

## The ecology of asociality in Namibian leopards

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(With 4 figures in the text)

Data on the ecology of leopards (*Panthera pardus*) from north-eastern Namibia are presented and discussed in terms of the possible costs and benefits of solitary behaviour. In an area of low leopard density, where individuals lived alone, both males and females occupied large home ranges, ( $\bar{X}$  = 210–1164 km<sup>2</sup>;  $\bar{X}$  = 183–194 km<sup>2</sup>). Despite resource and reproductive advantages in maintaining exclusive ranges, the degree of range overlap both between and within sexes was substantial. Average overlap between males was 46% and between females 35%. The cost of dispersal appeared high as all three marked sub-adults died, and most recorded mortalities were of sub-adults. Females with dependent young showed a significant increase in per capita food intake compared to single females and males. Higher foraging success by females with cubs was revealed through two energy expenditure parameters (kg/km travelled/day and kg/hunt/day). Differential food intake between females with cubs, single females and males can be explained partly by differences in day ranges, body size and costs of parental care. Females shared 27% of their food with cubs and the costs of sharing food does not appear as high as previously suggested. Inter-specific competition over food and the defence of carcasses is suggested as an important cost to group living. Leopard kills were visited by other large carnivores (12%) but food loss was minimal (2%). Leopards successfully avoided conflict with inter-specific competitors by dragging and hiding kills in thick vegetation. We argue that solitary and secretive behaviour enables leopards to avoid the costs of defending carcasses against larger and gregarious carnivores.

### Introduction

Most felids show similar social organization. All species are asocial, except lions (*Panthera leo*: Schaller, 1972; Bertram, 1978) and male cheetahs (*Acinonyx jubatus*: Caro & Collins, 1986). Sociality has been argued to be beneficial since individuals may derive benefits such as anti-predator vigilance (Rood, 1986) and improved foraging success (Bertram, 1979; Lamprecht, 1981; Packer, 1986), especially in areas where larger prey are abundant (Caro, 1994). Feeding efficiency may be improved through locating and subduing large prey (Lamprecht, 1981) and co-operation during hunting (Stander, 1992*a, b*). Grouping can aid the defence of carcasses (Lamprecht, 1981; Cooper, 1991), or the defence of young and the maintenance of territories (Schaller, 1967; Packer, Scheel & Pusey,

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1990). Males may benefit from grouping by increased reproductive success and the defence of territories (Packer & Pusey, 1982; Packer, 1986; Caro & Collins, 1987). However, the costs of sociality can be high and may explain why most felid species are strictly solitary. Group-living species have to share food resources (Packer *et al.*, 1990) and as a result have to capture prey more frequently by spending more time foraging or by resorting to larger prey (Caro, 1989). Larger carcasses and larger congregations around carcasses increase the risk of inter-specific competition (Sunquist & Sunquist, 1989).

Most studies addressing sociality have focused on the social segment of the Felidae (lions and male cheetahs) with some comparative reviews between social and asocial species (Sunquist & Sunquist, 1989; Caro, 1989). Assessing the cost and benefits of sociality among solitary species is more difficult owing to the lack of comparison between different group sizes, except when females support large cubs. Solitary felids, like the leopard, are notoriously difficult to study and most data on ecology and behaviour are scant. Furthermore, the structure of felid social systems and basic ecological adaptation is shaped by ecological constraints imposed by diverse environmental conditions (Gittleman & Harvey, 1982; Macdonald, 1983; East, 1984; Sunquist & Sunquist, 1989). The assessment of felid social systems is complicated by these ecological and behavioural variations within and between species.

In this paper, we present data on the ecology and behaviour of leopards, the largest solitary African felid, from the woodland habitat of northern Namibia. Data on densities, population characteristics, home ranges and behaviour related to the food habits are compared with available accounts in the literature. This comparison identifies ecological and behavioural variations among different leopard populations. This variation is argued to be the result of constraints imposed by the environment which shapes the structure of leopard ecological adaptation and social organization. The ecology of a solitary strategy is presented and the possible costs and benefits of sociality in an asocial felid are discussed.

### Methods

The study was conducted between August 1992 and December 1995 in the adjoining Kaudom Game Reserve and Bushmanland communal area, north-eastern Namibia (15 000 km<sup>2</sup>; 18° 20'–20° S, 19° 30'–21° E), which lie within the southern savannah woodland biotic zone (Skinner & Smithers, 1990). This area (referred to as NE Namibia) is dominated by tall deciduous woodland savannah, with *Burkea africana* as the predominant species, and forest and shrub savannah woodland (Giess, 1971), dominated by *Commiphora africana*, *Terminalia sericea*, *Combretum hereroensis* and *Grewia* spp. at densities of 152 ± 82 woody plants (≥ 60 cm) per hectare. The region falls within the 400–500 mm rainfall isohyet with annual evapotranspiration equalling 2800–3000 mm (Van der Merwe, 1983). The climate is described as warm semi-arid steppe with summer rainfall and temperatures fluctuating between 5 and 36 °C. The soil is classified as arenosols (interior sands) and the region forms part of the northern extension of the Kalahari desert. During 1995, there were 215 (S.E. ± 139) wildebeest (*Connochaetes taurinus*); 230 ± 82 giraffe (*Giraffa camelopardalis*); 262 ± 64 gemsbok (*Oryx gazella*); 215 ± 64 ostrich (*Struthio camelus*); 382 ± 92 kudu (*Tragelaphus strepsiceros*); 5690 ± 706 steenbok (*Raphicerus campestris*) and 1500 ± 454 duiker (*Sylvicapra grimmia*) in NE Namibia (Stander, 1995). A 500 km<sup>2</sup> study area (19° 35' S, 20° 25' E) was subjectively selected for being representative of the habitat. Most of the marked leopards ( $n = 15$ ) used this study area. Data on group size and sex ratio were collected throughout NE Namibia, whereas density, population structure, home range and predation were collected in the study area.

All leopards ( $n = 18$ ) were captured and radio-collared. After following the spoor of a new leopard, and locating a fresh kill, the leopard was immobilized using a traditional Ju/hoan (San) bow and arrow (Stander *et al.*, 1996). A combination of Zoletil and xylazine hydrochloride (Stander & Morkel, 1991) was used as immobilizing agent and reversed with tolazoline hydrochloride (Van Wyk & Berry, 1986). Leopards were immobile for approximately 1 hour, during which time they were weighed ( $\delta$ :  $\bar{x} = 44.6$  kg ± S.E. 0.5;  $\text{♀}$ :  $\bar{x} = 25.0$  ± 2.2 kg).

photographed, and their age determined based on tooth wear (Stander, In press). The animal's respiration and heart beat were monitored throughout, and care was taken to avoid exposure to heat, and to avoid dust in unprotected eyes. The leopard was then fitted with a radio-collar and monitored from a distance until safely recovered.

Marked leopards were then regularly located (mean interval = 3.8 days; S.D. = 6.4;  $n = 1084$ ) with the use of light aircraft and vehicles. Most data collected were derived from tracking. The spoor of leopards was assessed for age of the animal, sex, recognition of individual leopards, and the age of the spoor. The spoor of leopards was then followed to reconstruct a wide and detailed range of behavioural activities. Tracking by Ju/hoan Bushmen is a reliable method in behavioural ecology with high levels of accuracy (< 5% coefficient of variance; Stander *et al.* (1997). The study area was regularly scanned for leopard spoor either by driving (4076 km) at 20 km h<sup>-1</sup> with one of us sitting on the bumper of the vehicle, or walking (595 km). High reliability of identifying individuals from spoor ( $P < 0.001$ ) ensured that all unmarked or new leopards were radio-collared and included in the study. The spoor of marked leopards was followed for between one and five consecutive 'leopard days'. A 'leopard day' was treated as a discrete unit of activity from one mid-day rest spot to the next (Bothma & le Riche, 1990). During each 'leopard day' spoor was followed (daily follows) step by step and all activities recorded. Marked leopards were also radio-tracked during the day and then approach on foot. Upon spotting fresh spoor, a detailed reconstruction of the animal's activities that morning and during the latter part of the previous night was performed. These reconstructions consisted of both 'back-tracking' (following spoor in the opposite direction that the leopard had moved; range 2-8 km) and following the spoor of the leopard in its true direction, up to the point where it fled at our approach. These observations consisted of consecutive days (range 2-12 days) or random 1 day assessments when data were collected on predation, hunting behaviour and food intake.

Daily distances travelled by leopards were measured on a vehicle's odometer, and distances relating to different hunting categories were paced or measured using a tape measure. Foraging was defined as searching for and hunting prey (Stander, 1992a). There is no clear definition of hunting that applies to all large carnivores (Kruuk, 1972; Schaller, 1972; Mills, 1990). Leopards were considered hunting when they stalked for more than 10 m. We determined the age and sex of species killed from horns and tooth eruption and wear, and estimated mass using data from Skinner & Smithers (1990). Following previous biomass calculations (Mills, 1990; Stander, 1992a; Caro, 1994) and weighing remains of kills, we estimated inedible proportions of 0% for carcasses < 5 kg, 5% for 5-25 kg, and 30% for > 25 kg. Based on body weight and size, cubs were estimated to consume 25% as much as an adult female when 1-3 months old, 50% 3-8 months, and the same amount between 10 months and independence (see Caro, 1989).

Home-range analysis was based on locating the daytime resting spots of leopards by radio-telemetry and tracking (fixes) with at least 24 h between fixes. The exact location where the leopard had been resting was recorded using a Global Position System (GPS). Home ranges were calculated with the WILDTRACK<sup>®</sup> programme, using the convex polygon (Mohr, 1947) and grid cell (Macdonald, Ball & Hough, 1980) methods. Sufficiency of sample size was tested by determining whether or not an asymptote of home-range estimate was reached (Harris *et al.*, 1990). Test for autocorrelation (Swihart & Slade, 1985) showed that the time interval between successive fixes was sufficient and that data were independent (Schoener, 1981 index < 2;  $n = 12$ ). This independence of successive locations is due to the fact that the nocturnal leopards were located during the day, with fixes  $\geq 24$  hours apart. The extent of static interaction and overlap between different individual home ranges was tested following Doncaster (1990).

Statistical computations of the relationship between two interdependent variables were fitted by ordinary least squares linear regression. Usually, an independent variable such as prey biomass or rainfall, was expressed in terms of a linear function of the dependent variable, leopard biomass, or home range. Where non-linear regression provided a better fit, we used polynomial regression by including significant quadratic terms (Sokal & Rohlf, 1995: 667). Data points relating to hunting and feeding were calculated per individual leopard per day following Packer *et al.* (1990). Means are given with standard error (S.E.) as a measure of the precision, and median values when these had biological significance. Data were tested for normality using a Komogorov-Smirnov 2 sample test and were transformed using  $\log(y + 1)$  when variances were high. Non-parametric tests were used where data could not be normalized. Significance was measured at 5% and all  $P$  values are 2-tailed.

## Results

*Density and population dynamics*

Leopards were present throughout NE Namibia (3.18 leopard spoor 100 km<sup>-1</sup>;  $n = 8205$  km). In the study area, a density of 1.5 leopards 100 km<sup>-2</sup> was maintained during the entire study period, despite a turnover of males in 1994. Density calculations are based on the fact that all leopards ( $n = 15$ ) using 500 km<sup>2</sup> were marked and that the area was scanned continuously for spoor of new animals.

Leopard densities vary widely in sub-Saharan Africa (Table I). Leopard density in the present study is similar to the Kalahari, and agrees with a significant correlation between leopard biomass and the available biomass of prey weighing between 15 and 60 kg in sub-Saharan Africa (Fig. 1).

In NE Namibia, 475 sets of leopard spoor were assessed for group composition and sex structure. Most spoor observed (94.2%) was of single animals. The spoor of females with a sub-adult was seen 10 times (2%) and females with small cubs on 14 occasions (3%). Similarly, in a sample of 496 observations, radio-collared leopards in the study area were mostly alone (84%) and occasionally in pairs (females with one sub-adult = 2%). Females with small cubs were observed at a higher frequency (13%;  $G$ -test;  $G = 35.7$ ;  $P < 0.001$ ).

Observations of leopard spoor in NE Namibia revealed a sex:age ratio of 1♂:0.7♀:0.2 cubs ( $n = 290$ ). At the end of 1993, in the study area, three adult males, one sub-adult male, three adult females and one cub (1♂:0.75♀:0.25 cub) used the 500 km<sup>2</sup>. During 1994 and 1995, two adult and

TABLE I  
*Densities of leopards in various conservation areas in sub-Saharan Africa. Conservation areas are listed in descending order of annual rainfall*

Conservation area	Leopard density (animals 100 km <sup>-2</sup> )
Queen Elizabeth, Uganda <sup>1</sup>	16
Lake Manyara, Tanzania <sup>2</sup>	11
Ngorongoro, Tanzania <sup>3</sup>	7.5
Serengeti, Tanzania <sup>4</sup>	5.6
Nairobi, Kenya <sup>5</sup>	8.5
Cape Fynbos, South Africa <sup>6</sup>	0.7
Cederberg, South Africa <sup>7</sup>	6-9
Tsavu, Kenya <sup>8</sup>	7.7
Hwange, Zimbabwe <sup>9</sup>	2.1
Matopo, Zimbabwe <sup>10</sup>	23.6
Londolozi, South Africa <sup>11</sup>	23.8
Kruger, South Africa <sup>12</sup>	5.1
This study	1.5
Etosha, Namibia <sup>13</sup>	0.5
Kalahari, South Africa <sup>14</sup>	1.3

Sources: <sup>1</sup> Van Orsdol (1981); <sup>2</sup> Schaller (1972); <sup>3</sup> Kruuk (1972), Estes & Small (1981); <sup>4</sup> Schaller (1972), Kruuk (1972); <sup>5</sup> Rudnai (1974), Eaton (1974); <sup>6</sup> Norton & Lawson (1985), Martin & de Meulenaer (1988); <sup>7</sup> Norton & Henley (1987); <sup>8</sup> Hamilton (1976); <sup>9</sup> Wilson (1975); <sup>10</sup> Smith (1977); <sup>11</sup> Le Roux & Skinner (1989); <sup>12</sup> Pienaar (1963, 1969), Smuts (1976), Bailey (1993); <sup>13</sup> Berry (1981), pers. obs.; <sup>14</sup> Bothma & le Riche (1984, 1986), Mills (1990)

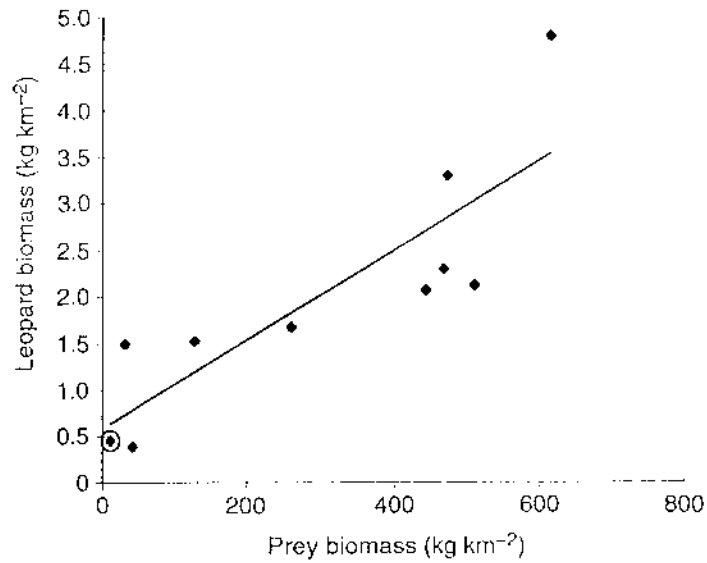


FIG. 1. Leopard biomass correlated with medium-sized prey (15–60 kg) biomass ( $b = 0.01 \pm 0.001$ ;  $r^2 = 0.72$ ;  $t = 4.57$ ;  $P < 0.01$ ) in 11 arid/eutrophic savanna conservation areas in Africa. The present study datum is circled. Biomass was calculated following Coe, Cumming & Phillipson (1976). Although unit weights of African mammals may vary from area to area, the extent of this variation is unknown. To standardize comparisons, herbivore mass was taken from Coe *et al.* (1976) and carnivore mass from Schaller (1972). See Table I for references.

TABLE II  
*Reproductive characteristics of three individually marked female leopards in Namibia*

Parameters	♀6	♀9	♀10	Total/average <sup>6</sup>
Age of leopard (years)	4–6	5–7	4–6	
Duration of monitoring (weeks) <sup>1</sup>	134	127	123	384
Female with suckling cub (%) <sup>2</sup>	32.1	22.8	70.7	41.4
Female with attendant cub (%) <sup>3</sup>	7.5	0	19.5	8.9
Total of female with cub (%) <sup>4</sup>	39.6	22.8	90.2	50.3
Observations of female leopards: <sup>5</sup>				
<i>n</i> (sample size)	71	111	128	310
Female alone (%)	48.4	86.1	58.6	68.2
Female with suckling cub (%)	48.4	13.9	24.3	24.3
Female with attendant cub (%)	3.2	0	17.1	7.5

<sup>1</sup> The total duration that individual leopards were monitored.

<sup>2</sup> The % of the time that female leopards had suckling cubs (< 8 months)/total duration of observation.

<sup>3</sup> The % of the time that female leopards had weaned cubs/total duration of observation.

<sup>4</sup> The % of the total time that female leopards had cubs/total duration of observation.

<sup>5</sup> The percentage of time that females with cubs were seen alone or with cubs at each cub stage. Observations of female leopards during the periods that they had cubs. Observation consisted of sightings or spoor reconstructions confirming whether female leopards were with their cubs or alone.

<sup>6</sup> Totals are given for duration of monitoring and number of observations; averages were calculated from untransformed data and given as percentages of the total sample size.

two sub-adult males, and two cubs died and new individuals were born or immigrated. By the end of 1995, four adult males, three adult females and two cubs (1 ♂ : 0.75 ♀ : 0.5 cub) utilized the study area.

Despite their solitary nature, female felids are expected to spend a large proportion of their life with dependent cubs (Prange, 1984; Gittleman, 1986) and Caro (1989) estimated that leopard females spend as much as 91% of their life with cubs. In the present study, three females were monitored for 384 'leopard weeks' (7.4 years). The females had dependent cubs for 50.3% of this time (Table II). The sample of three individuals is small given the large variation of between 22.8% and 90.2%. The large proportion of time (41.4%) that females spent with suckling cubs is the result of both juvenile mortality and sampling bias, e.g. the project was terminated when two cubs were at the age of weaning. During the 50.3% of their time that females had cubs they did not appear to spend many hours with their cubs. Females were alone on 68.2% of observations, and ♀9, who lost both her cubs before the weaning age, spent more time away from her cubs than the other two females who successfully reared their cubs. Females gave birth and kept very small (< 1 month) cubs in aardvark burrows ( $n = 5$ ). Surprisingly, larger (> 3 months) cubs did not follow females on foraging or wandering trips and were left alone for periods lasting between one and seven days. Females spent more time with suckling cubs than with attending cubs (Table II). On 12 occasions, the activities of both mother and cub were monitored simultaneously. Females always foraged alone. Upon capturing prey, and after feeding a small amount, the female would return to where she had left the cub and lead it to the meat. After the kill had been consumed, the cub would remain there while the female continued on another foraging expedition. Furthermore, females did not lead their cubs to all their kills. Females with mobile cubs were recorded to kill 26 prey and led their cubs to 73% of these. After seven kills (four of which weighed >10 kg) females consumed the carcass alone.

Dispersal appears to be a costly behaviour for leopards. Two male cubs in the study area were radio-collared and were nutritionally independent at 17 and 18 months of age. One remained close to his mother's home range for approximately eight months before dispersing 25 km to establish a new home range. This sub-adult lived within his new range for six months before dying from wounds inflicted by porcupine quills. The other sub-adult stayed within his mother's range for six months, then emigrated 162 km, but returned a few weeks later. He remained in his mother's range for another five months but was then killed by people after raiding domestic livestock. Despite using the same area, neither male associated with his mother after independence.

Vacancies in the study area were filled through immigration. At the end of 1994 two adult males died, and a sub-adult male emigrated. Within a few months (<2–4 months), two adult males moved in and established home ranges in the study area. A third male moved in after eight months but approximately 60% of his range was outside the study area.

Throughout NE Namibia (including the study area), 15 accounts of leopard mortality were recorded over four years. Two animals were very old, three were adult and ten were sub-adult. Most of these leopards ( $n = 11$ ) were killed by people after attacking domestic dogs and chickens at settlements, and four died of natural causes. All the leopards, except the three adults, were in poor condition.

#### *Home ranges*

Previous calculations indicate that the home ranges of male and female leopards may be different in size (Schaller, 1972). In the present study, sufficient fixes were obtained for reliable home-range estimates of six adult males, three adult females, and three sub-adults (Table III). The home ranges of adult males were significantly larger than those of adult females (Mann-Whitney  $U$ -test;  $U = 18.0$ ;  $P < 0.05$ ). Leopards moved an average distance of 9.8 km per day (median = 9.4; S.E. = 0.9;  $n = 31$ ;

TABLE III  
Home ranges of 13 leopards utilizing a 500 km<sup>2</sup> study area in Namibia

Age/sex and ID of leopard	Home range (km <sup>2</sup> )	No. of fixes	Accuracy of fixes <sup>1</sup>
A♂2	210.1	42	32 (76)
A♂4	285.0	35	27 (77)
A♂5	1163.5	113	48 (34)
A♂14	730.1	77	40 (52)
A♂15	210	44	32 (73)
A♂16	608.7	22	16 (73)
A♀6	187.9	109	30 (28)
A♀9	187.8	144	72 (50)
A♀10	194.4	175	60 (34)
SA♂7 <sup>2</sup>	117.3	22	20 (91)
SA♂7 <sup>3</sup>	191.9	26	19 (73)
SA♂12 <sup>4</sup>	88.1	82	50 (61)
SA♀11 <sup>5</sup>	143.7	9	Negative

<sup>1</sup> The number of fixes where the home-range estimate reached an asymptote of at least 95% of the home-range estimate. Percentage of fixes in parentheses

<sup>2</sup> Home range of SA♂7 during May 1993- January 1994 while nutritionally independent from his mother (♀6) but moving within her range

<sup>3</sup> Home range of SA♂7 during February-August 1994 after emigrating from his natal range. ♂7 died at the end of August 1994

<sup>4</sup> Home range of SA♂12 after independence in September 1994 up to his death in September 1995, but excluding a single excursion of 162 km

<sup>5</sup> SA♀11 moved into the study area during June 1994 but was shot two months later

range 0.8-17.8) with males ( $\bar{x} = 12.2$ ) travelling further than females ( $\bar{x} = 8.4$ ; Student's *t*-test, *t* = 2.21; *P* < 0.05). Within the limited time frame (2- 15 months) that sub-adults were monitored, their ranges averaged 129 km<sup>2</sup>. However, even though sub-adults may frequent a particular range within a given time frame, their ranges are by no means stable. Long distance movements and emigration are inevitable (Beier, 1995).

TABLE IV  
Home ranges (km<sup>2</sup>) of leopards in sub-Saharan Africa

Location	Males	Females	Unknown sex	Source
Serengeti	17.8	15.9		Bertram (1982)
Serengeti		40 & 60		Schaller (1972)
Matopo			18 ( <i>n</i> = 6)	Smith (1977)
Londolozi		23		Le Roux & Skinner (1989)
Tsavo	36.3 ( <i>n</i> = 4)	14.4		Hamilton (1976)
Kenyan ranches	32.8 ( <i>n</i> = 4)	14.0 ( <i>n</i> = 5)		Mizutani (1995)
Kruger	52 ( <i>n</i> = 5)	16.4 ( <i>n</i> = 5)		Bailey (1993)
Cederberg	51 ( <i>n</i> = 3)			Norton & Henley (1987)
Stellenbosch	388	487		Norton & Lawson (1985)
Kalahari			400	Bothma & le Riche (1984)
Namibia	451.2	188.4		This study

Note: For most locations data are not available on the accuracy of home-range estimates

The average calculated home ranges of leopards in different habitats in sub-Saharan Africa are highly variable ranging from  $10\text{ km}^2$  in Matopo, Zimbabwe, (Smith, 1977) to  $487\text{ km}^2$  in the Stellenbosch mountains of South Africa (Norton & Lawson, 1985) (Table IV). Range size is expected to be dependent on resource availability (Gittleman & Harvey, 1982). Data from 10 regions in sub-Saharan Africa (Fig. 2a) indicate that the relationship between home range and leopard density is not linear (Harvey & Mace, 1982), and is biased by three points on the graph; Kalahari, Stellenbosch and this study. The home-range estimate from Kalahari is disputable as it is not backed with data (Bothma & le Riche, 1984), and the Stellenbosch population exists under extremely marginal conditions and is persecuted (Norton & Lawson, 1985), leaving only one datum, which does not justify a curvilinear model. Excluding these data points, there appears to be no relationship between these two parameters ( $r^2 = 0.04$ ;  $P = 0.67$ ). Similarly, when home range is expressed as a linear function of rainfall (Fig.

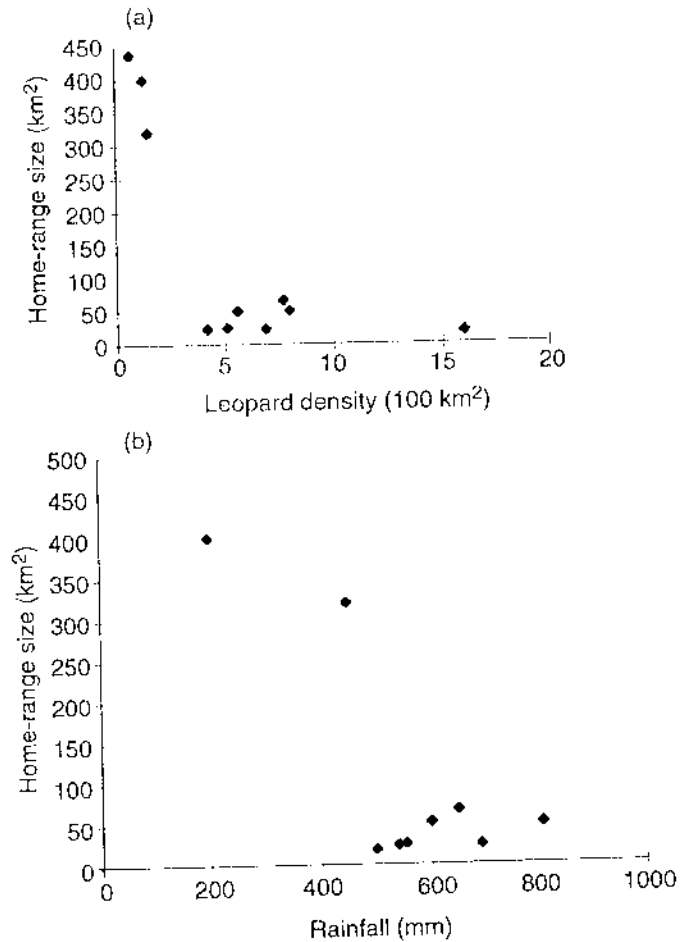


FIG. 2. Leopard home-range size correlated with: (a) leopard density and (b) annual rainfall in 10 arid/eutropic savannah conservation areas in Africa. Leopard density and annual rainfall are expressed as functions of resource availability, as a result of significant relationships between rainfall, primary production (Deshmukh, 1984), prey biomass (East, 1984) and leopard biomass or density (East, 1984; Martin & de Meulenaer, 1988; this study—Fig. 1). See Tables I & IV for references.



2b), the relationship is influenced only by data from the Kalahari and this study. Rainfall data in the Stellenbosch mountains are too erratic (80-2000mm; D. Pepler, pers. comm.) to merit inclusion. Excluding the two points, no correlation is apparent ( $r^2 = 0.28$ ;  $P = 0.2$ ).

During the study period, there were two distinct tenure structures amongst the adult male population. Data on land tenure use and distribution were thus split to represent two periods: up to the end of 1993 (referred to as 1993); and from the beginning of 1994 to the end of 1995 (referred to as 1995). The overlap percentages between the ranges of individual leopards of both sexes in both tenure periods were extensive (Table V).

In 1993, excluding the sub-adult female No. 11, all female ranges overlapped, as did all male ranges. The ranges of one male and one female did not overlap. Similarly, in 1995, all female ranges overlapped and all the male ranges overlapped with female ranges. Among the males, the ranges of two individuals did not overlap. The overlap between males for the two tenure periods ranged between 17.5 and 59.4%. On average, male ranges overlapped 46% (S.E. = 9.7) in 1993 and 29.3% (S.E. = 2.9) in 1995. Overlap between females ranged from 27.8% to 50.5% and were, on average, 35.3% (S.E. = 1.5) in 1993 and 42.7% (S.E. = 7.5) in 1995.

The overlap of ranges between males and females did not differ from the overlap within each sex. This overlap represented 31.7% (S.E. = 8.7) of the female range in 1993 and 51.4% (S.E. = 0.7) in

TABLE V  
Overlap as a percentage of the home ranges of leopards utilizing a 500 km<sup>2</sup> study area in Namibia: (i) up to the end of 1993 and (ii) during 1994 and 1995. The letters refer to individual leopards

		% of home-range overlap between two individual leopards <sup>1</sup>							
(i) 1993	♂2	♂4	♂5	♂7	♀6	♀9	♀10	♀11 <sup>2</sup>	
♂2	—	81.3	82.1	14.9	38.7	19.7	54.2	32.5	
♂4	59.9	—	86.7	4.5	22.5	19.0	40.8	17.9	
♂5	68.0	94.8	—	6.7	25.9	18.9	44.7	18.0	
♂7	26.8	11.1	14.5	—	81.2	0	14.1	0	
♀6	55.2	43.6	44.6	64.8	—	22.2	43.2	0.3	
♀9	40.9	53.7	47.5	0	32.3	—	38.5	2.3	
♀10	84.4	86.2	83.9	67.5	46.9	28.7	—	16.1	
♀11	47.7	35.6	32.2	0	0.3	1.6	15.1	—	
(ii) 1995	♂5	♂12 <sup>3</sup>	♂14	♂15	♂16	♀6	♀9	♀10	
♂5	—	93.2	48.8	73.4	96.7	67.1	97.9	80.6	
♂12	7.1	—	34.8	1.2	10.2	41.4	12.0	45.4	
♂14	9.6	90.9	—	0	11.0	86.7	8.6	61.7	
♂15	13.2	3.0	0	—	5.1	6.3	59.7	4.5	
♂16	50.6	70.5	29.1	14.3	—	43.7	44.5	54.6	
♀6	9.6	86.0	69.0	5.5	13.1	—	25.7	70.3	
♀9	15.8	25.7	7.0	53.5	13.7	26.5	—	29.6	
♀10	13.4	100	52.0	4.2	17.5	74.4	30.5	—	

<sup>1</sup> Figures indicate overlap of the home ranges of two leopards (rows and columns) as a percentage of each home range. Overlap between two individuals (co-ordinating row and column) is calculated as the percentage overlap relevant to the home range of individuals listed by columns

<sup>2</sup> ♀11 is a sub-adult female that immigrated and lived in the study area for two months

<sup>3</sup> ♂12 was a sub-adult, the cub of ♀10. Data presented here are for a period of 12 months before his death while not associating with ♀10 and being nutritionally independent

1995. It was a smaller part of male ranges (1993—28%, S.E. = 2.8; 1995—22.9%, S.E. = 6.8) since males had larger ranges, encompassing those of several females, which often extended beyond the 500 km<sup>2</sup> study area. During two months in 1993, SA ♀11 ranged over an area that overlapped the ranges of all the study animals except one male. The overlaps were small, 22.8% for males and only 6.2% for females. In 1995, however, the range of SA ♂12 overlapped extensively with all the study animals. Despite being nutritionally independent from his mother (♀10) his range overlapped 100% with her. The average overlap between him and other leopards was 70.6% for females and 64.4% for males.

Percentage overlap of home ranges, however, does not give an indication of the extent of aggregation between individuals in the shared range. Calculations of the static interaction between individuals (Doncaster, 1990) showed that, despite large percentage overlaps during both tenure periods, concordance was low for both sexes (Table VI, i & ii). In other words, leopards concentrated their activities in the same parts of the overlapping range at different times. In 1995, both SA ♂12 and ♂14 showed high *r* values in relation to ♀10 (Table VI, ii), indicating that the leopards (♂12 & ♀10 or ♂14 & ♀10) were sometimes located in the same area at the same time. Spoor reconstructions during these apparent static interactions revealed that the leopards were in fact between 100 and 300 m apart, but there was no evidence of direct visual interactions.

TABLE VI

Amount of range overlap (horizontal axis) and static interaction (Spearman's rank correlation coefficient; vertical axis) of leopards utilizing a 500 km<sup>2</sup> study area in Namibia: (i) up to the end of 1993 and (ii) during 1994 and 1995. The letters refer to individual leopards

	Overlap area (km <sup>2</sup> )							
	♂2	♂4	♂5	♂7	♀6	♀9	♀10	♀11
(i) 1993								
♂2	—	170.7	172.4	31.4	81.2	41.3	113.9	68.1
♂4	-0.63	—	283.5	0.87	64.1	54.2	116.4	50.9
♂5	0.76	-0.73	—	-0.69	65.6	48.0	113.3	46.1
♂7	-0.74	0.87	-0.69	—	95.2	0	16.5	0
♀6	-0.86	-0.9	-0.75	-0.34	—	-0.89	-0.6	0.5
♀9	-0.77	-0.79	-0.83	-0.9	-0.89	—	38.8	2.4
♀10	-0.49	-0.84	-0.56	-0.68	-0.6	-0.81	—	21.8
♀11	-0.47	-0.79	-0.8	-0.81	-0.84	-0.77	-0.57	—
(ii) 1995								
♂5	—	82.1	112.2	154.2	588.9	112.7	184.1	156.3
♂12	-0.51	—	80.1	2.6	62.1	75.8	22.6	88.1
♂14	-0.63	-0.24	—	0	67.0	158.6	16.1	119.6
♂15	-0.65	-0.87	-0.89	—	30.8	11.6	112.3	8.8
♂16	-0.45	-0.87	-0.81	-0.91	—	80.0	83.6	106.3
♀6	-0.81	-0.71	-0.57	-0.85	-0.72	—	48.4	136.1
♀9	-0.50	-0.75	-0.82	-0.25	-0.74	-0.85	—	57.4
♀10	-0.49	+0.01	-0.07	-0.84	-0.72	-0.67	-0.78	—

Note: The Spearman rank correlation coefficient, *r*, measures the degree of concordance or association in overlap between different individuals. Analyses are based on the number of grid-cells shared in time, when using the grid-cell method of calculating home range (Macdonald *et al.*, 1980). When *r* is positive it indicates attraction or concordance in utilization of shared cells; whereas when *r* is negative it indicates repulsion or discordance in utilization of shared cells (Doncaster, 1990)

*Hunting behaviour*

Leopards foraged mainly at night. Of the 508 km over which spoor was followed, 85.6% of the distance was covered by leopards during the night. Late afternoons and early mornings contributed only 2.1% and 12.3%, respectively, to the total distance. Of 100 recorded hunts, 96 took place at night and four during the early morning. Leopards always hunted alone ( $n = 100$ ), even on eight occasions when females were accompanied by sub-adults.

During all recorded hunts, leopards employed a solitary method of hunting, typical of the Felidae (Ewer, 1973), consisting of stalking, followed by a short chase ( $n = 94$ ). Four structural phases of each successful hunt were measured as a descriptive breakdown of hunting behaviour (Table VII). The median stalking distance for all prey species of 29 m ( $\bar{x} = 45.1$  m) was subject to high variability (S.E. 8.9). This variation may be due to habitat constraints as it was not a function of variation among individuals, sex, or prey species. Stalking distances by male leopards were similar to those of females (ANOVA;  $F_{2,97} = 0.01$ ;  $P = 0.92$ ). Similarly, there was no individual variation during hunts of duiker ( $F_{3,54} = 1.29$ ;  $P = 0.32$ ), steenbok ( $F_{6,31} = 1.652$ ;  $P = 0.23$ ), or the rest of the prey species combined ( $F_{4,68} = 0.99$ ;  $P = 0.44$ ). Stalks of duikers were not significantly different from those of steenbok or from the other prey species combined ( $F_{4,16} = 2.26$ ;  $P = 0.112$ ). The extraordinary stealth of the leopard is illustrated by its ability to stalk, undetected, to within a few metres of the prey. The distance at the end of the stalk (the crouch), before initiating a charge, averaged 4.4 m with the median distance being 4 m (Table VII). This distance was similar between species with a slightly lower median of 3 m for steenbok. It is to be expected that, during successful hunts, the chase distance (averaging 10.3 m) is

TABLE VII

*Analyses of four structural phases of a hunt (distances measured in metres) by nine individually known leopards in Namibia*

Hunt parameters		Duiker	Steenbok	Rest of prey	All prey
Stalk	$\bar{x}$	40.4	52.9	55.1	45.1
	Median	26.5	32.5	49	29
	S.E.	5.26	3.33	14.1	8.88
	Range	3-161	0-184	0-218	0-218
	$n$	38	14	23	75
Distance from prey <sup>1</sup>	$\bar{x}$	5	4.5	4.5	4.4
	Median	4	3	4	4
	S.E.	0.4	0.56	0.83	0.25
	Range	2-15	0-10	0-12	0-15
	$n$	40	17	19	76
Chase	$\bar{x}$	9.7	9.8	10.9	10.3
	Median	7	3	5	7
	S.E.	0.74	3.41	2.44	1.33
	Range	0-58	0-117	0-41	0-117
	$n$	41	17	19	76
Drag carcass <sup>2</sup>	$\bar{x}$	178	104	97.6	140
	Median	108	69.5	84	82.5
	S.E.	32.0	57	11.3	27.2
	Range	0-762	0-378	0-312	0-762
	$n$	31	12	13	56

Note: Sample sizes ( $n$ ) are irregular as a result of unavoidable environmental conditions

<sup>1</sup>Distance from prey is the straight line distance from the position of the leopard at the end of the stalk to the position of the prey before flight

<sup>2</sup>The distance the carcass was dragged by the leopard to a feeding spot

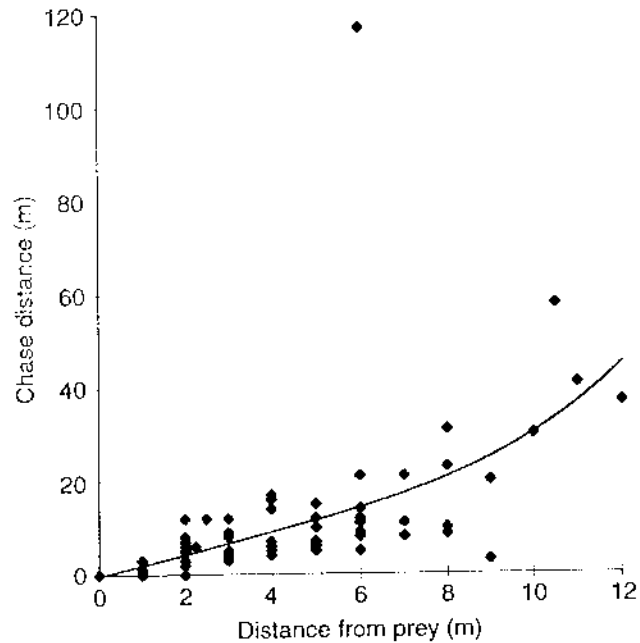


FIG. 3. The distance that leopards chased their prey correlated with the initial distance from the prey at the start of the chase, for successful hunts only.

a function of the distance from the leopard to the prey at the start of the chase. This relationship, however, is non-linear ( $y = 0.897 + 0.419x + 0.108x^2$ ;  $F_{2,07} = 76.31$ ;  $P < 0.001$ ) with the chase distance increasing markedly when leopards were more than 8 m from the prey (Fig. 3). Up to the 8 m distance, a linear model provided the best fit ( $b = 2.88 \pm 1.21$ ;  $r^2 = 0.09$ ;  $t = 2.37$ ;  $P = 0.021$ ). This relatively weak slope suggests that up to a distance of 8 m from prey, chase distance was not markedly influenced by the distance from which leopards pounced and captured prey.

All carcasses, except hares and birds, were dragged an average of 140 m (median 82.5) to a suitable feeding spot. From a sample of 93 kills, leopards dragged their kills into trees on only three occasions (3%), despite the availability of tall forked trees. Instead, kills were dragged for up to 762 m (Table VII) and often stored in thick undergrowth. Some kills were dragged more than once (52%;  $n = 56$ ). When leopards were disturbed by other carnivores (8.9%) they dragged their kill to a second hiding spot. Our tracking activities sometimes (7.1%) caused leopards to move their kills. However, leopards mostly (33%) moved their kills for no apparent reason. When kills were moved, the second drag distance ( $\bar{x} = 199$ ; median 204;  $n = 29$ ) was longer than the first ( $t = 1.739$ ;  $d.f. = 17$ ;  $P < 0.1$ ) and in total these drag distances were longer than those that had not been moved a second time ( $U = 638$ ;  $P < 0.001$ ).

During 41 systematic observations of hunting success ( $n = 16$  duiker; 7 steenbok; 18 rest of prey species combined) leopards averaged one kill for every 2.7 hunts, which gives a success rate for all prey species combined of 38.1%. The distance to which the leopard approached the prey at the end of the stalk was closer for successful hunts than for unsuccessful hunts ( $U = 73$ ;  $P < 0.01$ ). Chase distances of successful hunts had a non-significant tendency to be shorter than those of unsuccessful hunts ( $U = 76.8$ ;  $P < 0.1$ ). The scant data do not allow further analyses of the various factors that may influence hunting success.

*Predation and foraging success*

Leopards killed 17 different prey species (Table VIII). Duiker formed the most important element in their diet in terms of both numbers killed and biomass. Steenbok were the second highest contributor, followed by a combination of different carnivorous animals (aardwolf, cheetah, genet, bat-eared fox, African wild cat and python) at 12% of the food items and 11% of the biomass. Leopards killed most of the food items they were observed to feed on, and only scavenged two partly consumed steenbok carcasses (1.3% biomass), one from another leopard, and the other from a caracal (*Felis caracal*). Carcasses were consumed in full, with only skin, a few bones, or feathers remaining. Smaller carcasses (<5 kg) were consumed within a few hours but larger carcasses (> 5 kg) were stored in dense vegetation and consumed over several days ( $\bar{x} = 2.5 \pm 0.9$ ; range 1- 5 days).

Leopards interacted with four species of other large carnivores. They killed and consumed two adult male cheetahs. Spotted hyenas (*Crocuta crocuta*;  $n = 11$ ) and wild dogs (*Lycan pictus*;  $n = 2$ ), lions ( $n = 2$ ) and other leopards ( $n = 1$ ) visited leopards with kills on 11 occasions (12%;  $n = 93$  kills). A total of three kills (3%) was lost to these competitors. Kills that were taken into trees ( $n = 3$ ) always attracted other carnivores, whereas only 8.9% of those that were dragged and hidden under thick vegetation attracted carnivores (Fisher tests:  $P = 0.001$ ). Leopards lost two out of the three kills in trees but only one of the 90 that were dragged ( $P = 0.002$ ). A female leopard was killed by lions as a result of dragging a duiker carcass into a tree. The tree advertized her position and the kill, and did not provide her with sufficient protection. Occasionally ( $n = 5$ ) we enticed leopards to bait that we tied to

TABLE VIII  
Analysis of numbers of prey killed and estimated biomass consumed by leopards in woodland habitat during the present study

Species <sup>1</sup>	No. of kills	% of kills	Edible biomass <sup>2</sup>	% of biomass
Duiker	43	32.8	756.2	59.2
Steenbok	17	13.0	182.5	14.3
Eland	4	3.1	120.0	9.4
Aardwolf	4	3.1	24.7	1.9
Porcupine	3	2.3	34.2	2.7
Cape hare	3	2.3	5.1	0.4
Cheetah	2	1.5	97.2	7.6
Small-spotted genet	2	1.5	5.0	0.4
Guineafowl	2	1.5	3.6	0.3
Red-crested korhaan	2	1.5	1.4	0.1
Cape turtle dove	2	1.5	0.4	0.0
Gemsbok	1	0.8	31.5	2.5
African python	1	0.8	11.0	0.9
Bat-eared fox	1	0.8	4.1	0.3
Great-spotted cuckoo	1	0.8	0.1	0.0
Total	131		1277.0	

<sup>1</sup>Scientific names of species not mentioned in text: aardwolf (*Proteles cristatus*), African python (*Python sebae*), bat-eared fox (*Otocyon megalotis*), Cape hare (*Lepus capensis*), Cape turtle dove (*Streptopelia capicola*), eland (*Tragelaphus oryx*), great-spotted cuckoo (*Clamator glandarius*), guineafowl (*Numida meleagris*), porcupine (*Hystrix africaeaustralis*), red-crested korhaan (*Eupodotis* sp.), small-spotted genet (*Genetta genetta*)

<sup>2</sup>Calculated by subtracting the estimated percentage wastage (< 5 kg = 0%; 2-25 kg = 5%; > 25 kg = 30%; unpubl. data; Mills, 1990) from the average mass of each carcass

the upper branches of tall trees. Four of these attracted vultures and spotted hyenas, whereupon the leopards withdrew and abandoned the bait.

Daily per capita food intake showed variation between different groups of leopards (Fig. 4). Three different methods were used to calculate food intake. Daily follows, consecutive day and random day assessments (see **Methods**) produced similar food intake calculations within each of the leopard groups ( $G = 0.14$ ;  $P = 0.9$ ). By measuring the ratio of kills by weight ( $> 5$  kg;  $< 5$  kg), daily follows ( $1:0.33$ ), used as a control, did not reveal a higher proportion of smaller kills than consecutive or random day assessments ( $1:0.39$ ;  $G = 0.03$ ;  $P = 0.85$ ). Calculations of food acquisition was therefore based on the latter group because of larger sample size. There was a distinct difference in daily per capita food intake between single females, females with dependent cubs and males, for both consecutive day ( $G = 10.62$ ;  $P < 0.01$ ) and random day assessments ( $G = 29.4$ ;  $P < 0.001$ ). Females with dependent cubs killed prey at a frequency (one kill every 3.9–4.4 days) only slightly higher than single females (5.1–5.6 days;  $G = 0.96$ ;  $P = 0.32$ ) but killed larger-sized prey ( $t = 2.49$ ;  $P < 0.01$ ) resulting in a higher per capita food intake ( $2.5 \pm 0.5$  kg/leopard/day) than single females ( $1.6 \pm 0.5$ ;  $G = 5.3$ ;  $P < 0.05$ ). Females with dependent cubs actually acquired  $3.4 \pm 1.2$  kg per day but shared 27% with cubs of various ages. There was little difference in daily per capita food intake between females with dependent cubs ( $2.4$ – $2.5$  kg/day) and males ( $3.1$ – $3.3$  kg/day), both in terms of the frequency of kills (one kill every 4.4 and 4.6 days, respectively;  $G = 0.01$ ;  $P = 0.97$ ) and in the quantity of food acquired ( $G = 1.2$ ;  $P = 0.28$ ). The size of prey animals killed was also similar ( $t = 0.18$ ;  $P = 0.43$ ).

Energetic returns to individuals among social carnivores has been shown to be an important parameter in testing foraging success (Creel & Creel, 1995). Following the energetic considerations described by Creel & Creel (1995), female leopards with cubs had the highest foraging returns with 2.45 kg of food obtained for each km travelled per day compared with single female leopards

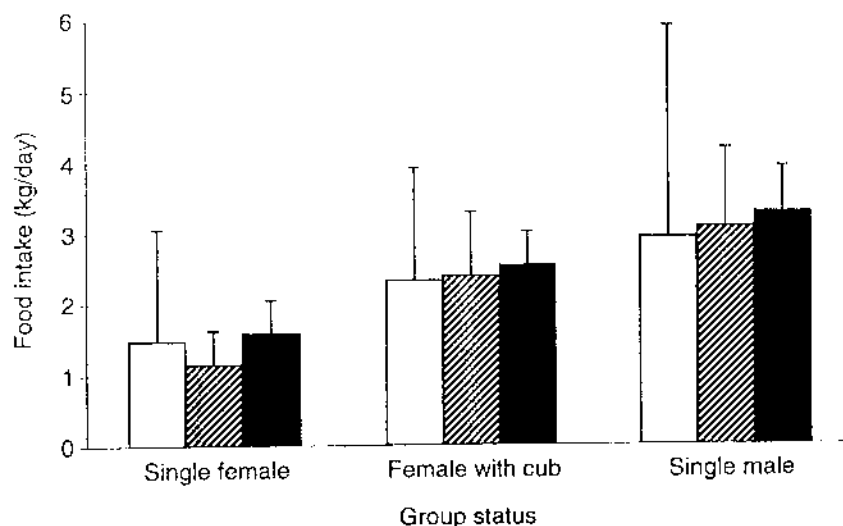


FIG. 4. Daily per capita food intake (kg/leopard/day) for single female leopards, females with dependent cubs and males, as estimated by three different techniques. Daily follows (□), consecutive day assessments (▨), and random day assessments (■). Standard errors are shown.

(0.28 kg/km/day) or males (0.35 kg/km/day). Another form of presenting energetic return (kg food/hunt/day) revealed similar results. Females with cubs had the highest foraging returns (6.9 kg/hunt/day), followed by males (4.4 kg/hunt/day) and single females (3.7 kg/hunt/day).

The large discrepancy in daily food intake between single females and males could be a function of body size and energetic requirements (McNab, 1963; Gittleman & Harvey, 1982) since larger males have larger ranges and travelled further per day than single females ( $\bar{x} = 6.8$  km;  $U = 11.5$ ;  $P < 0.01$ ). On the basis of body weight, males still showed higher food acquisition (68–73 g food/kg leopard/day) than did single females (41–57 g/kg/day). Females with dependent cubs had the highest per ratio food intake (85–90 g/kg/day) which may be due to the higher energetic needs imposed by dependent cubs. They travelled ( $\bar{x} = 10.5$  km) slightly further than single females ( $P = 0.07$ ) but similar distances to males ( $\bar{x} = 12.2$  km;  $P = 0.2$ ).

## Discussion

### *Densities and population dynamics*

Large African carnivores occur at a variety of densities and social structures, as a response to varied environmental constraints (East, 1984; Sunquist & Sunquist, 1989). The variance in leopard densities in sub-Saharan Africa is explained by correlations with rainfall (Deshmukh, 1984; East, 1984; Martin & de Meulenaer, 1988) and hence prey density. Namibian leopards maintained similar figures of low comparative density, and age/sex ratios, throughout the two tenure periods of the study. By utilizing patchy resources they are expected to maintain large and exclusive ranges (Gittleman & Harvey, 1982; Macdonald, 1983). The high costs of grouping are expected to promote asociality (Caro, 1994).

Leopards are solitary and generally are social only during mating or when rearing cubs, with little variation shown by various studies (Turnbull-Kemp, 1967; Schaller, 1972; Hamilton, 1976; Smith, 1977; Bertram, 1982; Bailey, 1993). Namibian leopards have similar patterns, including solitary hunting behaviour even when accompanied by sub-adult cubs. Despite their highly solitary nature, it has been suggested that female leopards live a mostly social life as a result of rearing cubs (Caro, 1989). Data from the present study suggest that females spend only half their adult life with dependent cubs. They always foraged alone, they were alone on 68.2% of mid-day rest spot observations, and did not share all their kills with their cubs.

The costs of dispersal among asocial species is high (Packer, 1986; Wrangham & Rubenstein, 1986) and the difference in time scale of dispersion from the natal area depends on social circumstances and resource availability (Sunquist, 1983). Both dispersing leopards in the present study died within six months. Most deaths of leopards (excluding very small cubs) in the present study were of sub-adults. These leopards were mostly in poor condition and were killed by people, after resorting to desperate measures in raiding livestock around settlements. In the Kruger, Bailey (1993) reported mortalities of 43% of old adults and 43% of sub-adults, with starvation as the leading cause of death. Vacancies, in the present study, due to deaths in the resident population, were filled quickly through immigration. Similar mechanisms have been recorded for leopards (Seidensticker, Sunquist & McDougal, 1990; Bailey, 1993; Mizutani, 1995); jaguars (*Panthera onca*) (Rabinowitz & Nottingham, 1986), and cougars (*Felis concolor*) (Beier, 1995). Despite a low survival rate among dispersing cougars, young females were more readily integrated into the resident adult population (Beier, 1995), whereas resident males were replaced by relatively mature immigrants (Laing & Lindzey, 1993). We suggest that the ecological carrying capacity of Namibian leopards (and perhaps most asocial felids) are controlled by density-dependent processes (Begon, Mortimer & Thompson, 1996). High sub-adult/dispersal

mortality and rapid occupation of vacancies may serve as the functional mechanisms for maintaining a density status quo, as was evident between 1993 and 1995.

#### *Home range and land tenure systems*

Large variations in home-range size between different leopard populations can be explained by differential density (Gittleman & Harvey, 1982), dispersion and richness of resources (Macdonald, 1983; Wrangham, Gittleman & Chapman, 1993). The relationship between home-range size and resource availability, expressed in terms of leopard density and rainfall, however, was not linear. Only under low densities and rainfall were home ranges notably larger.

The basic pattern of felid social organization has males occupying larger ranges than females. Within-sex ranges tend not to overlap, although each male's range usually encompasses that of several females (tigers: Sunquist, 1981; leopards: Bertram, 1978; Bailey, 1993; cougars: Seidensticker *et al.*, 1973; jaguars: Rabinowitz & Nottingham, 1986; Crawshaw & Quigley, 1991). Bertram (1978) described layers of mosaics of leopard ranges within an area; the resident female layer superimposed by a layer of resident males with larger ranges. A male's range could cover up to six female ranges and another layer could be added to the picture, namely dispersing young or adults moving through from other areas (Bailey, 1993). Under particular conditions, however, when resources are abundant range overlap can be an economically efficient strategy (Davies & Houston, 1984). Among some felids within-sex overlap has been recorded (leopards: Schaller, 1972; Norton & Henley, 1987; jaguars: Rabinowitz & Nottingham, 1986; Crawshaw & Quigley, 1991; cougars: Laing & Lindzey, 1993; snow leopards: Jackson & Ahlborn, 1989).

In the present study, the ranges of leopards (between-sex and within-sex) showed extensive overlap. During both tenure periods male ranges (except for two individuals) overlapped all other males in the study area. All female ranges overlapped during both periods. All adult female ranges overlapped with all male ranges during both periods. These data do not agree with theoretical predictions which state that under low density, such as in the study area, leopards should maintain exclusive ranges to reduce feeding competition (Gittleman & Harvey, 1982; Mace, Harvey & Clutton-Brock, 1983). Female reproductive success is dependent on resource availability (Trivers, 1972), whereas that of males is limited by access to females (Emlen & Oring, 1977). Males should form groups if this would improve their reproductive success, as do lions (Bygott, Bertram & Hanby, 1979; Packer & Pusey, 1982) and cheetahs (Caro & Collins, 1986, 1987). Hence, with typically solitary felids, in which females occupy exclusive ranges, males are expected to remain alone and gain higher reproductive options by limiting incursions by all other males (Caro, 1989). Alternatively, where females have overlapping ranges, and where densities are high, males are expected to form groups (Caro, 1994). Under low densities Namibian leopards remain solitary, and with the possible energetic costs of large daily movements and large ranges, we propose that individuals may simply not be capable of maintaining exclusive ranges, despite the resource and reproductive advantages.

Within the overlapping parts of leopard ranges, there was no indication of aggregation and contact was clearly avoided. Similar to the present study leopards in the Kruger National Park, South Africa (Bailey, 1993) and snow leopards in Nepal (Jackson & Ahlborn, 1989) staggered their activities in different parts of the shared ranges.

#### *Hunting and feeding behaviour*

Little is known about the foraging habits of leopards. Hunts during the present study occurred mostly at night and uniformly consisted of stalking, to within an average of 4 m of the prey, followed



by a short charge. This behaviour is typical of solitary felids (Ewer, 1973; Smith, 1977; Leyhausen, 1979; Bothma & le Riche, 1990; Bailey, 1993). Stalking distances varied substantially and are probably a function of habitat variability. Our data showed that stalking distances did not vary between prey species, individual leopards, or between male and female leopards. Stalking appears to be a very important behaviour as, during successful hunts, leopards approached prey to within closer range than during unsuccessful hunts. In addition, chase distances increase markedly when leopards are not able to stalk within 8 m of prey. Hornocker (1970) also suggested that the approach to prey is as the most crucial part of the hunt. Recognizing the lack of sufficient data on hunting success, the uniformity of successful hunts in terms of structure suggests a stable and effective solitary hunting strategy.

Leopards are catholic in their diet, depending on the availability of potential prey species, and have been recorded as killing between 16 (Mills, 1990) and 31 (Pienaar, 1969; Bertram, 1982) different species, with a body mass range of 5 to 70 kg (Schaller, 1972; Bothma & le Riche, 1986; Norton *et al.*, 1986; Bailey, 1993). These include primates and carnivores as well as other mammals, birds, reptiles and insects. Leopards in the present study conformed to behaviour elsewhere and killed the available and abundant species. These were mainly small antelopes, approximately half to two-thirds the body mass of adult female leopards. Other carnivores (mainly small-sized, but including cheetahs) also made a marked contribution to their diet. Scavenging was rare, although records of leopards scavenging and eating old, even putrid meat are common (Bothma & le Riche, 1986; Bailey, 1993; Mizutani, 1995). A study in China reported dietary shifts over a seven-year period, attributed to either pure opportunism or changing habitat and resource availability (Johnson *et al.*, 1993).

Interaction between leopards and other large carnivores during the present study occurred at 12% of their kills. Only three kills were stored in trees, instead kills were dragged, often a considerable distance from the kill site, and hidden beneath a bush. Despite the energetic costs of dragging carcasses over long distances, the benefits are clear. Dragging reduces the frequency of visits by competitors and the loss of carcasses to scavenging. Taking kills into trees appears to be a costly behaviour, despite small sample sizes, and indicates a significant loss of food and can even be lethal. Elsewhere, especially in open areas, leopards regularly store food in trees (Eisenberg & Lockhart, 1972; Schaller, 1972; Hamilton, 1976). In Kruger, 57% of leopard kills were visited by other carnivores and 84% of kills were stored in trees (Bailey, 1993). However, other studies showed that most kills were not stored in trees (Smith, 1977; Bothma & le Riche, 1986) and that vegetation cover reduces scavenging, even by vultures (Sunquist & Sunquist, 1989). We suggest that habitat and the degree of interspecific competition determines the likelihood of detection, which drives the options leopards use to hide their kills. Avoiding detection is of primary importance and leopards probably only take kills into trees if the chance of detection on the ground is high, due to high competitor densities and/or sparse vegetation cover.

#### *Food acquisition*

Namibian leopards showed distinct differences in daily food intake between single females (1.6 kg/day), females with cubs (2.5 kg/day), and males (3.1 kg/day). Data from Kruger ( $\sigma = 3.5$  kg/day,  $\text{♀} = 2.8\text{--}4$  kg/day; Bailey, 1993) and Kalahari ( $\sigma = 3.5$  kg/day,  $\text{♀}$  with cubs = 4.9 kg/day; Bothma & le Riche, 1986) indicate much higher daily food acquisition. This is surprising as Namibian leopards, with larger home ranges, would be expected to have higher daily food intake as a result of higher metabolic needs (Gittleman & Harvey, 1982). When observations are not random, which might be the case with data from Kruger and Kalahari, biases such as inflated food intake estimates might be prevalent (Mills, 1992).

The discrepancy in daily food intake between males, single females and females with cubs in the present study was consistent in terms of two energy expenditure parameters (kg/km travelled/day and kg/hunt/day). Females with cubs gained more food per body weight than single females by killing larger-sized prey. Variations in daily per capita food intake between the three groups can be explained partly by differential energy expenditure as a result of variations in daily ranges, body size (McNab, 1963; Gittleman & Harvey, 1982) and the costs of parental care (Caro, 1994; Laurenson, 1995a). Bothma & le Riche (1986) showed that females with cubs were more active and effective hunters than solitary males, and in Kruger (Bailey, 1993) females with cubs were more active than single females. Increased expenditure of energy may also occur with the effects of increased hunger, resulting in increased daily ranges and longer stalking distances (Bothma & le Riche, 1990).

#### *Asociality*

We have demonstrated how ecological constraints like rainfall and prey density may determine leopard density. Namibian leopards, living under low densities, conform to theory by occupying large home ranges and living strictly solitary lives. However, they did not maintain exclusive ranges, despite predicted advantages in doing so (Gittleman & Harvey, 1982; Mace *et al.*, 1983; Caro, 1994). Leopard populations may furthermore be regulated by density-dependent processes, mainly through sub-adult mortality. Constraints imposed by ecological factors may thus play an active role in shaping leopard social structures.

Despite advantages of group-living, Caro (1989) suggested that sociality in felids is limited by the costs of grouping. We discuss the potential costs of sharing food resources and inter-specific competition to group-living in leopards.

Under conditions where individuals live in exclusive ranges, under low density, utilizing low quality resources (Mace *et al.*, 1983), sociality is not favoured since the costs of sharing an unreliable food resource are too high (Caro, 1994). In the present study, female leopards, at comparatively low densities, have largely overlapping ranges, and females with dependent cubs increase their per capita food intake to surprisingly high levels. The combination of the two observations could favour grouping. Modal prey mass was  $\leq$  that of adult females, contrary to predictions that increased food intake is dependent on the availability of prey equal or twice the mass of an adult female (Caro, 1989). Cubs did not act as a constant drain on females (see Caro, 1989, 1994) as females spent only about half of their lives with dependent cubs. During this period, they did not appear to spend much time with their cubs, which consumed only 27% of the food acquired by females. However, females with dependent cubs killed larger-sized prey than single females, therefore acquiring significantly higher per capita food intake per day. The cost of sharing food may not be as important a constraint to social development as previously suggested (Packer, 1986; Packer & Rutten, 1988; Caro, 1994), since individuals in several species have been demonstrated to raise per capita food intake when supporting dependent cubs or by forming groups (cheetahs: Laurenson 1995a; leopards: this study; wild dogs: Creel & Creel 1995; lions: Stander, 1992a, b).

Inter-specific competition between carnivores may be a factor limiting populations of some species (cheetahs: Caro, 1994; Laurenson, 1995b; wild dogs: Creel & Creel, *In press*). The cost of defending food against larger or gregarious carnivores has been well documented (Kruuk, 1972; Schaller, 1972; Cooper, 1991; Laurenson, 1995b), and some species such as cheetahs and wild dogs are more common in areas of low densities of spotted hyena and lion (Laurenson, 1995a; Creel & Creel, 1996; Mills & Gorman, *In press*). Lions are a major cause of wild dog mortality and wild dogs avoid areas of high lion densities (Mills & Gorman, *In press*). In areas where visibility is good, wild dogs are more susceptible

to inter-specific competition (Fanshawe & Fitzgibbon, 1993; Creel & Creel, In press), resulting in lower wild dog densities (Mills & Biggs, 1993). Forming large groups in order to outnumber competitors (Cooper, 1991), or limiting advertisement of food, are the only two options for avoiding competition.

Namibian leopards utilized available cover by dragging and hiding kills in thick cover. They did not take kills into trees since this would advertize their food and attract other carnivores (see Sunquist & Sunquist, 1989). Smaller-bodied felids, like the leopard, are elusive, are not easily detected by inter-specific competitors, and avoid competition through their ability to conceal themselves and their food. This behaviour is arguably restricted to the solitary animal. The costs of inter-specific competition may be important in limiting sociality, especially in areas of high visibility. By forming groups, felids would increase the risk of competition over food. Groups would be more visible and would be expected to capture larger prey (Laniprecht, 1981) or at higher frequencies (Caro, 1994). Although known as an opportunistic generalist (Eltringham, 1979; Sunquist & Sunquist, 1989), leopards living in woodland habitat in Namibia appear from our data to be highly specialized. They exhibit homogeneous hunting behaviour, are capable of increasing food intake to meet requirements, and overcome the costs of inter-specific competition through solitary and concealed behaviour.

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