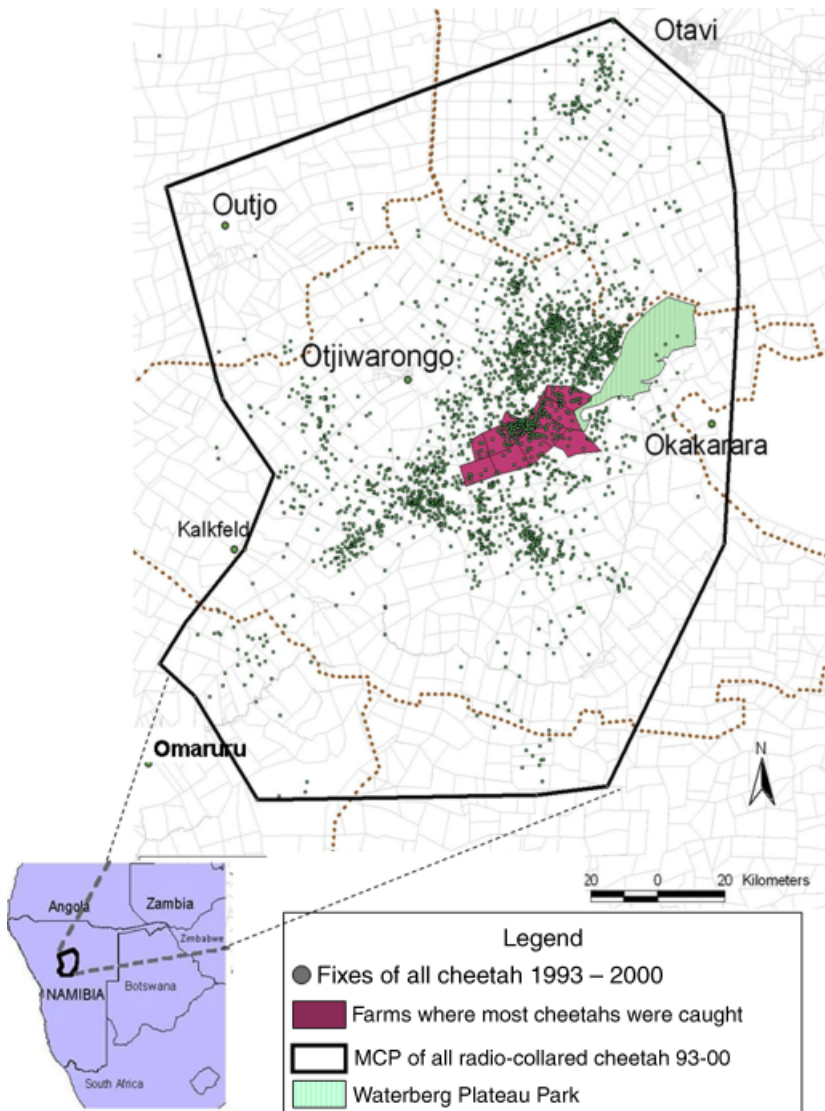
Figure 1 Radio tracking study area, in the north-central Namibian commercial farmland, used to track radio collared cheetahs *Acinonyx jubatus* between 1993 and 2000.

of cheetah spatial ecology have been documented previously (Caro, 1994; Durant, 1998; Broomhall, Mills & du Toit, 2003), but the only detailed, long-term study to date has been conducted in Serengeti National Park. This study provides the first long-term information regarding cheetah ranging behaviour outside of protected areas.

Study area

Radio tracking was conducted within an 18 000 km^2 area in north-central Namibia. The study area primarily consisted of commercial farmland, but also encompassed the Waterberg Plateau (a 48×16 km protected area), communal farmland and several fenced game-farms (Fig. 1). The area received an average of 472 mm rainfall annually, with 93% rain falling in the wet season (15th September to 14th April) and 7% in the dry season (15th April to 14th September).

The area was generally flat, with slow rainfall run-off, no permanent rivers and numerous man-made semi-permanent water reservoirs.

Land use in the area was primarily commercial cattle and wildlife farming, with a low human population density, averaging 2.3 people km^2 (CIA, 2003). The majority of commercial farms were individually owned and ranged in size from 50 to 200 km^2, with a mean of 80 km^2 (Marker-Kraus *et al.*, 1996). The area was situated in the Thornbush Savannah vegetation zone (Geiss, 1971), with *Acacia*, *Dichrostachys*, *Grewia*, *Terminalia* and *Boscia* being the dominant woody plant genera.

Methods

Between 1993 and 2000, radio collars were fitted onto 41 wild caught cheetahs on Namibian commercial farmland.

Cheetahs were captured opportunistically, mainly by local farmers but also by CCF researchers, using box traps (see Marker *et al.*, 2003*a* for details). Cheetahs were classified as being in one of the following social groupings: male coalition, single male or female (with or without cubs) for analyses. If one cheetah was caught, further traps were placed beside it until there was confidence, from lack of spoor or other signs of other cheetahs nearby, that the animal was a singleton or that all members of the social group had been captured.

Cheetahs were examined either at the capture site or at CCF headquarters. Immobilization was achieved using Telazol® (tiletamine-HCl and zolazepam-HCl; Warner Lambert, Ann Arbor, MI, USA), administered at 4 mg/kg intramuscularly. Cheetahs were fitted with a neoprene radio tracking collar with an external antenna (Advanced Telemetry Systems, Isanti, MN, USA), which had a life expectancy of > 36 months. Radio collars weighed 280 g, equivalent to 0.56% of body mass for a 50 kg male and 0.76% for a 37 kg female, well below the 3% limit recommended by Kenward (2001). We found no evidence of collars affecting survival or behaviour, and the same design has been used previously without evidence of significant adverse effects (Laurenson & Caro, 1994).

Age classification was based on experience with captive cheetahs and upon information from previous studies (Burney, 1980; Caro, 1994) and derived from weight, body measurements, tooth condition, gum recession, pelage condition, reproductive condition and social groupings of animals (Marker & Dickman, 2003). We categorized adult cheetahs at the time of collaring as: newly independent (> 18–30 months), young adults (> 30–48 months), prime adults (> 48–96 months) and old adults (> 96–144 months). None of the cheetahs radio collared was estimated to be over 144 months old. To give confidence to the above process, a cementum ageing model, as described in Matson (1981), was used on a subsample of individuals recovered after death, as well as from known-age animals, which revealed a good correlation between estimated and actual ages (Matson's Laboratory, LLC, Milltown, MT, USA; Marker *et al.*, 2003*a*). Full details of the criteria used to assign cheetahs to age classes are provided in Marker & Dickman (2003).

Depending on the landowner who had caught the animal, cheetahs were either released at the capture site, or on other farms where ranchers had given permission. The distance from capture to release site ranged from 0 to 600 km (Table 1). Only one cheetah per social group was radio collared, and cheetahs were released in the grouping with which they had been captured. Young, dependent cheetahs were only released if they were captured with their mothers, and animals were not collared unless they were fully grown. Wherever possible, radio collars were retrieved at the end of the project, but this was not always feasible due to the opportunistic nature of cheetah capture, and occurred in 63% of the cases.

Radio tracking

Following release, radio-collared cheetahs were tracked from a Cessna 172 aeroplane, utilizing a dual antenna procedure, with the animal's location determined using a portable global positioning system. Between May 1993 and May 1996, aerial tracking was conducted twice a week, while from June 1996 to December 2000 it was conducted once a week.

Home-range area and overlap calculations

Data were plotted and analysed using ArcView GIS (version 3.2, ESRI, Redlands, CA, USA) and the Animal Movement extension (Hooge, Eichenlaub & Soloman, 1999). Latitude and longitude recordings were used to calculate 95% minimum convex polygon (MCP) home ranges (White & Garrott, 1990), as well as 95 and 50% adaptive kernel home-range estimates (Worton, 1989; Seaman *et al.*, 1999). Four estimates of home-range size were calculated: (1) overall (the entire length of time a cheetah was tracked); (2) annual (based on 12-month periods from the time of collaring); (3) dry season; (4) wet season home-range size. Analysis was restricted to cheetahs with enough fixes to reach an asymptotic level, as determined using Ranges V (Kenward & Hodder, 1996), and was set at ≥ 30 fixes within a year for overall and annual home range and ≥ 15 fixes within a season for seasonal home range. When the effect of age on range size was being investigated, analyses were restricted to the first year after collaring, to improve the likelihood that cheetahs remained in the age group in which they had originally been classified.

Core home-range size was defined as the 50% probability kernel, and was determined for all cheetahs whose overall home range had been calculated. The degree of home-range overlap between cheetahs tracked concomitantly was calculated for each year of the study using the dynamitic interaction analysis as described in Ranges V (Kenward & Hodder, 1996). This analysis uses Jacob's Index (Jacobs, 1974), which compares the observed and possible distances between each range and provides a single index for each pair of animals.

Habitat selection

The habitat type in which each radio-telemetry fix occurred was visually classified from the air, and categorized in terms of bush density, namely sparse (< 30% canopy), medium (30–75% canopy) and thick bush (> 75% canopy). We also flew stratified random transects 20 km apart over the entire study area, and every 5 km, bush density was visually classified as above. This allowed estimation of the relative proportions of each habitat type available to cheetahs in the study area, providing a baseline for assessing habitat selection.

Prey density in different habitat types was calculated by driving strip counts across 70 km² of the study area, while the availability of different habitat types across that area was assessed using aerial photographs and ground observations. A minimum of three counts, over a standardized 50 km route, was conducted each month. The program DISTANCE (Thomas *et al.*, 1998) was used to estimate

Table 1 Information regarding all cheetahs *Acinonyx jubatus* radio-tracked on the Namibian farmlands during this study

Cheetah ID#	Social grouping	Distance (km) from capture site to release site	Estimated age group at collaring	Body mass (kg)	Dates tracked	No. of months tracked	Total no. of fixes	% flights located	Overall HRS 95% kernel	95% MCP	Core HRS (50% kernel)	Wet season HRS No. of fixes	95% kernel	Dry season HRS No. of fixes	95% kernel
821	SM	0	3	43.5	June 93–June 94	13	69	73.4	272	596.1	38.8	31	193.3	38	715.3
842	SM	50	3	50.0	May 93–November 94	19	124	93.9	1146.5	774.2	254.1	40	940.2	84	1009.6
867	SM	75	2	40.0	July 93–January 94	7	50	84.8	1763.7	1343.0	171.4	22	1474.8	28	1178.2
868	SM	75	2	42.0	July 94–December 96	30	132	77.2	1723.8	4221.5	268.0	57	909.5	75	2607.3
881	SM	0	3	46.0	August 93–April 95	21	120	89.6	281.6	419.1	16.9	65	260.7	55	362.7
952	SM	0	3	48.5	June 95–April 96	11	56	96.6	119.6	266.3	16.8	28	117.6	28	210.4
977	SM	0	2	48.0	June 95–July 95	2	8	80.0	–	–	–	–	–	–	–
985	SM	0	4	43.0	October 95–March 97	18	71	84.5	3938.1	2514.9	833.3	43	3281.5	28	3864.4
1025	SM	0	3	55.0	October 96–March 98	18	64	90.1	574.1	989.5	47.6	40	390.1	24	599.8
1043	SM	350	3	50.0	June 97–February 98	9	25	75.8	–	–	–	–	–	17	6244.8
1061	SM	200	3	54.0	July 99–December 00	18	58	98.3	1297.9	917.2	57.1	31	1331.5	27	1540.4
1062	SM	200	3	47.0	September 97–October 97	2	3	60.0	–	–	–	–	–	–	–
1105	SM	50	3	43.0	June 98–May 99	12	30	71.4	2205.4	5658.2	345.6	18	1298.5	12	6045.1
1158	SM	0	2	42.0	February 99–October 00	21	83	91.2	1227.7	382.0	135.5	28	900.8	33	1431.6
1163	SM	200	2	40.5	April 99–October 00	19	59	98.3	3333.1	2292.3	450.9	26	2519.6	33	3125.6
All single males (n=15) Mean		80	–	46.2	–	14.7	63.5	84.3	1490.3	1697.9	219.7	35.8	1134.8	37.1	2225.8
SD		107.8	–	4.7	–	7.7	39.3	11.2	1202.9	1700.1	239.3	14.0	957.8	21.5	2051.8
831	CM	50	2	43.0	April 93–April 95	24	140	85.4	1406.4	3402.8	140.9	63	1156.3	77	1828.2
835	CM	0	2	45.0	October 95–November 95	2	6	66.7	–	–	–	–	–	–	–
865	CM	0	1	48.0	July 93–August 95	26	172	94.0	710.7	824.6	78.8	72	452.2	100	937.3
869	CM	75	2	46.0	October 93–April 94	7	44	93.6	644.1	385.3	98.0	41	621.3	–	–
937	CM	150	2	38.5	September 94–October 94	2	7	87.5	–	–	–	–	–	–	–
974	CM	0	2	48.0	June 95–June 99	49	216	96.4	1076.2	1371.6	138.5	101	904.6	115	1324.0
979	CM	0	3	51.0	August 95–December 96	17	80	97.6	680.4	712.8	74.6	40	807.5	40	552.3
990	CM	0	3	54.5	December 95–April 98	41	115	95.8	544.5	2437.6	49.1	63	312.6	52	1129.3
1063	CM	200	1	50.0	September 97	1	3	42.90	–	–	–	–	–	–	–
1164	CM	0	2	40.0	April 99–July 99	4	12	100.0	–	–	–	–	–	–	–
1167	CM	0	1	42.0	September 97–May 98	9	30	83.3	4347.6	2124.2	872.3	20	2837.7	10	8496.4
All coalition males (n=11) Mean		43.2	–	46.0	–	16.5	75.0	85.7	1344.3	1608.4	207.5	57.1	1013.2	65.7	2377.9
SD		70.8	–	4.9	–	16.6	75.3	17.0	1358.2	1091.0	295.1	26.3	852.7	39.2	3027.1
All males (n=26) Mean		64.4	–	46.1	–	15.5	68.3	84.9	1436.5	1664.9	215.2	43.6	1090.0	46.1	2273.8
SD		94.1	–	4.7	–	12.0	56.3	13.7	1226.5	1471.4	253.1	21.5	898.1	30.4	2314.5
878	F	450	1	35.0	September 93–October 93	2	9	81.8	–	–	–	–	–	–	–
948	F	260	1	34.0	October 94–December 00	79	257	86.9	4024.7	6353.7	473.4	129	3617.9	128	3920.9
967	F	0	4	–	February 95–August 99	43	218	92.0	1029.3	1445.8	157.7	100	206.8	118	619.8
978	F	300	3	46.0	October 95–March 97	18	67	98.5	999.9	1190.8	217.6	45	1473.2	22	147.8
984	F	275	1	30.0	October 95–December 00	63	220	94.4	1282.5	1041.7	221.5	119	1357.5	101	1232.0
986	F	0	3	34.0	October 95–March 96	6	29	96.7	–	–	–	28	1219.2	–	–
992	F	350	3	42.0	January 96–February 96	2	8	61.5	–	–	–	–	–	–	–
1026	F	50	3	31.0	November 96–July 97	9	33	82.5	553.9	324.0	67.2	22	479.8	11	430.7

Table 1. Continued

Cheetah ID#	Social grouping	Distance (km) from capture site to release site	Estimated age group at collaring	Body mass (kg)	Dates tracked	No. of months tracked	Total no. of fixes	% flights located	Overall HRS 95% kernel	95% MCP	Core HRS (50% kernel)	Wet season HRS No. of fixes	95% kernel	Dry season HRS No. of fixes	95% kernel
1084	F	0	3	40.0	January 98–May 98	5	19	95.0	–	–	–	15	957.3	–	–
1100	F	600	3	36.0	June 98–December 99	19	48	94.1	7063.3	3012.1	1795.3	19	2686.2	29	6654.4
1107	F	125	1	25.0	September 98–October 98	2	3	100.0	–	–	–	–	–	–	–
1144	F	0	2	35.0	December 98–March 99	4	10	83.3	–	–	–	–	–	–	–
1154	F	0	2	35.0	March 99–September 00	19	56	98.2	1705.6	1016.0	126.7	28	1369.7	28	2090.8
1177	F	600	2	39.0	December 99	1	1	100.0	–	–	–	–	–	–	–
1184	F	0	1	34.0	October 99–December 00	14	47	97.9	626.3	306.6	122.7	30	683.8	17	444.0
All females (n = 15) Mean		200.7	–	35.4	–	19.1	68.3	90.9	2160.7	1836.3	397.8	53.5	1405.1	56.8	1942.6
SD		222.4	–	5.2	–	23.9	87.3	10.3	2269.4	2010.3	578.0	44.4	1032.4	49.7	2272.3
All cheetahs (n = 41) Mean		114.3	–	42.4	–	16.8	68.3	87.1	1651.1	1715.7	269.3	47.0	1198.7	49.3	2175.7
SD		165.1	–	7.1	–	17.1	68.1	12.7	1594.2	1610.4	376.2	30.9	940.4	36.4	2263.3

Social group categories are as follows: SM, single male; CM, coalition male; F, female. Cheetahs were assigned to one of the following age groups at time of radio collaring: 1 = newly independent (>18–30 months), 2 = young adult (>30–48 months), 3 = prime adult (>48–96 months) and 4 = old adult (>96–144 months). None of the radio collared cheetahs was estimated to be >144 months old. MCP, minimum convex polygon; HRS, home-range size.

prey density, and the strip was classified by habitat type, as above. The relative utilization of habitat types by prey species was examined alongside cheetah habitat selection, to investigate whether cheetahs' favoured habitat that was selected for by ungulates.

Data analysis

Analyses were conducted using the statistical package SPSS version 12.0.1 (SPSS Inc. Chicago, IL, USA). The statistical tests used depended on the distribution of the data and included χ^2, t-test, z-test, Kruskal–Wallis (KW) χ^2, analysis of variance and Spearman's and Pearson's correlations, with $P < 0.05$ considered to be significant.

Results

Forty-one cheetahs (26 males, 15 females) were radio-tracked between April 1993 and December 2000 (Table 1). Cheetahs were located on 87.4% (± 12.6) of the flights, during which they were searched, and overall, annual and seasonal home ranges were determined from a mean of 68.34 (± 68.14) fixes per cheetah, and 7.4 (± 2.8) days between fixes.

Because cheetahs were opportunistically caught, we examined their ages in order to reveal potential biases in sampling before comparing social groupings and sexes (Table 1). There was no significant difference between sexes regarding age category at collaring ($z = -0.562$, $P = 0.602$); however, there was between social groupings (KW $\chi^2 = 6.549$, $P = 0.038$), as single males were significantly older at the time of collaring ($z = -2.73$, $P = 0.006$) when compared with other groupings. There were no significant differences between the mean number of fixes ($F = 0.087$, $P = 0.917$), percentage of flights on which they were located ($F = 1.070$, $P = 0.353$) or the number of months tracked (KW $\chi^2 = 0.472$, $P = 0.790$).

Overall home-range size

Twenty-seven cheetahs yielded sufficient fixes to estimate overall home-range size, which revealed a mean overall range size of 1651.1 km² (± 1594.2 km²) and a median overall range size of 1146.5 km² (Table 1). Estimates of overall home-range size produced using the 95% kernel method did not vary significantly from those using the 95% MCP, for any of the social groupings (single males: $z = -0.115$, $P = 0.908$; coalition males: $z = -0.831$, $P = 406$; females: $z = -0.315$, $P = 0.753$). Therefore, the 95% kernel method was used for further estimates of home-range size.

No statistically significant differences were detected in home-range size between sexes ($t = -1.081$, $P = 0.290$) or social groupings ($F = 0.580$, $P = 0.586$). For all social groupings, the overall home-range sizes estimated here were significantly larger than those reported elsewhere (single males: $t = -5.15$, $P = 0.036$; coalition males: $t = -18.9$, $P = 0.001$; females: $t = -15.8$, $P < 0.001$: Table 2). Despite the general trend for vast ranges, some individuals still managed to exist within relatively small areas. Three single males, with a mean of 46 months of age, each occupied

Table 2 Estimates of cheetah *Acinonyx jubatus* home ranges sizes, and methods of estimation, reported in this study and elsewhere in Africa

Area	Method of HRS estimation	Female	Coalition male	Single male	Male (unspecified)	References
Namibia (north-central farmlands)	95% kernel	2161 (15)	1344 (11)	1490 (15)	–	This study
Namibia (north-central farmlands)	95% MCP	1836 (15)	1608 (11)	1698 (15)	–	This study
Serengeti Plains*	Minimum polygon	833 (19)	37 (22)	777 (9)	–	Caro (1994)
Kalahari Gemsbok/Gemsbok National Parks	Sightings	320 (4)	125 (3)	–	–	Mills (1998)
Kruger National Park	95% MCP	161 (2)	126 (1)	195 (1)	–	Broomhall *et al.* (2003)
Kruger National Park	95% kernel	212 (2)	188 (1)	250 (1)	–	Broomhall (2001)
Kruger National Park	Convex polygon	160 (2)	332 (2)	–	–	Mills (1998)

Figures in parentheses indicate sample size, that is the number of single males, single females or coalitions of males radio collared.

MCP, minimum convex polygon; HRS, home-range size.

*Male ranges given for the Serengeti refer to resident and non-resident males rather than coalitions and singletons respectively.
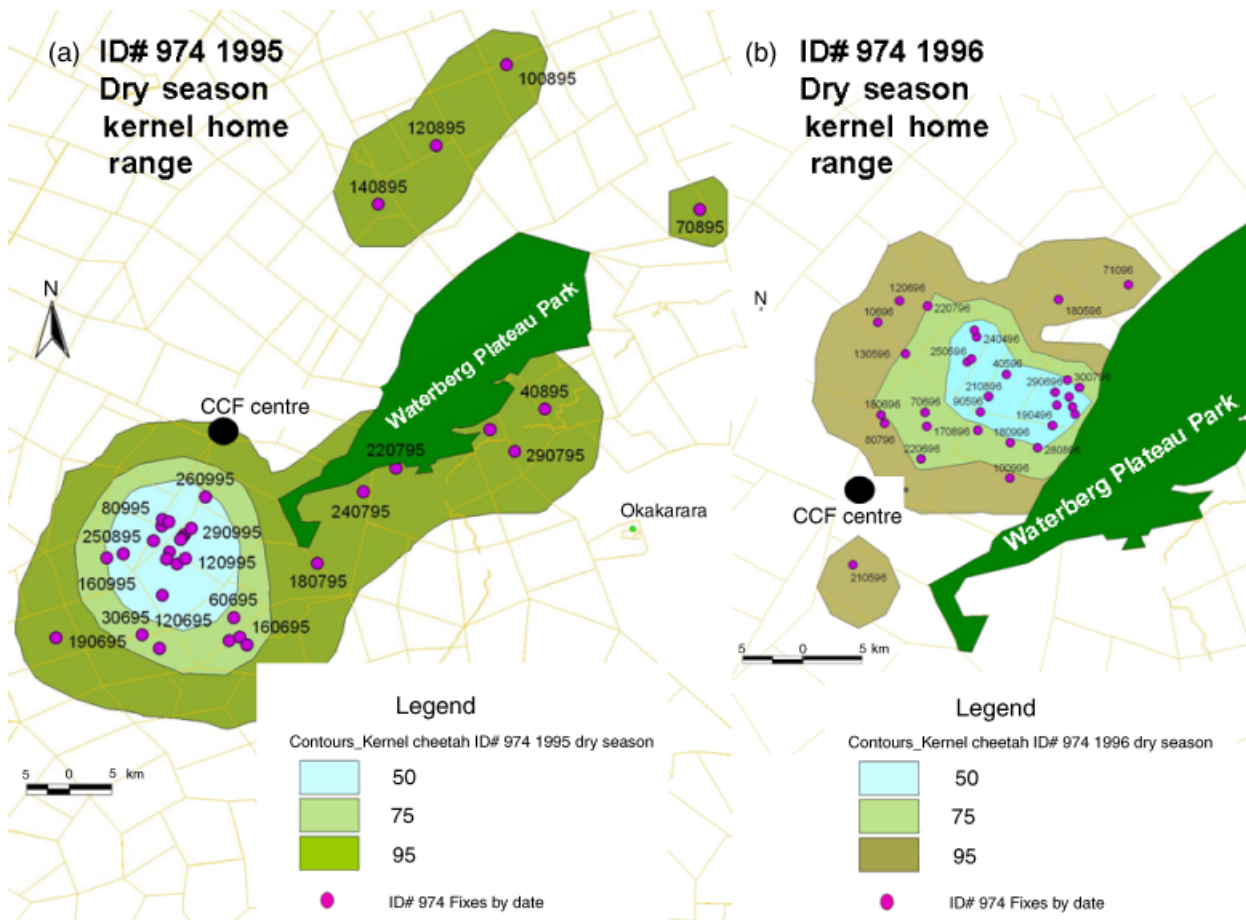
Figure 2 Home range of a male coalition group (cheetah ID# 974) during the dry season of 1995 (a) and 1996 (b) showing a major shift in home range between the 2 years.

overall ranges of $<300 \, \text{km}^2$, which might be considered to be large for cheetahs elsewhere, but tiny compared with the averages found here. In addition, ranges shifted between years (Fig. 2), and some home ranges were shown to increase when a male coalition was reduced to a single male (Fig. 3).

Annual home-range size

Annual home-range sizes could be calculated for 23 cheetahs (Table 3). The mean annual range sizes did not differ significantly from the overall home-range size for any of the
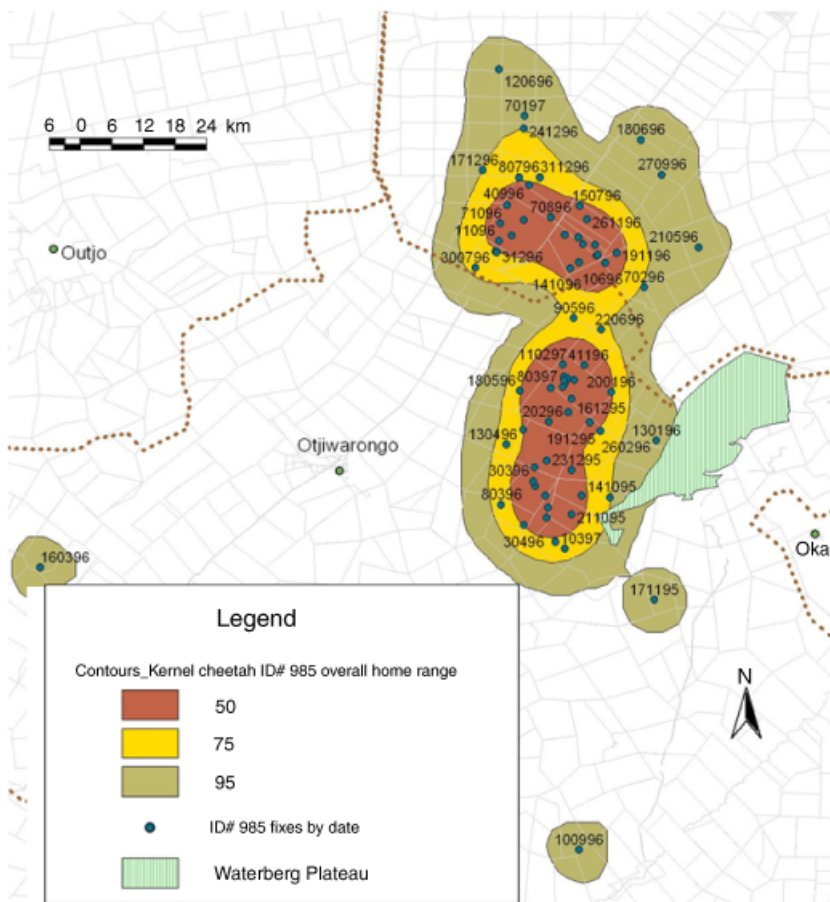
Figure 3 One of the largest home ranges during the 10-year study was of a single male cheetah *Acinonyx jubatus* (ID# 985), which, after losing his coalition member, continued to shift his movement patterns and increase his home-range size.

social groupings, and did not vary significantly between age groups, sexes or social groupings.

Seasonal home-range size

Neither wet nor dry season home-range size differed significantly between sexes, social groupings or age groups (Table 1). There was no significant difference between the size of wet and dry season home ranges for any of the social groupings: their boundaries shifted over time but did not differ significantly in terms of overall size.

Core home-range size

No significant seasonal variation was observed regarding core home-range area for any of the social groupings. Core areas comprised a significantly smaller percentage of single males' overall home range in the wet season ($11.3 \pm 5.0\%$) than in the dry season ($14.5 \pm 2.9\%$; $z = -2.13$, $P = 0.034$), but no significant difference was found for the other social groupings.

The sizes of coalition males' core home ranges were significantly smaller than those of females ($z = -2.19$, $P = 0.028$), but there were no detectable differences between other social groupings. Core areas comprised on average $13.9 \pm 5.3\%$ of the home-range size, with no significant difference between social groupings.

Effect of distance moved between capture and release sites

The distance moved from capture to release site was positively correlated to the overall home-range size (Table 4), but this may be an artefact of social groupings moved: coalition males, which tended to have smaller home ranges, accounted for 35% of those released at the capture site, but only 19% of animals moved. When examined separately, there was no significant relationship between distance moved and overall home-range size for any of the social groupings. Distance moved had some effect on spatial ecology, however, releasing a cheetah further from the capture site was linked to larger core home ranges for females, and to ranging further in the first year for single males (Table 4). There did not seem to be a marked effect of cheetahs' rapidly travelling long distances to return to original locations: cheetahs released away from their capture site did not range over larger areas in the first year than in subsequent years ($t = 0.576$, $P = 0.577$).

Home-range overlap

The large sample size of cheetahs collared, and the close proximity of their capture sites (Fig. 1) allowed range overlap to be calculated for cheetahs utilizing the same area

Table 3 Mean annual home-range size (HRS) (estimated using the 95% kernel method) for all cheetahs *Acinonyx jubatus* radio-tracked during the study for at least 12 months, split by sex and social group by age

Cheetah ID#	Social grouping	Estimated age group at collaring	Years radio tracked	Mean annual HRS (km^2)
985	Single male	Old adult	96	4191.5
821	Single male	Prime adult	93–94	272.0
831	Single male	Prime adult	94	519.9
842	Single male	Prime adult	93–94	907.5
881	Single male	Prime adult	94	246.3
952	Single male	Prime adult	95–96	119.6
1025	Single male	Prime adult	97	706.7
1061	Single male	Prime adult	2000	1203.0
1105	Single male	Prime adult	98–99	2205.4
868	Single male	Young adult	95–96	722.5
1158	Single male	Young adult	99–2000	736.6
1163	Single male	Young adult	99–2000	1524.9
All single males ($n=12$)	Mean			1113.0
	SD			1134.1
974	Coalition male	Prime adult	96–98	514.5
979	Coalition male	Prime adult	96	541.7
990	Coalition male	Prime adult	96–97	862.5
865	Coalition male	Newly independent	93–95	615.4
All coalition males ($n=4$)	Mean			633.5
	SD			158.5
All males ($n=16$)	Mean			993.1
	SD			997.1
967	Female	Old adult	96–98	984.3
978	Female	Prime adult	96	561.3
1100	Female	Prime adult	99	2323.9
1154	Female	Young adult	99–2000	1000.7
948	Female	Newly independent	95–2000	1678.7
984	Female	Newly independent	96–2000	905.7
1184	Female	Newly independent	2000	637.9
All females ($n=7$)	Mean			1156.1
	SD			629.2
All cheetahs ($n=23$)	Mean			1042.7
	SD			889.8

in the same year. Mean home-range overlap averaged $15.8 \pm 17.0\%$ (minimum = 0%, maximum = 74%, median = 9.83%) across all collared cheetahs (Fig. 4), with males exhibiting a significantly greater intra-sexual range overlap than females ($z = -2.23$, $P = 0.026$). However, more males than females were tracked in the study area, which could lead to underestimation of the true extent of female intra-sexual overlap. Single males overlapped with one another significantly more than females did ($z = -2.10$, $P = 0.036$), but there were no significant differences when other social groupings were compared. There are caveats to interpreting these data, however, they do not take account of overlap with cheetahs that were not radio-tracked, and extensive movements by animals released far from their capture sites (particularly single males in the first year) may increase the range overlap that those cheetahs exhibited with others, at least in the short term.

Habitat selection

Overall, radio-collared cheetahs appeared to utilize the three habitat types approximately in proportion to their availability, but when examined by social grouping, female cheetahs seemed to use thickly bushed areas less than their availability, preferring medium bush ($\chi^2 = 7.37$, $P = 0.025$). Conversely, coalition males appeared to select for areas of thick bush while utilizing medium bush areas far less than expected ($\chi^2 = 23.9$, $P < 0.001$). Single males showed no evident selection, utilizing all habitat types in approximate proportion to availability.

The habitats in which radio-tracked cheetahs were recorded were not closely correlated with those in which ungulates were detected. The majority of ungulate species, particularly large prey, showed a preference for dense bush (Fig. 5a and b), whereas overall, radio-collared

Table 4 Relationship between distance moved from capture to release site, and overall, core, first season and first annual home-range size, for cheetahs *Acinonyx jubatus* of various social groupings radio-tracked on the Namibian farmlands

Social group	Variable being examined	Correlation with distance moved		
		r	n	P
All cheetahs	Overall home-range size	0.440	28	0.019*
	Core home-range size	0.482	28	0.009**
	Home-range size over the first season	0.181	30	0.339
	Home-range size over the first year	0.394	22	0.069
Coalition males	Overall home-range size	−0.089	7	0.849
	Core home-range size	0.267	7	0.562
	Home-range size over the first season	−0.439	6	0.383
	Home-range size over the first year	0.707	5	0.182
Females	Overall home-range size	0.27	9	0.483
	Core home-range size	0.714	9	0.031*
	Home-range size over the first season	−0.524	10	0.12
	Home-range size over the first year	−0.213	6	0.686
Single males	Overall home-range size	0.541	12	0.07
	Core home-range size	0.466	12	0.127
	Home-range size over the first season	0.671	12	0.017*
	Home-range size over the first year	0.553	11	0.008

*$P<0.05$, **$P<0.01$.

cheetahs were recorded in dense bush in proportion to its availability.

When examined by social group, however, coalition males did show some preference for the dense bush preferred by ungulates ($r = 1.00$, $P = 0.019$), and particularly for habitat preferred by large prey ($r = 1.00$, $P = 0.009$). Single males showed no relationship between their habitat preferences and those of prey species, while females actually seemed to avoid those habitats preferred by ungulates ($r = −1.00$, $P = 0.046$).

Discussion

Understanding the factors influencing cheetah spatial ecology in Namibia is fundamental to developing effective and appropriate regional conservation strategies for the species. The most striking result of this study was the very large home-range sizes of cheetahs, found across all sexes, social groupings, age groups and seasons. The long-distance movements of cheetahs elsewhere, particularly of females in the Serengeti, have been attributed to seeking out migratory prey after ephemeral rains (Caro, 1994), and Broomhall (2001) also found in Kruger National Park that dependence upon migratory prey was linked to large ranges. This explanation was inappropriate for the large ranges revealed for Namibian farmland cheetahs, where both sexes and all social groupings ranged extensively while reliant upon sedentary prey.

It is well established that intra-guild hostility from larger carnivores can lead to high levels of juvenile mortality and kleptoparasitism among cheetahs (Caro, 1994; Laurenson, 1994), which may therefore attempt to avoid competitors to minimize such risks (Durant, 2000). Such avoidance may result in cheetahs ranging across larger areas than would be predicted on the basis of prey availability. However, both

lions and spotted hyaenas have been widely eradicated on Namibian farmlands (Marker, 2002), but cheetah ranges were nonetheless much larger than those recorded where cheetahs coexist alongside larger carnivores. Furthermore, in the Serengeti consistent differences between the sexes and social groupings have been reported, with females occupying large, overlapping ranges and territorial males maintaining much smaller areas (Caro, 1994). In this study, we did not have the behavioural data needed to assess territoriality, but found no significant differences between sexes or social groupings in range size, with all utilizing very large areas. However, the smallest home ranges were of single males of prime breeding age, the age group most frequently removed by people from the farmlands (Marker et al., 2003b). These cheetahs may be seen more regularly by farmers, and therefore are removed. Namibian cheetahs were found to be as highly mobile and often closely related to others in their home-range areas (Marker et al., accepted), possibly contributing to the lack of exclusivity. We found that most home ranges shifted over time, which may be affected by fluctuating drought cycles; for instance, during the worst drought of the past two decades in 1996, one of two radio-collared groups moved into the other's territory and were killed by the other coalition (L. L. Marker, pers. obs.).

An explanation, therefore, for the ubiquitously large ranges recorded here could be low annual rainfall, averaging 468 mm in Namibia (Marker, 2002), compared with 600–700 mm on the Serengeti plains (Maddox, 2002). Precipitation is often a corollary of prey biomass, with most expansive ranges in the driest areas (Stander et al., 1997), but this effect may be diminished on farmland with man-made waterpoints. Moreover, range sizes in Namibia did not differ significantly between the wet and dry seasons, indicating that another factor aside from rainfall is influencing the need for such large areas. Most cheetahs also did
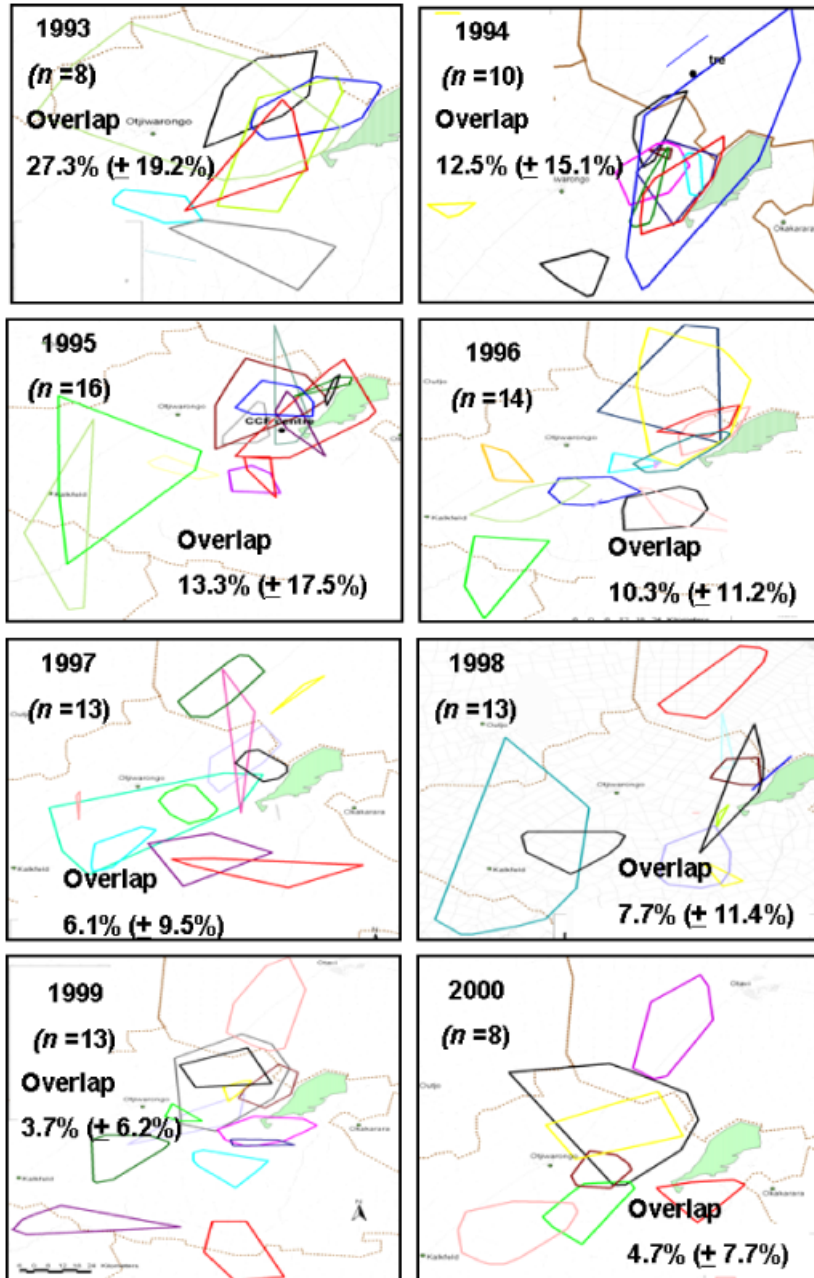
Figure 4 Degree of home-range overlap for cheetahs *Acinonyx jubatus* tracked concomitantly on the commercial farmland, shown for each year of the study. The mean overlap for all cheetahs tracked that year is shown at the top of each map, while the figure in parentheses denotes the standard deviation.

not appear to select for areas based simply on prey density, suggesting again that some other variable is affecting home-range size and configuration.

Understanding cheetah spatial ecology here may require examination at a finer scale: Muntifering *et al.* (2006) used these radio-telemetry data to define 'high-use' areas that cheetahs occupied relatively frequently – these were relatively small habitat patches with good visibility and grass cover, which may be advantageous for stalking. Observations of cheetah hunting have revealed the use of edges of dense habitat patches to provide cover for stalking, and so cheetahs

may configure range use to include a matrix of these different habitat patches (Frame & Frame, 1980; Caro, 1994). However, it should be noted that using weekly radio-telemetry fixes may not be the best technique for assessing habitat importance, and these data will be influenced by the time of day that the fix was obtained – more accurate information on daily habitat use would require finer-resolution studies such as the use of collars with frequent fixes. Despite this caveat, differences between 'high-use' and 'low-use' areas (Muntifering *et al.*, 2006) suggest that there may be important small-scale variation in habitat and vegetation determining which
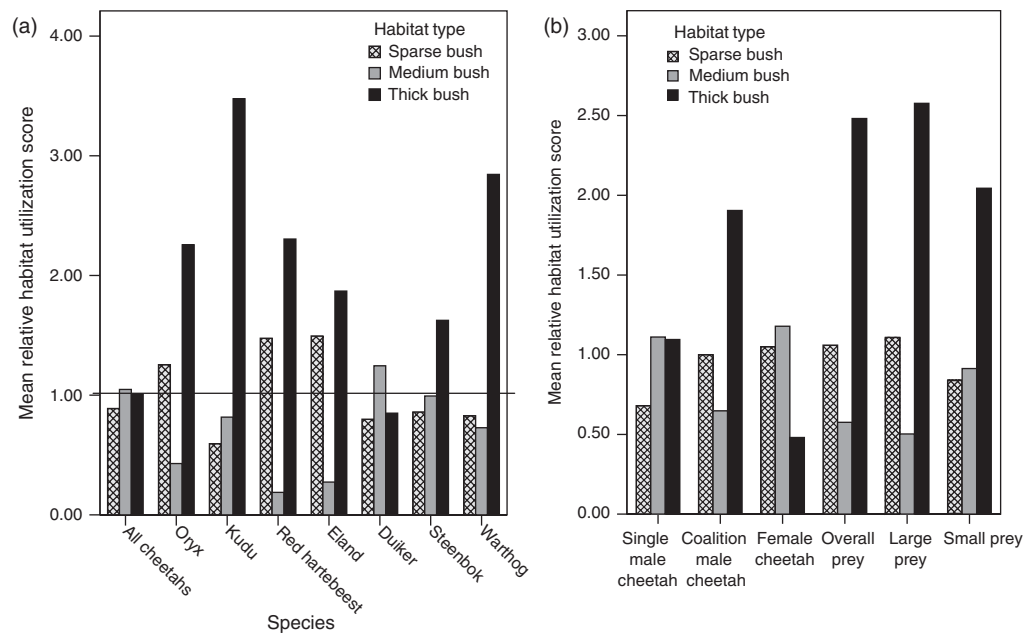
Figure 5 (a) Relative habitat utilization scores for radio-collared cheetahs *Acinonyx jubatus* and for the seven key prey species monitored during the study. Scores above 1.0 indicate utilization of a habitat proportionally more than its availability in the study area, while scores below 1.0 indicate lower usage than would be expected from the amount of that habitat available. The horizontal line indicates parity, that is the level (1.0) at which habitat is used in direct proportion to its availability. (b) Relative habitat utilization scores for radio-collared cheetahs of various social groupings; namely, coalition males, single males and females, and for prey species monitored during the study. The prey species are classified as either large (oryx, kudu, red hartebeest and eland) or as small (duiker, steenbok and warthog).

parts of their ranges cheetahs are likely to utilize more intensely, which could have important implications for understanding and resolving conflicts on farmlands.

Despite having such large home ranges, a finer-scale examination of core areas revealed that cheetahs tended to utilize intensively only a small fraction of their overall ranges, with very large 'peripheral' areas used less intensely.

The reason for this is unclear, but the size of the overall ranges and the use of such large peripheral areas could feasibly be linked to the serious perturbation recently suffered by this population due to removals from the farmlands (Marker *et al.*, 2003b). One of the largest home ranges was from a male cheetah (ID# 985) that had lost its male coalition partner, which was killed by a farmer. Such perturbation has been shown to affect a species' ecology and behaviour (Tuyttens & Macdonald, 2000), and high levels of human intervention are likely to have had a substantial impact on Namibian cheetahs, and so the consequences of disturbance could be an important factor affecting cheetah spatial ecology in this region. Further work on the features of intensively utilized patches compared with peripheral range areas, the spatial stability of 'core' areas across seasons and years and the impact of human disturbance on cheetah movements would provide useful information regarding the determinants of cheetah range use and habitat selection on the Namibian farmlands, which could in turn have important implications for cheetah management and conflict resolution.

Conservation implications

The range sizes found for cheetahs on Namibian farmland were unexpectedly large, considering that the region is typified by widely available water and a sedentary prey base. These very large, overlapping home ranges have important conservation implications, in that each cheetah will likely range over many farms, and so even a few hostile farmers could have a significant effect on the local cheetah population with these farms acting as population sinks. Given the average farm size of $80 \, km^2$ in the study area, the mean cheetah home-range size revealed here ($1651 \, km^2$) shows that each home range could well incorporate 21 different farms during the course of the year. Assuming an average group size of 2.5, this would lead to an estimate of 53 'cheetah-farm encounters' in one home range alone. Bearing in mind the degree of range overlap (16% here, which is almost certainly conservative, as it does not incorporate non-collared cheetahs in the study area), this would rise to an estimated 60 'cheetah-farm encounters' within one home range annually. Sightings of cheetahs on multiple, discontinuous farms could mistakenly be taken as evidence for many cheetahs in an area, whereas it could easily be the same cheetah or group of cheetahs simply moving through its range. It would be easy for farmers to overestimate local cheetah population numbers based on encounter rates: just one of those farmers killing cheetahs could have impacts over an area of more than $1500 \, km^2$. In Kenya, research

found that the actions of just one rancher, on a $180\,km^2$ ranch, had direct impacts on lion populations over $2000\,km^2$ (Woodroffe & Frank, 2005). Given that adult females, potentially the most valuable component of the population in terms of long-term viability, range over the largest areas, the size of these ranges is of particular significance for cheetah conservation in Namibia. It is important to implement effective conservation strategies over very large areas of unprotected rangeland to achieve country-wide cheetah conservation in Namibia, and reduce human-cheetah conflict on the farmlands. Fundamental to this is developing economic advantages to maintaining carnivores on private land (Sillero-Zubiri & Laurenson, 2001), such as through ecotourism, trophy hunting and incentives for predator-friendly farming (Archabald, 2000; Lindsey *et al.*, 2005; Woodroffe, Thirgood & Rabinowitz, 2005). Additionally, if cheetah are to survive on farms without depending on domestic stock, then creating conservancies where wild prey survive sustainably will be essential (Marker, 2002). Such strategies, integrating conflict resolution with more effective land and wildlife management, will be critical to conservation outside protected areas, both for cheetahs and for other threatened large carnivores.

Acknowledgements

References

Archabald, K. (2000). *Can revenue-sharing save wildlife? A case study of Jozani Chwaka Bay conservation area, Zanzibar, Tanzania*: 95. Wisconsin: University of Wisconsin.

Barnard, P. (1998). *Biological diversity in Namibia: a country-wide study*. Cape Town: Namibian National Biodiversity Task Force. ABC Press.

Broomhall, L.S. (2001). *Cheetah Acinonyx jubatus in the Kruger National Park: a comparison with other studies across the grassland-woodland gradient in African savannas*. Pretoria, South Africa: Department of Zoology and Entomology, University of Pretoria.

Broomhall, L.S., Mills, M.G.L. & du Toit, J.T. (2003). Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *J. Zool. (Lond.)* **261**, 119–128.

Burney, D.A. (1980). *The effects of human activities on cheetah (Acinonyx jubatus) in the Mara region of Kenya*. Nairobi: University of Nairobi.

Caro, T.M. (1994). *Cheetahs of the Serengeti plains: group living of an asocial species*. Chicago: University of Chicago Press.

CIA (2003). The World Factbook – Namibia. http://www.cia.gov/cia/publications/factbook/geos/wa.html.

Durant, S. (1998). Competition refuges and coexistence: an example from Serengeti carnivores. *J. Anim. Ecol.* **67**, 81–92.

Durant, S.M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.* **11**, 624–632.

Frame, G.W. & Frame, L.H. (1980). *Cheetahs: in a race for survival*: 712–728. Washington DC: National Geographic.

Geiss, W. (1971). A preliminary vegetation map of South West Africa. *Dinteria* **4**, 1–114.

Hooge, P.N., Eichenlaub, W. & Soloman, E. (1999). *The animal movement program*. Alaska: USGS, Alaska Biological Science Center.

Jacobs, J. (1974). Quantitative measurements of food selection. *Oecologia* **14**, 413–417.

Kenward, R. (2001). *A manual for wildlife radio-tagging*. San Diego, London: Academic Press.

Kenward, R.E. & Hodder, K.H. (1996). *Ranges V*. Dorset, UK: Institute of Terrestrial Ecology.

Laurenson, M.K. (1994). High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *J. Zool. (Lond.)* **234**, 387–408.

Laurenson, M.K. & Caro, T.M. (1994). Monitoring the effects of non-trivial handling in free-living cheetahs. *Anim. Behav.* **47**, 547–557.

Lindsey, P.A., Alexander, R.R., du Toit, J.T. & Mills, M.G.L. (2005). The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biol. Conserv.* **123**, 339–348.

Maddox, T. (2002). *The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone*. London, UK: Department of Anthropology, University of London.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature* **405**, 243–253.

Marker, L. (2002). *Aspects of cheetah (Acinonyx jubatus) biology, ecology and conservation strategies on Namibian farmlands*: 476. Oxford, UK: Department of Zoology, University of Oxford.

Marker, L.L. & Dickman, A.J. (2003). Morphology, physical condition and growth of the cheetah (*Acinonyx jubatus jubatus*). *J. Mammal.* **84**, 840–850.

Marker, L.L., Dickman, A.J., Jeo, R.M., Mills, M.G.L. & Macdonald, D.W. (2003*a*). Demography of the Namibian cheetah (*Acinonyx jubatus jubatus*). *Biol. Conserv.* **114**, 413–425.

Marker, L.L., Dickman, A.J., Mills, M.G.L. & Macdonald, D.W. (2003*b*). Aspects of the management of cheetahs, *Acinonyx jubatus jubatus*, trapped on Namibian farmlands. *Biol. Conserv.* **114**, 401–412.

Marker, L.L., Mills, M.G.L. & Macdonald, D.W. (2003*c*). Factors influencing perceptions and tolerance toward cheetahs (*Acinonyx jubatus*) on Namibian farmlands. *Conserv. Biol.* **17**, 1–9.

Marker, L.L., Pearks-Wilkerson, A.J., Sarno, R.J., Martenson, J., Breitenmoser-Würsten, C., O'Brien, S.J. & Johnson, W.E.(in press). Molecular Genetic Insights on Cheetah (Acinonyx jubatus) Ecology and Conservation in Namibia. *Journal of Heredity*. in press.

Marker-Kraus, L. & Kraus, D. (1990). Investigative trip to Zimbabwe and Namibia. *Cat News* **12**, 16–17.

Marker-Kraus, L., Kraus, D., Barnett, D. & Hurlbut, S. (1996). *Cheetah survival on Namibian farmlands*. Windhoek: Cheetah Conservation Fund.

Matson, G.M. (1981). *Workbook for cementum analysis*. Milltown, MT: Matson & Matson.

Mills, M.G.L. (1998). Cheetah ecology and behaviour in East and South Africa. In *Symposium on cheetahs as game ranch animals*: 18–22. Penzhorn, B.L. (Ed.). Onderstepoort, South Africa: Wildlife Group of South African Veterinary Association.

Morsbach, D. (1987). Cheetah in Namibia. *Cat News* **6**, 25–26.

Muntifering, J.R., Dickman, A.J., Perlow, L.M., Hruska, T., Marker, L.L., Ryan, P.G. & Jeo, R.M. (2006). Managing the matrix for large carnivores: a novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. *Anim. Conserv.* **9**, 103–112.

Newmark, W.P. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.* **9**, 512–526.

Richardson, J.A. (1998). Wildlife utilization and biodiversity conservation in Namibia: conflicting or complementary objectives? *Biodiver. Conserv.* **7**, 549–559.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. *J. Wildl. Mgmt.* **63**, 739–747.

Sillero-Zubiri, C. & Laurenson, M.K. (2001). Interactions between carnivores and local communities: conflict or co-existence? In *Carnivore conservation*: 282–312. Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (Eds). Cambridge: Cambridge University Press.

Stander, P.E., Haden, P.J., Kaqece & Ghau (1997). The ecology of asociality in Namibian leopards. *J. Zool. (Lond.)* **242**, 343–364.

Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strindberg, S., Hedley, S.L., Burt, M.L., Marques, F., Pollard, J.H. & Fewster, R.M. (1998). *Distance 3.5. Research unit for wildlife population assessment*. UK: University of St. Andrews.

Tuyttens, F.A.M. & Macdonald, D.W. (2000). Consequences of social perturbation for wildlife management and conservation. In *Behaviour and conservation*: 315–329. Gosling, L.M. & Sutherland, W.J. (Eds). Cambridge, UK: Cambridge University Press.

White, G.C. & Garrott, R.A. (1990). *Analysis of wildlife radiotracking data*. San Diego: Academic Press.

Wilson, V.J. (1975). *Mammals of the Wankie National Park*. Rhodesia: National Museums and Monuments of Rhodesia.

Woodroffe, R. & Frank, L.G. (2005). Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Anim. Conserv.* **8**, 91–98.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds). (2005). *People and wildlife: conflict or coexistence?* Cambridge, UK: Cambridge University Press.

Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.