INDIVIDUAL VARIATION IN SPACE USE BY
FEMALE SPOTTED HYENAS

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Large carnivores range more widely than many other terrestrial mammals, and this behavior tends to bring them into frequent conflict with humans. Within any carnivore population, individual variation in patterns of space use should be expected to make some animals more vulnerable than others to risks of mortality from humans and other sources. In this study, our goal was to document variation among individuals in space use by female spotted hyenas (*Crocuta crocuta*). We examined predictions of hypotheses suggesting that space use by female hyenas is affected by reproductive state, social rank, and local prey abundance. Home-range size, distance at which females were found from the current communal den, and distance at which they were found from the nearest territorial boundary all varied significantly with the 3 independent variables. Females with den-dwelling cubs had smaller home ranges, were found closer to the communal den, and were found farther from the territorial boundary than were females with no den-dwelling cubs. Neither social rank nor prey availability significantly influenced the space-use patterns of females with den-dwelling cubs. Among females with no den-dwelling cubs, high-ranking females had smaller home ranges, were closer to the communal den, and were farther from the territorial boundary than were low-ranking females. The females ranging most widely were low-ranking individuals with no den-dwelling cubs when they were observed during periods of prey scarcity.

Key words: carnivores, *Crocuta*, geographic information system, home range, hyena, utilization distribution

Among mammalian carnivores, home-range size and other aspects of space use are strongly influenced by dispersion patterns of resources, particularly food (e.g., Macdonald 1983; Spong 2002). In addition to food dispersion, however, other factors such as social status and reproductive condition might be expected to exert powerful effects on space use by carnivores (Hofer and East 1993c). In this study, we sought to evaluate the effects of social rank and reproductive status on patterns of space use by spotted hyenas (*Crocuta crocuta*).

Spotted hyenas live in fission–fusion societies in social groups called clans (Holekamp et al. 1997a, 2000; Kruuk 1972). Within the territory defended by each clan, individuals travel, rest, and forage alone or in subgroups (Holekamp et al. 2000). Composition of subgroups typically changes several times during the course of a single day, and sizes of subgroups range from 1 to tens of animals (Holekamp et al. 1997a, 2000). Hyenas assemble for reasons ranging from such cooperative activities as territorial defense (Boydston et al. 2001; Henschel and Skinner 1991) to intense direct competition during group feeding at kills of

ungulates (Frank 1986b; Tilson and Hamilton 1984). Hyenas also frequently congregate at the communal den, which serves as the clan's social center. Females with young cubs visit the den regularly to nurse their dependent offspring, and subadults, adult males, and adult females without den-dwelling cubs also visit the communal den frequently. Thus, in the fission–fusion societies of spotted hyenas, patterns of space use should be expected to vary among individuals on the basis of social, reproductive, and ecological parameters. Indeed, in the Serengeti National Park, Tanzania, where resident *C. crocuta* frequently commute long distances from their dens to feed on migratory prey, commuting behavior of females varies with their reproductive state (Hofer and East 1993c). However, because commuting behavior is not observed in other *C. crocuta* populations (Hofer and East 1993a), our objective in this study was to document variation in space-use patterns among adult female members of 1 large hyena clan in which commuting does not occur. We sought to examine reproductive condition, social rank, and local prey abundance as potential sources of this variation. We expected females with den-dwelling cubs to contract their home ranges and act much like central-place foragers (Orians and Pearson 1979), whereas we expected the movements of females having no den-dwelling cubs to be relatively unconstrained by location of the communal den. Because high-ranking females breed at far higher rates than low-ranking females, they are more likely to have cubs at the den at any given time. Therefore, to determine whether social rank has effects on use of space other than those mediated directly by differential reproductive rates, we examined effects of social rank on use of space by females while controlling for reproductive state. Finally, while controlling for female rank and reproductive state, we compared patterns of space use among individuals observed during periods of prey abundance and those

observed in the same animals during periods of prey scarcity.

MATERIALS AND METHODS

Study animal and study site.—A spotted hyena clan contains multiple adult females, their offspring, and 1 to several immigrant males that join the clan as adults. Female hyenas are generally philopatric, whereas most males disperse shortly after puberty (East and Hofer 2001; Frank 1986b; Henschel and Skinner 1987; Holekamp and Smale 1998; Smale et al. 1993, 1997). Social relationships within a clan are organized on the basis of a linear dominance hierarchy, and an individual's position in the clan's hierarchy determines its priority of access to food (Frank 1986b; Mills 1990; Tilson and Hamilton 1984). Access to food, in turn, profoundly affects the reproductive performance of adult females; although all adult female clan members breed, they do so at rates that increase dramatically with social rank (Frank 1986b; Holekamp et al. 1996, 1999). Females give birth to litters with a modal size of 2 cubs (Holekamp et al. 1996; Kruuk 1972; Mills 1990), which are reared at dens for the 1st several months of life.

The study clan, which usually contains 70–80 hyenas, defends a territory encompassing 62 km² (Boydston et al. 2001) in the Talek region of the Masai Mara National Reserve, Kenya. This is an area of open rolling grasslands grazed year-round by large concentrations of several resident ungulate species. These are joined for 3–4 months each year by large migratory herds of antelope from the southern part of the Serengeti. Boundaries of the territory defended by the Talek clan were known from observations of group territorial behaviors including border patrols and clan wars (Boydston et al. 2001). These territorial boundaries remained stable throughout the current study.

Food resources available to Talek hyenas were monitored weekly by counting all prey found within 100 m of 18 km of transect lines. Prey numbers summed over 11 transects were then averaged for each biweekly interval. For the entire study period, half the biweekly census intervals in which the highest numbers of prey animals were counted were designated as intervals when prey were abundant (>900 prey items counted). The other half of the census intervals were considered intervals when prey were scarce (<900 prey items counted). The number

of ungulates counted when prey were abundant was $1,353 \pm 159$ ($n = 20$), and the number counted when prey were scarce was 548 ± 27 ($n = 21$).

Collection of spatial data.—Between July 1996 and April 1998, we documented space-use patterns of adult female members of the Talek clan. Researchers were present in the study area on over 90% of days during the 20-month study period. We conducted regular daily observations between 0600 and 0900 h and again between 1700 and 2000 h, but observations were also conducted at other times of the day and at night with the aid of night-vision binoculars.

At any given time, approximately half the adult females in the clan were fitted with radio-collars (Telonics Inc., Mesa, Arizona) with signals in the 150- to 151-MHz range. Thirteen collared adult females were included in this study, spanning a range of social ranks from rank 2 (highest) to rank 26 (lowest). We radiotracked the 13 females from vehicles equipped with scanning receiver units. Locations of tagged hyenas were pinpointed by either visually sighting the animal or localizing the signal to an area less than 200 m^2 when the hyena was not visible.

Each week, researchers attempted to acquire at least 3 radiotracked locations per female. We drove through the clan's entire territory at least once every 2 days and made special efforts both inside and outside the territorial boundaries defended by the Talek clan to radiotrack any collared females not found during the preceding few days. We also recorded locations of radio-collared females that were found without use of telemetry equipment. Each time a radiocollared female was found, her geographic location was recorded with reference to local landmarks or as geographic coordinates in the Universal Transverse Mercator (UTM) system calculated from the average of 3–5 readings on a handheld Magellan (Thales Navigation, Santa Clara, California) global positioning system accurate to ±100 m. Date, time, context (den, fresh kill, old ungulate carcass, or other), and other data were also recorded each time a female was located.

To avoid autocorrelation among sequential locations, any location for a particular female that was not separated by at least 1 h from the previous location for the same female was excluded from the data set, irrespective of whether the location was identified with or without tracking. One hour allowed enough time for hyenas to cross the Talek territory and was thus sufficient for statistical independence of observations (White and Garrott 1990), but >6 h elapsed between consecutive sightings in 88% of cases. All locations that were within 200 m of the current communal den were also excluded to avoid biasing locations of females toward the site of the communal den, which observers usually visited at least twice daily.

Assignment of social rank, age, and reproductive state.—All individual members of the Talek study clan were recognizable by their unique spots. Sex was determined by the dimorphic glans morphology of the erect phallus (Frank et al. 1990). Social ranks of all clan members were known based on their positions in a matrix of outcomes of dyadic agonistic interactions (Smale et al. 1993).

Females were considered to be adults when they conceived their 1st litter or at 3 years of age, whichever came first. Talek females usually maintain their cubs at dens during the first 8 months of life. Dates of birth of cubs were estimated to ±7 days based on pelage, size, and other aspects of appearance when cubs were initially observed above ground. Dates of conception were calculated by subtracting the length of the gestation period, 110 days (Kruuk 1972; Schneider 1926), from cub birth dates, so conception dates were also known to ±7 days. Weaning in the Talek population occurs, on average, when cubs are 13.4 months old (Holekamp and Smale 1993; Holekamp et al. 1996), but weaning age ranges from 7 to 21 months (Holekamp et al. 1996; Szykman et al., in press). Weaning conflicts and cessation of nursing indicated that cubs had been weaned. Weaning dates were determined as described previously (Holekamp et al. 1996; Szykman et al., in press) and were accurate to ±10 days.

For each day during which a female's location could be pinpointed, she was assigned to 1 of 4 possible reproductive states. Pregnancy (P) encompassed the 110 days from conception to parturition. The lactation interval was divided into 2 phases. During the 1st phase of lactation (L1), litters resided at dens. L1 ended when cubs became independent of the communal den or died there. Before den independence, cubs were regularly seen at the communal den. When a cub was found at least 200 m from the den on 4 or more consecutive occasions, that cub was considered to be "free-roaming" and independent

of the communal den. Females that continued nursing free-roaming cubs were classified as being in the 2nd phase of lactation (L2), which ended at weaning. Females that were neither pregnant nor lactating were assigned a reproductive state of "other" (O). Nulliparous adult females were also assigned to this "O" state. Three females became pregnant while still in the 2nd phase of lactation. In these cases, their reproductive states were assigned as L2. For some analyses, females were further classified as either with (L1) or without (L2, O, and P) den-dwelling cubs.

Geographic information system analyses and statistical methods.—Global positioning system coordinates were recorded for about 40 landmarks distributed throughout the study site, and these were used to create a digital photomosaic map for use in a geographic information system (GIS) as a base map. Air photos taken in 1991 by Kenya Wildlife Service and Kenya Rangelands and Ecological Monitoring Unit were scanned into a computer at 1-m resolution. Using ERDAS IMAGINE software, ver. 8.3 (ERDAS, Atlanta, Georgia), we created a digital map of the study site on which landmarks were clearly visible. The boundaries of the Talek clan's territory were digitized as a separate overlay coverage (Boydston et al. 2001), as were the locations of all dens used by the hyenas during the study period. Locations of all collared females were digitized so that each point in space at which an animal was tracked or found without tracking was associated with UTM coordinates.

To document space-use patterns, we calculated linear distances and home-range estimates using ArcView GIS software with the Animal Movement Extension (Hooge and Eichenlaub 1997). For each location for each female, we obtained the straight-line distance from that point to the communal den and also the distance between that point and the nearest territorial boundary or "edge." When 2 communal dens were in use concurrently, the "distance to the den" was measured between the female's location and the midpoint between the 2 dens. The distance to the nearest territorial boundary ("distance to the edge") was used as a measure of a female's tendency to be peripherally located. If a female was found outside the Talek territory, her distance to the nearest boundary was assigned a negative value. In comparing distance to the den or edge for females in different re-

productive states, we used mean distance per female per sampling interval. We calculated means for only those females for which at least 30 locations had been recorded in a given reproductive state.

Sizes of areas used by individuals were initially estimated for each female based on all recorded locations, except when females were found at the communal den or found less than 1 h after an earlier sighting. We calculated minimum convex polygons (MCPs—Hayne 1949) and fixed-kernel utilization distributions (UDs—Powell 2000; Worton 1989) with 50% and 95% probabilities to compare the results of the traditional and widely used MCP method with those obtained using the fixed-kernel UD method. Because MCPs rely on only the outermost points at which an individual was observed, they do not require independence among observations (Swihart and Slade 1985). However, MCPs do not show intensity of use (Harris et al. 1990), which is revealed by UDs. The number of observations needed to estimate home-range size with MCPs has been suggested to be 29–150 for large carnivores (Bowen 1982; Fritts and Mech 1981; Messier and Barrette 1982; Pierce et al. 1999), but fixed-kernel UDs do not depend on sample sizes as large as those required for MCPs (Powell 2000; Seaman et al. 1999).

The sizes of areas used by individual females in each reproductive state (with and without den-dwelling cubs) were estimated from 95% UDs. Utilization distributions were calculated only for females in particular reproductive states for which sample sizes of more than 50 locations had been recorded. These UDs were calculated from data collected during continuous periods of 3–4 months. When more than 1 UD could be calculated for a female in a particular reproductive state because she cycled repeatedly during the study, the mean UD size was reported for that female in that state.

SYSTAT 8.0 (Systat Software, Inc., Richmond, California) was used for all statistical analyses. Dependent variables examined were distance to the den, distance to the nearest territory edge, and size of UDs. Rank, reproductive state, and current prey abundance were the independent variables. For some analyses, females were divided into 2 groups according to rank: females in the top half of the dominance hierarchy were assigned to the "high" rank group, and those in the lower half were assigned to the

''low'' rank group. Because we calculated mean values of distance to den or territory edge for females in all statistical analyses, sample sizes equaled the number of females. These mean values were normally distributed. Fixed-kernel UDs were transformed to a logarithmic scale for analyses. Differences among females in various reproductive states were assessed with analysis of variance (ANOVA). Paired *t*-tests were used to compare space use by the same females found under 2 different conditions (with cubs at a den or no cubs at dens). Spearman's rank correlation coefficients were used with female social rank as the independent variable in linear regression analyses. Values are presented as mean $\pm$ *SE*. Differences among groups were considered significant when $P < 0.05$.

RESULTS

General patterns of space use.—The territory of the Talek clan shared its northern border with the edge of the Reserve (Fig. 1A). Seventeen different communal dens were used by the Talek clan during the study period (Fig. 1B), although 3 of these den sites were used 2 or 3 times. Each communal den was occupied for 1.5 ± 0.4 months between den moves. During 9 months in 1996–1998, there was only 1 active communal den site; during the remaining time, there were 2 active communal dens. Most communal dens used by Talek hyenas during the study period were situated in the northwest quadrant of the clan's territory, except from December 1997 to March 1998, when active communal dens were located concurrently in the eastern and western parts of the territory.

In a comparison of home-range estimates using UD and MCP methods, the MCPs for 1 high-ranking female (Fig. 2A) and 1 low-ranking female (Fig. 2B) more closely matched the defended borders and size of the Talek clan's territory than did UDs. However, MCP calculations did not reveal the differences between these individuals that were apparent with UD calculations. Even though all locations falling within 200 m of an active den were excluded from analyses, areas of core use (50% UDs) re-
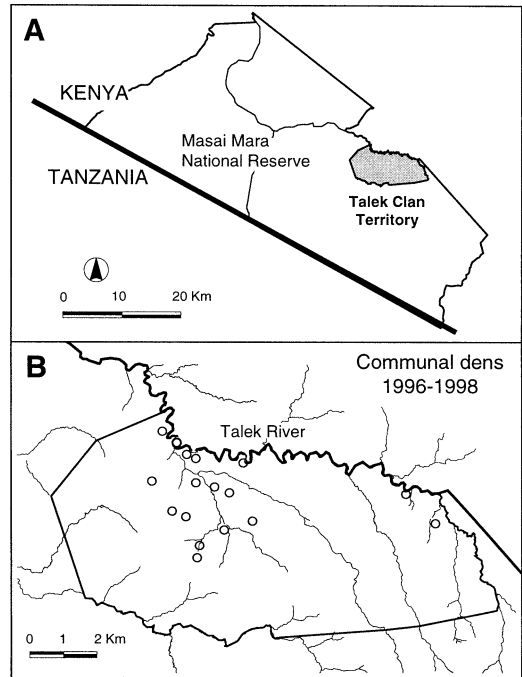
FIG. 1.—A) Location of the territory (in gray) defended by the Talek clan of spotted hyenas within the Masai Mara National Reserve in southwest Kenya. Area of the territory = 62 km². B) Territory of Talek clan, with water courses and locations of the 17 communal den sites used by hyenas during 1996–1998 (3 sites were used more than once each).

flected intensive use by both females of areas near communal den sites. Areas of core use were not always contiguous, and some females had two 50% UDs that were kilometers apart (Fig. 2B). In addition to having 2 areas of core use, the low-ranking female (Fig. 2B) had a 50% UD that was twice as large as the 50% UD of the high-ranking female (Fig. 2A). The size of the 95% UD of the low-ranking female (Fig. 2B) was also larger and extended farther east than that of the high-ranking female (Fig. 2A).

Ten females were radiocollared for at least 17 months during the study, and 3 additional females had radiocollars for 8–9 months. Excluding sightings at the communal den and all sightings made within an hour of a previous sighting of the same fe-
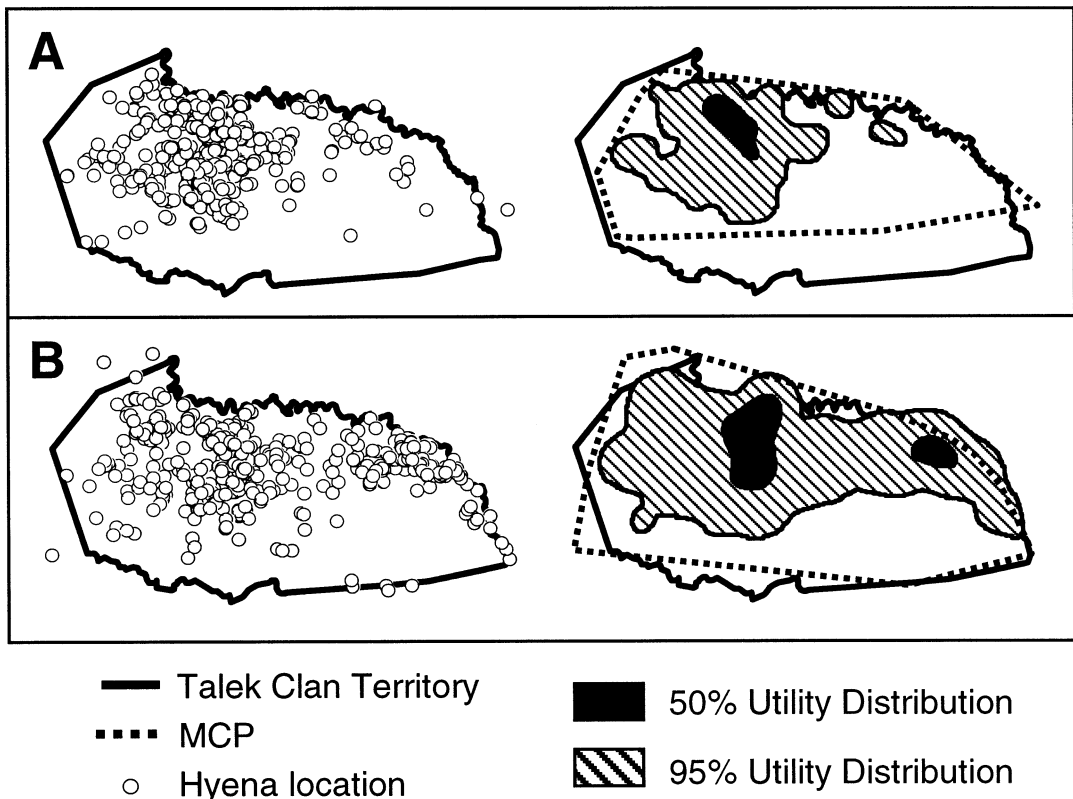
FIG. 2.—All locations of hyenas of the Talek clan, Masai Mara National Reserve, Kenya, and the resulting minimum convex polygons (MCP) and utilization distributions (UDs) for the entire 20-month study period for A) 1 high-ranking female (rank = 5, n = 469 locations) and B) 1 low-ranking female (rank = 20, n = 476 locations). Sizes of MCP and UDs are given in Table 1.

male, a total of 4,838 locations were determined for the 13 females. Most (64 ± 2%) of the locations for each female were established by radiotracking. The size of 95% UDs based on all locations for the 10 females was 30.2 ± 2.2 km^2 (Table 1). On average, 90 ± 2% of each UD fell inside the clan's territorial boundaries (Table 1). On average, only 44 ± 3% of the entire territory was covered by the 95% UD of Talek females (Table 1), and all individual UDs together covered only 69% of the 62 km^2 of the territory. Thus, approximately 30% of the territory was not regularly used by any one of these females during the study period. The 95% UDs overlapped on average 76 ± 2% (Table 1). Percentage of overlap decreased significantly with social rank, with UDs of low-ranking females overlapping least with those of other females (Spearman's rank correlation r_s = −0.80, P = 0.01, n = 10).

Effects of reproductive state, rank, and prey abundance.—Distance to the communal den varied significantly among the 4 reproductive states L1, L2, O, and P (ANOVA: F = 3.40, $d.f.$ = 3, 37, P = 0.03; Fig. 3). Nonlactating females (states O and P) were found significantly farther from the den than were lactating females with den-dwelling cubs (L1, Fig. 3). The difference in distance to the den was not significant between the 2 phases of lactation, although the value for L2 was intermediate between those for the L1 and the 2 nonlactating states. Although cubs of females in L2 no

Table 1.—UD calculations for each individual female over the entire study period of spotted hyenas in southwest Kenya. Numbers in parentheses are results for 3 females collared for only 8–9 months; these were excluded from calculations. All other females ($n = 10$) were collared for at least 17 months.[a]

Social rank	100% MCP (km²)	50% UD (km²)	95% UD (km²)	Percentage of 95% UD inside territory	Percentage of territory covered by 95% UD	Mean % overlap of 95% UD with other females
(2)	(38.7)	(4.4)	(36.9)	(90)	(54)	(66)
5	45.3	1.5	17.1	95	26	87
7	63.6	2.9	25.9	93	39	82
9	62.7	2.3	25.6	96	40	83
11	46.7	3.1	27.3	99	44	82
13	60.5	2.5	36.1	86	51	73
14	89.0	7.1	34.7	89	50	73
15	55.6	6.4	37.9	86	53	66
20	63.5	4.6	37.7	90	55	70
(21)	(28.9)	(5.2)	(31.6)	(95)	(49)	(70)
24	59.2	4.5	34.2	87	48	74
25	76.0	1.9	25.1	82	33	70
(26)	(69.5)	(15.9)	(62.5)	(57)	(58)	(35)
Mean	62.2	4	30.2	90	44	76
SE	4.1	0.6	2.2	2	3	2

[a] MCP, minimum convex polygon; UD, utilization distribution.

longer resided at the communal den, these cubs often remained in the vicinity of the den, gradually increasing their ranging distances. Thus, mothers in state L2 returned relatively frequently to the general vicinity of the den or tended to remain in that area.

Log-transformed UD sizes varied significantly with reproductive state (ANOVA: $F = 21.294$, *d.f.* $= 1, 18$, $P < 0.001$; Fig. 4), with the actual sizes of 95% UDs increasing from 18.6 ± 2.6 km² when females had den-dwelling cubs to 36.4 ± 2.4 km² when females had no cubs at the den. The log-transformed UD sizes also varied significantly between high- and low-ranking females (ANOVA: $F = 5.077$, *d.f.* $= 1, 18$, $P = 0.04$; Fig. 4), with 95% UD size being 23.1 ± 2.5 km² for high-ranking females compared with 31.8 ± 2.5 km² for low-ranking females. Log UD size was not correlated with female social rank when females had den-dwelling cubs ($r_s = 0.15$, $F = 1.35$, $P = 0.28$, $n = 10$). However, when females had no den-dwelling cubs, the log of UD size increased significantly with rank ($r_s = 0.73$, $P = 0.03$, $n = 10$; Fig. 5).

Use of space by low-ranking females was more strongly influenced by reproductive state and prey abundance than was that of high-ranking females (Fig. 6). Even though all locations falling within 200 m of an active den were excluded from all analyses, females with den-dwelling cubs were often found in the general vicinity of the active communal den regardless of rank or prey availability (Fig. 6A). Distance to the communal den during state L1 was unrelated to rank during periods of both prey abundance ($r_s = 0.67$, $P = 0.35$, $n = 10$; Fig. 6A) and prey scarcity ($r_s = 0.15$, $P = 0.89$, $n = 10$; Fig. 6A). Similarly, distance to the nearest territorial edge did not vary with rank or prey availability for females in L1 (prey abundance $r_s = -0.35$, $P = 0.61$, $n = 10$; prey scarcity $r_s = 0.37$, $P = 0.51$, $n = 10$; Fig. 6C). However, both distance measures were correlated with social rank when females had no den-dwelling cubs (states L2, O, or P), and this was true during periods of both prey abundance and prey scarcity (Figs. 6B and 6D). Low-ranking females without den-dwelling cubs were found sig-
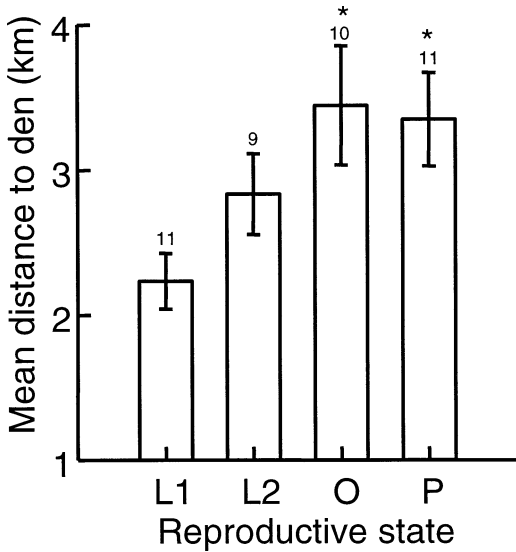
FIG. 3.—Mean distances ± SE to the communal den during each of 4 reproductive states (L1 = lactation with den-dwelling cubs, L2 = lactation with free-roaming cubs, O = other, P = pregnant) for spotted hyena females of the Talek clan, Masai Mara National Reserve, Kenya. Numbers over bars indicate numbers of females monitored in each state. Total numbers of locations represented in each reproductive state were as follows: 1,977 observations for females in state L1; 1,039 for state L2; 1,017 for state O; and 1,145 for state P. Asterisk indicates significant difference from L1 (Tukey's post hoc test).

nificantly farther from the communal den than were high-ranking females when prey were abundant (r_s = 0.64, P < 0.01, n = 12) and also during periods of prey scarcity (r_s = 0.68, P < 0.01, n = 12; Fig. 6B). Low-ranking females without den-dwelling cubs were also found closer to borders than were high-ranking females when prey were abundant (r_s = −0.87, P < 0.01, n = 12; Fig. 6C) as well as during periods of prey scarcity (r_s = −0.83, P < 0.01, n = 12; Fig. 6D). When prey were scarce, low-ranking females were found even farther from the den than they were when prey were abundant (paired t-test, t = 2.68, P = 0.02, n = 12; Fig. 6B), but the relationship between distance to the edge of the territory
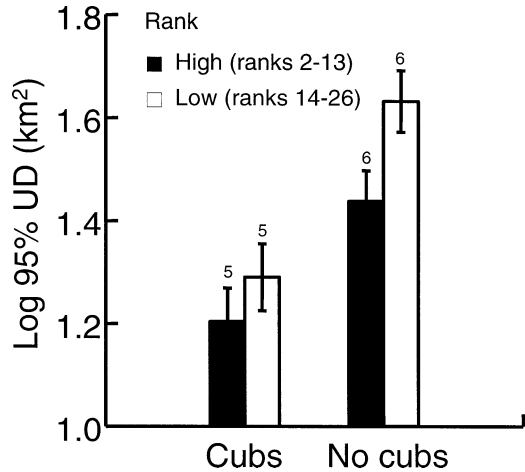
FIG. 4.—Effects of reproductive state and rank on log of 95% fixed-kernel utilization distribution for spotted hyena females of the Talek clan, Masai Mara National Reserve, Kenya. Sample sizes over bars indicate numbers of females.

and social rank did not change with the abundance of prey (paired t-test, t = 0.36, P = 0.72, n = 12; Fig. 6D).

DISCUSSION

Female members of the Talek clan used surprisingly little of their territory on a reg-
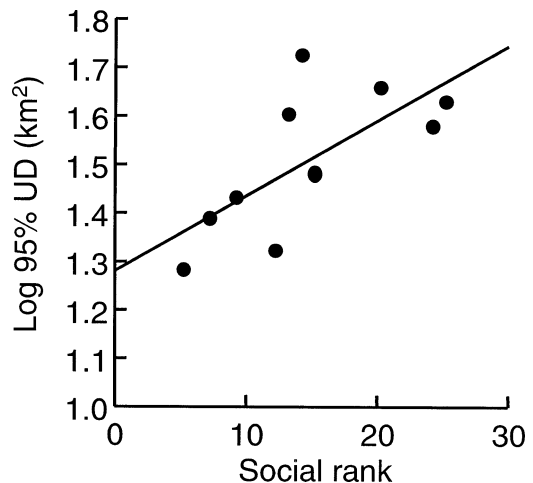
FIG. 5.—Sizes of 95% fixed-kernel utilization distributions in the Talek clan of spotted hyenas in southwest Kenya were correlated with social rank among females having no den-dwelling cubs.
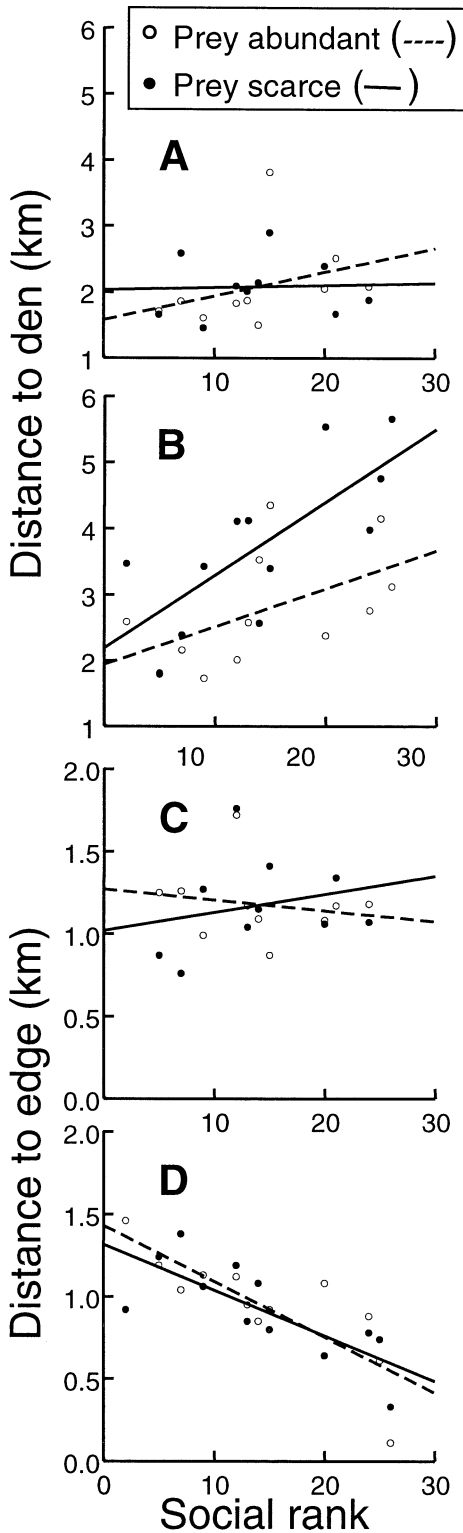
ular basis. Territories defended by mammalian carnivores are usually of the same size as or smaller than home ranges (Ewer 1973; Powell 2000). However, if the 95% UD is used to define a home range, then the territory defended by the entire group was actually larger than individual home ranges measured in the present study or by Henschel and Skinner (1991). Even the overlapping UDs for 10 Talek females covered only 69% of the territory. Maintaining a territory larger than the area regularly used by any 1 individual may be unique to fission–fusion societies in which the economics of territorial defense presumably differ from those proposed for groups that associate tightly (Lowen and Dunbar 1994).

Traditional MCPs more accurately reflected the size and shape of the Talek clan's group territory than did UDs, but only UDs revealed variation in overlap among female home ranges and individual variation with respect to areas within the territory that were most intensively used. The lowest mean percentage of overlap between the UD of any individual female and those of all other monitored females was 66% (Table 1), similar to the minimum 65% overlap that Henschel and Skinner (1987) found between pairs of clan members in Kruger National Park. In the current study, overlap with other females was greater for high-ranking females than for low-ranking females, as could be predicted from patterns of association in hyenas in which animals

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FIG. 6.—Mean distance at which each spotted hyena female was found from the communal den and from the nearest edge of the Talek clan's territory in southwest Kenya. A) Distance to the communal den when females had den-dwelling cubs (state L1). B) Distance to the communal den when females had no den-dwelling cubs (states L2, P, and O). C) Distance to the nearest territorial edge when females had den-dwelling cubs (state L1). D) Distance to the nearest territorial edge when females had no den-dwelling cubs (states L2, P, and O).

of all ranks prefer to associate with higher-ranking females (Holekamp et al. 1997a), except when hunting and feeding (Holekamp et al. 1997b).

The space-use patterns of females of the Talek clan were influenced by female reproductive state, abundance of prey, and social rank. Females with den-dwelling cubs had smaller home ranges than other females and were generally found closer to the communal den. When low-ranking females had no den-dwelling cubs, home-range size and distance to the communal den increased. Low-ranking females without den-dependent cubs ranged most widely, particularly during periods of prey scarcity. When their movements were not constrained by the needs of den-dwelling cubs, low-ranking females may have been using areas farther from the communal den to avoid competition over food with high-ranking females. Space-use patterns of high-ranking females were less strongly affected by reproductive state and prey abundance. High-ranking females were consistently found closer to the communal den, and although the den was sometimes located near the edge of the territory, high-ranking females were more likely to be found deeper inside the territory than were low-ranking females.

The relatively small home ranges of high-ranking females may enable them to conserve energy by traveling less than low-ranking females (Mills 1990). High-ranking females may also benefit from being more centrally located than low-ranking females and from rarely needing to venture outside the territory. Talek females that enter the territories of neighboring clans risk attack from residents if they are detected and recognized as intruders (Boydston et al. 2001). Similarly, Talek females that are absent from the center of the Talek clan's territory for several months may be targets of severe aggression from resident hyenas on return, and they may fall in social rank, as do females that absent themselves from the territory for extended periods (Holekamp et al. 1993). The large UDs of low-ranking fe-

males may reflect a strategy that attempts to balance the costs of competition with higher-ranking females in the vicinity of the communal den against the costs of prolonged absence or a trade-off between better resources in the center of the home range (Frank 1986a) and increased competition for these resources.

Most terrestrial carnivores bear altricial young that reside at a den or creche for some time before offspring travel around the home range. The contraction of home ranges during denning observed in female *C. crocuta* also occurs in other carnivores, including caracals, *Caracal caracal* (Avenant and Nel 1998); wild dogs, *Lycaon pictus* (Burrows 1995; Schaller 1972); cheetahs, *Acinonyx jubatus* (Durant 1998); arctic foxes, *Alopex lagopus* (Landa et al. 1998); and black bears, *Ursus americanus* (Hirsch et al. 1999). However, spotted hyenas maintain a group territory even when individuals contract their ranges. This also may be true for other carnivores living in fission–fusion societies and defending group territories (e.g., lions, *Panthera leo*— Packer et al. 1990). Furthermore, because adult female hyenas participate in group territorial activities regardless of reproductive state (Boydston et al. 2001), the contracted 95% UD does not mean that females with den-dwelling cubs do not venture to the border of the territory.

The point distributions and home-range sizes based on data from females are probably conservative estimates of space-use patterns for spotted hyenas. While dispersing, male hyenas move over larger areas than females and may traverse up to 4–5 clan territories (Smale et al. 1997). Long-distance commuting is not a regular feature of hyena behavior in the Mara as it is in the Serengeti, where hyenas frequently make extended forays away from their group territories to forage in areas of high prey abundance (Hofer and East 1993a, 1993b, 1993c). Where hyenas occur at low population density, or where hyenas exhibit commuting behavior, individual home rang-

es should be much larger than those observed among Talek females.

Vulnerability to "edge effects" is a significant contributor to local extinction of mammalian predators inhabiting protected areas, and sizes of female home ranges can be used to predict the critical size of reserves needed to sustain populations of carnivores (Woodroffe and Ginsberg 1998, 2000). Because large carnivores tend to be wide-ranging, individuals in protected areas may frequently encounter reserve boundaries where they face higher risks of mortality due to human activity (Woodroffe and Ginsberg 1998, 1999). For gregarious carnivores, the viability of the social group may be contingent on variation in ranging behavior among group members. The widest-ranging individuals in a social group are likely to be at the greatest risk of mortality due to interactions with humans. Given the position of the Talek clan's territory at the edge of the Mara Reserve and the movements of females outside the territory on some occasions, all Talek hyenas may be at risk of mortality due to edge effects. In this case, those at greatest risk are likely to be low-ranking females without den-dwelling cubs, particularly during periods when prey are scarce. In the Serengeti, lactating females tend to travel long distances most frequently and as a result may be more likely than other females to be victims of snares (Hofer et al. 1993). Because the widest-ranging individuals are unlikely to be a random subset of a social group, edge effects might increase inbreeding potential and decrease effective population size (Creel 1998; Parker and Waite 1997). A better understanding of individual variation in space-use patterns and the mechanisms by which edge effects can lead to extinction should aid in planning for the protection of wide-ranging carnivores around the world.

ACKNOWLEDGMENTS

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