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Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal

Morten Odden & Per Wegge

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Space use and activity of radio-collared leopards *Panthera pardus* (two adult males and one adult female) were monitored during 3-25 months in a prey-rich part of the Royal Bardia National Park, Nepal. Annual home ranges of the two males were 47 and 48 km^2 and had an overlap of only 7%, whereas the overlap between the female's home range (17 km^2) and that of one of the males was 56%. The range sizes were larger than reported from other studies in south-east Asia, but much smaller than some ranges in Africa. When comparing different studies, the sexual difference in range size increased significantly with increasing average range size. Thus, the cost by males of traversing large home ranges is probably not a determinant factor in shaping leopard communities. The female's seasonal home ranges (5.2 and 6.6 km^2) were smallest during the seasons when her cubs were less than six months of age. She moved her home range closer to agricultural fields during the season when the abundant and important prey axis deer *Axis axis* visits these areas most frequently. No such pattern was detected among the two males. Instead they frequented human settlements throughout the year, probably in order to hunt easily accessible domestic animals. Home ranges in similar seasons in consecutive years overlapped more (female = 64%, male = 75%) than ranges in different seasons in the same year (female = 38%, male = 64%). Intensive tracking sessions of 24 hours revealed that the diel activity levels of the two sexes were similar (female: 62.3%, males: 62.6%). However, their patterns of activity were different as the males moved mainly at night (day: 1,582 m, night: 5,244 m) and the female moved similar distances day and night (day: 2,381 m, night: 2,698 m). The female may have restricted her movement at the time when conspecific males were likely to be active in order to protect her cubs from infanticide. The males moved in a more linear manner than the female, and the linear distances between radio locations from consecutive days differed significantly between the sexes (male: 3,324 m, female: 881 m), but the actual distances moved during the 24-hour cycles were fairly similar (male: 6,826 m, female: 5,079 m).

Key words: activity, home range, leopard, Panthera pardus, spacing, subtropical forest

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Previous radio-telemetry studies of leopards *Panthera pardus* have revealed pronounced variations in spacing patterns between different study areas. The variation is particularly evident when comparing home range sizes, which range from 6 km^2 (Seidensticker et al. 1990) to more than 2,000 km^2 (Bothma et al. 1997). Moreover, the degree of overlap between neighbours has been described as both extensive (Stander et al. 1997) and small (Rabinowitz 1989, Seidensticker et al. 1990, Mizutani & Jewell 1998). The variability among the previous studies is probably related to differences in the spatial distribution of food resources, as the density and movement of prey are essential determinants of predator behaviour (Schaller 1972, Malcolm & Van Lawick 1975, Frame et al. 1979, Bailey 1993). The variation may also be due to small sample sizes, or due to differences in sex, reproductive and social status and metabolic needs (Gittleman & Harvey 1982, Bailey 1993).

In this study, we describe the spacing and activity patterns of leopards in a prey-rich area of lowland Nepal and relate intersexual differences to season, prey conditions and reproductive status. We also evaluate home range estimators and attempt to identify a general trend in spacing pattern by comparing our findings with those from other studies.

Material and methods

Our study was conducted within a 100-km^2 area in the southwestern part of the Royal Bardia National Park (986 km^2). The park is situated in southwest Nepal where the foothills of the Himalayas flatten out on the Indian lowlands (about 100 m a.s.l.). The climate is subtropical monsoonal with heavy rains from July to September/October. Sal forest, interspersed with patches of *Imperata cylindrica*-dominated grasslands, and riverine forest and tallgrass flood plains are the dominating plant associations (Dinerstein 1979a, Sharma 1999). Of the 32 different mammal species recorded in the Park (Dinerstein 1979b), axis deer *Axis axis* contributes nearly 90% of the herbivore biomass (Andersen & Næss 1993). Other commonly occurring prey species are hog deer *Axis porcinus*, barking deer *Muntiacus muntjak*, wild boar *Sus scrofa*, and barasingha *Cervus duvauceli*. Until the late 1970s, a large number of domestic animals grazed within the park, but since then grazing has virtually ceased. Ungulate prey density is high with > 200 animals/km^2 within the study area (Andersen & Næss 1993, Støen & Wegge 1996). Tiger *Panthera tigris* is the dominant carnivore. Leopard coexists at lower density, and sloth bear *Melursus ursinus*, striped hyena *Hyaena hyaena*, and dhole *Cuon alpinus* occur in still fewer numbers (Heinen & Kattel 1992).

Table 1. Morphometric and tracking data of three adult leopards (one female, F1, and two males, M1 and M2) studied in the Royal Bardia National Park during 1999-2001.

	F1	M1	M2
Weight (kg)	36	44	58
Total length (cm)	180	203	223
Tail length (cm)	84	84	94
Shoulder height	70	70	75
Date of first capture	14.02.99	28.02.99	30.12.99
Date of recapture	08.01.00	30.01.00	
Number of locations	396	110	22
Date of last location	01.04.01	16.03.01	22.03.00

Three adult leopards, two males (M1 and M2) and one female (F1), were captured in box traps and immobilised with a combination of 8.7-10.4 mg/kg ketamine and 4.35-6.2 mg/kg xylazine in three captures, and a mixture of 3.6-5.9 mg/kg ketamine and 0.07-0.12 mg/kg medetomidine in two captures. The sedated animals were weighed, measured, fitted with radio collars in the 164-MHz frequency range and aged according to Bailey (1993). After handling, all animals were given an antidote (atipamezole) and monitored from a distance until they were mobile. Morphometric data and tracking data are listed in Table 1.

The leopards were located by triangulation from the ground using portable receivers and three-element Yagi antennas. At each compass bearing we determined whether the animal was active or passive based on variation in the signal strength. The range of the radio signals rarely exceeded 700 m, probably due to the dense vegetation and the flat topography within the study area. Nevertheless, locating the animals was usually not difficult, since several roads encompassed the study area and the home ranges of the leopards were relatively small. The short distance between the animal and the observer ensured a high level of precision; nearly all error polygons were within < 0.5 ha.

We conducted 24-hour continuous tracking sessions on 19 occasions (F1 = 13, M1 = 4, M2 = 2), during which activity was recorded every 15 minutes and precise radio fixes were obtained every hour. In the analysis of these data we defined the period between 06:00 and 18:00 as 'day', and the period between 18:00 and 06:00 as 'night'.

All radio locations were plotted on 1:10,000 topographic maps and digitised. Digitising, home range estimation and movement analysis were conducted using ArcView GIS 3.2. We used minimum convex polygon (MCP; Mohr 1947) and fixed kernel (95%, least squares cross validation and individual smoothing factor; Worton 1989) as home range estimators. We used

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Table 2. Estimated home range sizes (in km^2) of radio-collared leopards in Southeast Asia.

Study area	Sex	N	Home range size MCP	Home range size Kernel	Sampling durations (months)	Reference
Bardia, Nepal	♀	296	17.1	16.9	26	This study
	♂	95	50.4	46.8	25	
	♂	20	20.1	48.1	3	
Chitwan, Nepal	♀	?	7.0		5	Seidensticker et al. 1990
	♀	?	6.0		3	
	♀	?	13.0		6	
Nagarahole, India	♂	327	26.3	31.3	23	Karanth & Sunquist 2000
	♂	82	17.1	25.1	10	
Huai Kha Khaeng, Thailand	♀	45	11.4		3	Rabinowitz 1989
	♂	9	27.0		9	
Kaeng Krachan, Thailand	♀	92	8.8		?	Grassman 1999
	♂	42	17.3		?	
	♂	68	18.0		?	

bootstrap simulations to examine the relationship between sample size and home range size when using MCP and fixed kernel. In bootstrap simulations, range size is estimated from an increasing number of randomly selected radio locations. We started with 10 locations and increased the sample size with 10 until all radio locations were included in the calculations. We did five repetitions in each interval.

Seasonal home ranges were calculated whenever > 15 radio locations had been retrieved during a time span of more than one month during one season. We defined the period from November to March as the cool dry season, from March to July as the hot dry season and from July to November as the wet season. Overlap was calculated according to Minta (1993). Seasonal occupancy centres were calculated by averaging the coordinates of all the locations obtained during each season. We analysed day-to-day movement by measuring the distance between locations obtained on consecutive days. In all home range estimates and day-to-day movement analyses we used no more than one location per day. We used the location taken nearest 12:00 whenever more than one location had been obtained on a single day. Diel movement distances were calculated by adding up the distances between consecutive locations that were obtained during the 24-hour intensive tracking sessions.

In all tables and analyses which include home range data from previous studies only adult individuals were considered. If several methods had been used, we chose kernel home range estimates if available; otherwise we chose MCP. In the comparisons of sexual differences in home range size between the study areas we used the following definitions: sexual difference in range size was determined as the average range size of males divided by the average range size of females. Average range size was determined as the average range size of males + the average range size of females divided by two.

Results

Spacing pattern

The home ranges of the three leopards were located along the border of the park and consisted predominantly of sal forests with small patches of grasslands. The range size of the female leopard (F1) calculated by the kernel estimator was 16.9 km^2 when including the tracking data from the whole study period (hereafter termed 'total home range'), whereas the total ranges of the males, M1 and M2, were 46.8 km^2 and 48.1 km^2, respectively (Table 2). The home range sizes of F1 and M1 were 17.1 km^2 and 50.4 km^2, respectively, when using the MCP as estimator and thus fairly similar to the ones obtained using the kernel method. In contrast, the size of M2's total home range was only 20.1 km^2 with MCP, which is more than two times smaller than the kernel estimate. As seen in Figure 1, the MCP method is sensitive to small sample size, and as a consequence, the estimated home range of M2 is more reliable when using the kernel method.

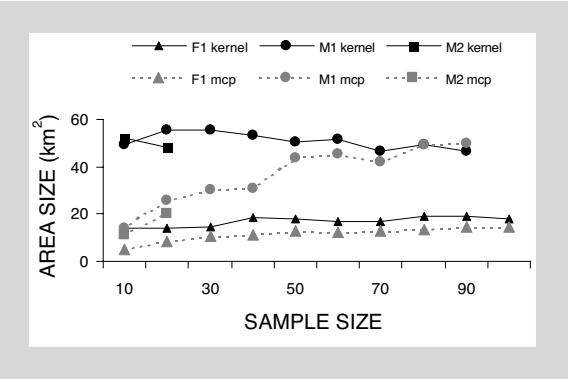


Figure 1. Relationship between sample size and home range size using MCP (100%) and fixed kernel methods (95%), respectively, as estimators for the female (F1) and the two male (M1 and M2) leopards in the Royal Bardia National Park, Nepal.

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Table 3. Average home range sizes (in km^2) of adult leopards in this and previous studies.

Study area	Habitat	Home range size (km^2) ♂ (N)	♀ (N)	Home range ♂♂/♀♀	Reference
Asia					
Bardia National Park, Nepal	Subtropical forest	47.4 (2)	16.9 (1)	2.8	This study
Royal Chitwan National Park, Nepal	Subtropical forest		8.7 (3)		Seidensticker et al. 1990
Nagarahole National Park, India	Tropical forest	28.2 (2)			Karanth & Sunquist 2000
Huai Kha Khaeng Wildlife Sanctuary, Thailand	Tropical forest	27.0 (1)	11.4 (1)	2.4	Rabinowitz 1989
Kaeng Krachan National Park, Thailand	Tropical forest	17.7 (2)	8.8 (1)	2.0	Grassman 1999
Africa					
Taï National Park, Ivory Coast	Tropical forest	86.0 (1)	24.4 (2)	3.4	Jenny 1996
Kaudom Game Reserve, Namibia	Semi-arid savannah	451.2 (6)	188.4 (3)	2.4	Stander et al. 1997
Serengeti National Park, Tanzania	Wooded grassland		15.9 (1)		Bertram 1982
Lolldaiga Hills Ranch, Kenya	Wooded grassland	37.1 (2)	16.9 (3)	2.2	Mizutani & Jewell 1998
Kruger National Park, South Africa	Woodland savannah	47.1 (5)	12.4 (6)	3.8	Bailey 1993
Kalahari Gemsbok National Park, South Africa	Semi-arid savannah	2182.4 (3)	488.7 (5)	4.5	Bothma et al. 1997
Stellenbosh Mountains, South Africa	Fynbos mountain	388.0 (1)			Norton & Lawson 1985
Sabi-sand Game Reserve, South Africa	Woodland savannah		23.0 (1)		LeRoux & Skinner 1989
Cedarberg Wilderness Area, South Africa	Fynbos mountain	51.0 (3)			Norton & Henley 1987

Even though the home ranges of the leopards in our study were relatively small compared to those of leopards living in more arid environments in Africa (Table 3), they were the largest ever recorded in southeast Asia (see Table 2). The average size of the home ranges of the males in our study was 2.8 times larger than the range of the female, whereas the corresponding values from previous studies average 3.0 (SD = 0.9, N = 7; see Table 3). When comparing different study areas, the sexual difference in range size was significantly correlated with the average range size (Spearman Rank Correlation Test, two tailed: $r = 0.762$, $N = 8$, $P < 0.05$; Fig. 2). The positive correlation implies that the sexual difference in range size becomes larger when the average range sizes increase.

The overlap between M1 and M2 was 7% when using 95% fixed kernel as home range estimator. The overlap between F1 and M1 was 56%, but between F1 and M2 there was no overlap. Hence, the spatial distribution of the ranges was in accordance with what should be expected for a solitary felid as there was a pronounced sexual difference in home range size, a high degree of intersexual overlap, and a small degree of intrasexual overlap (Fig. 3). Pugmark tracking and camera trapping indicated that there were no resident males located between M1 and M2 (Eliassen 2003), which would have increased the degree of overlap between the males.

The annual and seasonal home ranges of F1 and M1

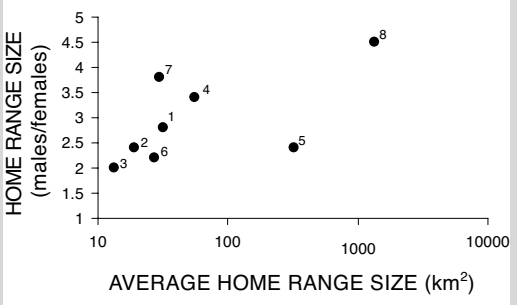


Figure 2. Relationship between sexual differences in home range size for male/females and the average home range size (male+female/2) in our study (1) and the following previous leopard studies: Rabinowitz 1989 (2), Grassman 1999 (3), Jenny 1996 (4), Stander et al. 1997 (5), Mizutani & Jewell 1998 (6), Bailey 1993 (7) and Bothma et al. 1997a (8).

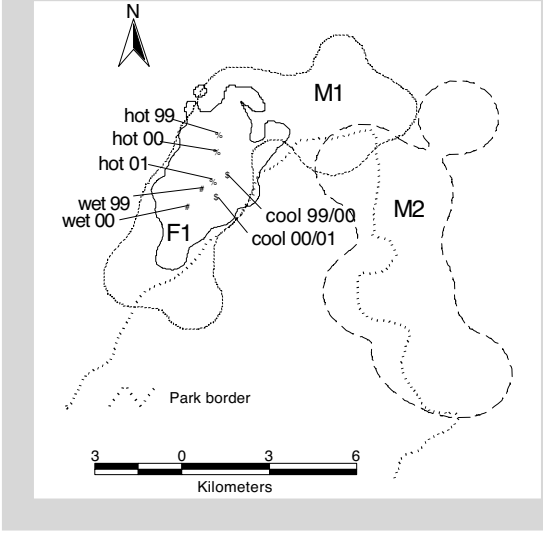


Figure 3. Total home range boundaries using 95% kernel of one adult female (F1 = ——) and two adult male (M1 = ….. and M2 = - - -) leopards in the Royal Bardia National Park, Nepal, and seasonal occupancy centres of the female.

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Table 4. Annual and seasonal home range sizes (expressed as fixed kernel (95%, in km^2) of two adult leopards (female F1 and male M1) in the Royal Bardia National Park, Nepal.

Tracking period	F1	M1
Hot 1999	9.5 (40)	33.5 (21)
Wet 1999	5.2 (49)	
Cool 1999/2000	12.8 (55)	50.8 (29)
Hot 2000	11.6 (36)	40.0 (22)
Wet 2000	2.5 (16)	
Cool 2000/2001	6.6 (67)	
Mar. 1999 - Feb. 2000	19.1 (118)	57.9 (56)
Mar. 2000 - Feb. 2001	13.2 (144)	45.2 (37)

varied in size (Table 4). The variation was probably not due to sampling as the bootstrap simulations showed that the kernel estimator produced fairly similar-sized ranges in the whole array of sample sizes. F1 gave birth to two cubs in late June of 1999 and two cubs in August of 2000. Hence, the smallest seasonal home ranges of F1 during the wet season of 1999, the wet season of 2000 and the cool season of 2000, coincide with the time when her cubs were < 6 months of age.

Seasonal range overlap was estimated for F1 and M1 separately (Table 5A). Range overlap between different seasons was smaller than the overlap between similar seasons in consecutive years. Also, the distances between the occupancy centres of similar seasons were shorter than the distances between different seasons in both M1 and F1 (Table 5B). For M2 we had too few data for it to be included.

F1 showed significant seasonal differences in the distances between radio fixes and the park border (Kruskal-Wallis ANOVA on ranks: H = 64.1, df = 2, P < 0.0001). A pairwise comparison revealed that F1 was significantly closer to the park border during the cool seasons than during the other seasons and most distant during the hot seasons (Dunn's method, cool seasons vs hot seasons: Q = 7.90, P < 0.05, cool seasons vs wet seasons: Q = 4.13, P < 0.05, hot seasons vs wet seasons: Q = 2.68, P < 0.05; Fig. 4). M1 showed no such seasonal difference in the distance to the park border (H = 2.59, df = 2, P = 0.2735). Contrary to F1, he seemed to be located close to the park border throughout the whole year (see Fig. 3). M2 was not included in the analysis due to lack of data.

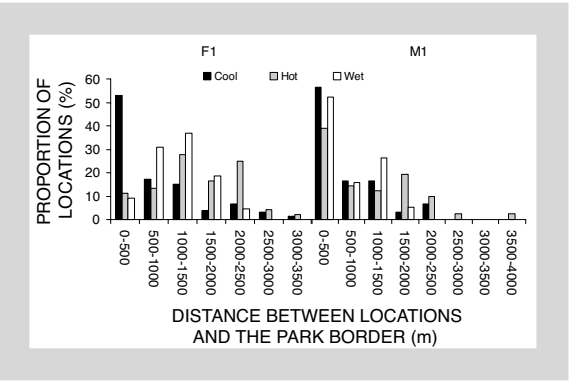


Figure 4. Distribution of the female F1's and the male M1's radio locations during different seasons in relation to the distance to the border of the Royal Bardia National Park.

Movement and activity

The distance between locations obtained on consecutive days averaged 881 m for F1 (N = 164, SD = 893 m). The distance between locations of M1 (Mean = 3,324 m, N = 26, SD = 2,912 m) was significantly longer (Mann-Whitney: T = 3,579.0, P < 0.0001). M2 was not included due to lack of data.

F1 was active in 76% of the radio locations obtained during daytime (SD = 35%, N = 335), while M1 was active in 66% (SD = 41%, N = 99) and M2 was active in 73% (SD = 35%, N = 17). The diurnal level of activity differed significantly between the three leopards (H = 8.20, df = 2, P = 0.0166). F1 was significantly more active during daytime than M1 (Q = 2.82, P < 0.05), and the difference in activity level was least pronounced between the two males (Q = 0.466, not significant).

The 24-hour intensive tracking sessions (F1 = 13, M1 = 4, M2 = 2) revealed that the two sexes had similar mean diel activity levels (t-test: t = 0.0798, P = 0.937); F1 was active in 62.3% of the measurements (SD = 8.28), and the males were active during 62.6% (SD = 8.51). The males' mean diel movement distance (6,826 m, SD = 3,510 m) was longer than the distance moved by F1 (5,079 m, SD = 2,133 m), but did not differ significantly (t = 1.34, P = 0.198). However, the two sexes moved

Table 5. Overlap (in %) between seasonal home ranges (using kernel 95%; A) and distance (in m) between seasonal occupancy centres (B) of a female (F1) and a male (M1) leopard in the Royal Bardia National Park, Nepal.

		Similar seasons in consecutive years					Different seasons (hot/wet/cool)		
	ID	Cool/cool	Hot/hot	Wet/wet	Mean	SD	Min	Max	N
A)	F1	66	73	52	38	17	6	62	12
	M1	75			64		56	72	2
B)	F1	910	625	821	1653	673	588	2890	12
	M1	651			1360		1081	1639	2

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at different times of the day. The female moved similar distances during the day and night (day: 2,381 m, SD = 1,923 m, night: 2,698 m, SD = 1,474 m, N = 13; t = 0.472, P = 0.641), whereas the males moved mainly during the night (day: 1,582 m, SD = 985 m, night: 5,244 m, SD = 3,441 m; T = 56.0, P = 0.004). Furthermore, F1 was never located outside of the park during the intensive tracking sessions, whereas M1 was outside the park border during three sessions and M2 during one session.

Discussion

Several authors have described an inverse relationship between food availability and territory size in territorial animals (e.g. Ebersole 1980, Hixon 1980, Schoener 1981, Saitoh 1991). This relationship seems evident when reviewing previous leopard studies conducted in Africa, where the drier habitats with a sparser prey distribution produce extremely large home ranges, and the more humid and prey-rich habitats produce smaller ranges. The difference in home range sizes in Asian studies is far less pronounced than in African studies, which is probably due to smaller differences in prey abundance between the study areas.

The sexual differences in home range size observed in our and previous leopard studies are considerably larger than expected from sexual differences in energy requirements of solitary carnivores (Sandell 1989). Hence, the basic social organisation of solitary felids, in which the limiting resource for females is access to food and the limiting resource for males is access to females, seems to be a common feature among leopards throughout their distribution range. Surprisingly, the sexual difference in home range size was significantly more pronounced in study areas where home ranges were large. Hence, males seem to expand their ranges proportionally more than females in areas where resources are more sparsely distributed. This implies that the cost by males of traversing large home ranges is not a determinant factor in shaping leopard communities.

Reproductive status seemed to affect the area use of F1, as her three smallest seasonal home ranges coincided with the time when her cubs were less than six months of age. This is in accordance with previous studies of leopard (Bailey 1993) and mountain lion *Felis concolor* (Hemker et al. 1984), which showed that rearing small cubs restricts movement of the mother.

Previous studies have demonstrated relationships between spatio-temporal changes in prey distribution and the movement patterns of leopards (Bailey 1993) and bobcats *Felis rufus* (Litvaitis et al. 1987, Koehler & Hornocker 1989). Accordingly, seasonal changes in the distribution of Axis deer, the main prey of leopards in our study area (Eliassen 2003), may explain why different parts of the total home range of our female leopard were more intensively used during different seasons. The recurrent movements of F1 close to the park border during the cool seasons (see Fig. 3) coincide with the time when axis deer visit the agricultural fields for foraging most frequently (Moe & Wegge 1994).

In contrast to F1, a large proportion of M1's radio locations were situated close to the park border in all seasons, not only during the cool season (see Fig. 3). The difference between the two leopards probably reflects the fact that male leopards are more prone to be stock-raiders than females (Hamilton 1981, Esterhuizen & Norton 1985). The 24-hour tracking sessions support this conclusion, since F1 was never located within human settlements in any of the 13 sessions, whereas the males were found in villages during four out of six sessions. According to Sukumar (1991), males of polygynous species more frequently cause conflicts with humans than females due to inherent higher risk-taking behaviour. The 'high risk-high gain' strategy is favoured among males of such species due to their greater variance in reproductive success (Trivers 1985).

An important and obvious factor affecting our results concerning space use was the choice of home range estimator. The MCP method, which has frequently been used as home range estimator in other leopard studies, is criticised for its sensitivity to small sample sizes, and because it usually incorporates large areas that are never used (Bekoff & Mech 1984, Powell 1987, White & Garrott 1990). Our bootstrap simulations and Mitzutani & Jewell's (1998) study confirmed that relatively large samples sizes were required to produce reliable home range estimates. Likewise, Bothma et al. (1997) concluded that the home range sizes of all nine leopards tracked in their study were underestimated when using MCP due to limited sample sizes. A common argument for choosing MCP is that it allows comparison with previous studies. In our opinion this argument is equivalent to saying that it is better to compare two unreliable estimates than comparing one good estimate with a bad one. We disagree with this argument and believe that other home range estimators, such as kernel methods, are more appropriate.

The sexual difference in day-to-day movement was 3.8:1, and thus, somewhat similar to the sexual difference in range size (2.8:1). Probably, the males moved longer distances every day in order to regularly frequent all parts of their larger territories. However, the inten-

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sive tracking sessions revealed that the actual distance moved during 24-hour periods differed to a lesser degree between the sexes. This implies that the primary cause of the pronounced sexual difference in day-to-day movement was a more linear movement pattern among the males.

The males were less active than the female during daytime. Moreover, the female moved similar distances during day and night, whereas males moved mainly at night. A more nocturnal behaviour in males was also found in studies of lynx *Lynx lynx* (Schmidt 1999) and bobcat (Wassmer et al. 1988). Seidensticker (1977) reported that a radio-marked female leopard rearing small cubs in the Chitwan National Park spent more time in the immediate vicinity of her cubs during night than during day. F1's cubs were 4-8 months old during the intensive tracking sessions, and her movement pattern seemed somewhat similar to the movements of the female in Chitwan. Infanticide has been recorded as a factor of mortality in previous studies of *Carnivora* (Swenson 2003), including solitary cats (leopards: Bailey 1993, Iliany 1990; mountain lion: Logan & Sweanor 2001) and inferred in tiger (Smith & McDougal 1991). In order to avoid infanticide F1 may have restricted her movement at night in order to be closer to her cubs at the time when conspecific males are more active.

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