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Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (*Crocuta crocuta*)

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Abstract

Observational and telemetry data were used in a geographic information system database to document the ontogenetic development of sexually dimorphic patterns of space use among free-living spotted hyenas *Crocuta crocuta* in Kenya. No measures of space use were sexually dimorphic among den-dwelling cubs, nor were sex differences apparent among hyenas that had ceased using dens for shelter until these animals were *c*. 30 months of age. Significant sex differences emerged late in the third year of life, and persisted throughout the remainder of the life span; males were found farther from the geographic centre of the natal territory than were females, and the mean size of individual 95 % utility distributions was larger for males than females. Most dispersal events by radio-collared males were preceded by a series of exploratory excursions outside the natal territory. All collared males dispersed, but no collared females did so. Most dispersing males moved only one or two home ranges away at dispersal, roughly 8–10 km distant from the natal territory, before settling in a new social group.

Key words: dispersal, emigration, sex differences, space use

INTRODUCTION

Natal dispersal, the permanent departure of an individual from its natal area, occurs in most birds and mammals, and tends to be strongly sexually dimorphic (Greenwood, 1980; Dobson, 1982). Among mammals, males are generally either more likely to disperse, more likely to move greater distances during dispersal than their female counterparts, or both (Lidicker, 1975; Greenwood, 1980; Holekamp, 1986; Pusey & Packer, 1987*a*). A dispersing mammal leaves its familiar physical and social environment and moves to a new site that is unfamiliar in both these respects (Waser & Jones, 1983; Smale, Nunes & Holekamp, 1997). Natal dispersal behaviour thus often sets male and female conspecifics onto radically different ontogenetic trajectories (Wiley, 1981). Because dispersal may be preceded by a great deal of exploratory behaviour during earlier ontogeny, and because it often involves travelling substantial distances across unfamiliar terrain, patterns of space use exhibited by young members of the dispersing sex might be expected to differ markedly from those of philopatric individuals (Holekamp, 1984; Fuller *et al.*, 1992; Thomson, Rose & Kok, 1992; Smale, Nunes *et al.*, 1997). However, little is known about the emergence of sex differences in patterns of space use during mammalian development. Our goal here was to document the ontogenetic emergence of sexually dimorphic patterns of space use in the spotted hyena *Crocuta crocuta*, a large mammalian carnivore in which males disperse from the natal site but females generally do not (Henschel & Skinner, 1987; Holekamp & Smale, 1993; Smale, Nunes *et al.*, 1997; East & Hofer, 2001).

METHODS

Subject animals and study population

Spotted hyenas live in large social groups, called clans (Kruuk, 1972), that defend group territories (Kruuk, 1972; Henschel & Skinner, 1991; Boydston, Morelli & Holekamp, 2001). The focus of this study was a single large clan that usually contains 65–75 hyenas, and defends a territory encompassing 61 km^2 (Boydston, Morelli *et al.*, 2001) in the Talek region of the Masai Mara National Reserve, Kenya (1°40′S, 35°50′E), which is an area of open rolling grassland interspersed with seasonal creek beds (Frank, 1986). When estimated as 100 % minimum convex polygons (Hayne, 1949), home ranges of individual female hyenas in the Talek clan approximated to the size and shape of the clan's territory (Boydston,

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Kapheim *et al*., 2003). Here, the term 'territory' is used to refer to the area defended by a hyena clan, and the term 'home range' is used to refer to the area used by 1 individual hyena. The territory of the Talek clan is surrounded by the territories of at least 6 other clans (Boydston, Morelli *et al*., 2001), and is embedded within a larger mosaic of clan territories covering the entire Reserve and environs (Ogutu & Dublin, 1998).

Each Talek hyena was individually identified by its unique spots, and its sex was known based on the dimorphic glans morphology of the erect phallus (Frank, Glickman & Powch, 1990). Social ranks of all clan members were known based on their positions in a matrix of outcomes of dyadic agonistic interactions (Smale, Frank & Holekamp, 1993). The maternal rank of each juvenile was assigned as its mother's position in the female dominance hierarchy. Other maternal kin relationships were also known for all natal Talek clan animals, as described previously (e.g. Holekamp, Ogutu *et al*., 1993; Van Horn, Engh *et al*., 2004).

Crocuta cubs rarely come above ground during the first few weeks of life, which they typically spend in an isolated natal den (Kruuk, 1972; East, Hofer & Turk, 1989; Holekamp & Smale, 1998*a*). After they are transferred to the clan's communal den, however, they emerge frequently from the den hole to socialize, nurse, and explore their environment. The communal den serves as the clan's social centre and provides shelter for cubs (Holekamp & Smale, 1998*a*). Various den sites within the clan's territory may be used as the communal den; usually there is only 1 communal den active at a given time, although sometimes there are 2 (Boydston, 2001). Talek cubs become independent of the communal den at *c*. 8–9 months of age, after which they travel alone, with their mothers, or with small groups of conspecifics. Den-independent cubs visit the communal den, but no longer use it for shelter (Holekamp & Smale, 1998*a*).

Talek females usually give birth to litters of 1 or 2 cubs, and breeding occurs throughout the year. Here cub birth dates were estimated to ± 7 days based on cub pelage, size, and other aspects of appearance when they were first seen above ground. Weaning in the Talek population occurs, on average, when cubs are 13.4 months old, but weaning age ranges from 7 months in the alpha matriline to 21 months among low-ranking females (Holekamp, Smale & Szykman, 1996; Szykman *et al*., 2001). Weaning conflicts and cessation of nursing indicated when cubs were weaned. If a particular mother and cub were found together infrequently, the weaning date for that cub was estimated to ± 10 days as the midway point between the last observed nursing bout and the next sighting of mother and cub together without nursing. Onset of puberty, as indicated by rising plasma androgen levels, occurs between 20 and 24 months of age in male *Crocuta* in both captivity and the wild (Glickman *et al*., 1992; Dloniak *et al*., 2004), and most females first bear young in their fourth year. Therefore males and females here were considered to be reproductively mature adults at 24 and 36 months of age, respectively, and all younger hyenas were considered to be juveniles.

Documentation of ontogenetic change in patterns of space use

Between 1988 and 2003, behavioural and telemetry data were collected daily, mainly from 06:00–09:00 and 17:00–20:00, but observation sessions and radio-tracking were also conducted at other times of the day and at night with the aid of night-vision binoculars. Each observation session involved recording the identity and behaviour of all hyenas found within 200 m of one another, and the duration of observation sessions ranged from 5 min to several h. The geographic location of an observation session was recorded in reference to local landmarks and also as geographic coordinates using a hand-held Magellan global positioning system unit. Date, time, context (den, fresh kill, old ungulate carcass, or other), and the identities and activities of all hyenas present were recorded at the start of every observation session. During each observation session, all aggressive and appeasement behaviours (Kruuk, 1972) were recorded as critical incidents (all-occurrence sampling, Altmann, 1974). Scan sampling (Altmann, 1974) was also conducted throughout all observation sessions at 30 min intervals, and 30-min focal animal surveys (FAS) (Altmann, 1974) were conducted between scans on selected individuals during some observation sessions.

At the communal den

Movements and space use were monitored in both members of 10 mixed-sex twin litters born between 1988 and 1990 while these cubs resided at the clan's communal den. Mixed-sex litters were used to examine effects of cub sex and maternal rank without introducing confounding effects of variation in litter size, different mothers, or environmental variables due to time of year at which cubs were born. Maternal ranks for these 10 pairs ranged from 1 (offspring of the alpha female) to 16 (offspring of a low-ranking female; 22 was the lowest possible maternal rank in the clan).

During all Scan and FAS samples at the communal den, distances at which individuals were observed from the entrance of the den were estimated and recorded in m. Because mean body length of adult Talek hyenas is 98.8 ± 0.7 cm (measured in 58 Talek hyenas immobilized when they were older than 36 months), the bodies of adults could be used as convenient standards for measuring distances at which cubs were found from den entrances by counting the number of adult body lengths between a cub and the den entrance. These distances were recorded for all 20 subject animals starting 1 month after birth until they demonstrated independence from the communal den several months later. The distance of each hyena to the main den entrance was recorded during each scan, and each hyena's average distance to the den during a session was calculated from the scans. During FAS, all movements of the focal subject were recorded in relation to the den, and from this record, a single maximum distance was obtained at which the focal hyena was observed from the den during that FAS. Typically one FAS was conducted per week per cub, and distances observed during these surveys were averaged for each cub for each month of age.

Den independence to 36 months of age

A juvenile hyena was considered independent of the communal den when it was observed in 4 consecutive observation sessions > 200 m from the communal den. The date of each cub's independence from the den was then identified as the first of those 4 observation sessions. Location data from 9 of the 10 twin litters mentioned above (in 1 litter, both cubs died by age 9 months), plus 2 more mixed-sex twin litters born in 1994–95, were analysed from age 9 months until 36 months of age, death, or dispersal, whichever occurred first. Locations of these 22 animals during observation sessions were plotted on 1:50 000 maps of the Talek study area and then digitized in a geographic information system (GIS) database. For each point in space at which each subject was found, its distance (km) was calculated from the current active communal den and also from the geographic centre of the Talek territory using ArcView GIS software. Communal dens were located near the borders of the Talek territory as often as they occurred near its centre (Boydston, 2001), so these measures were not redundant. Only 1 geographic location per animal per morning or evening was included in the dataset. If an animal was found more than once during morning or evening observation h, only the first sighting of that individual was included.

Documentation of space use by adults

To study sex differences in space use in adults, the locations of 10 natal males and 10 females that survived for several years after puberty and that we matched across sex according to their maternal ranks were monitored. Males had maternal ranks ranging from 1 to 18, and were born between 1987 and 1989. Females had maternal ranks ranging from 1 to 19. Nine of these females were born between 1987 and 1992, and one was born in 1995.

These 20 hyenas, all of which were first observed as juveniles, were anaesthetized as adults with Telazol (6.5 mg/kg) administered via a CO_2-powered darting rifle (Telinject Inc.; Saugus, California, U.S.A.), and fitted with VHF radio-collars transmitting in the 150–151 MHz range (Telonics Inc., Mesa, Arizona, U.S.A.). The collared animals were then tracked several times per month throughout the life span of each radio-collar (mean collar life span $= 40 \pm 3$ months), with the aid of antennas mounted atop our vehicles. Dead collars were replaced with fresh ones whenever possible. If an animal was lost for > 2 weeks from the ground, ground tracking was supplemented with aerial tracking from hot-air balloons. Geographic locations based on both opportunistic sightings and radio-tracking were recorded for each of these collared adults of both sexes from 1991 to 2000. The mean distance from the geographic centre of the Talek territory was calculated for each year of age for each collared individual. The fixed kernel utilization distribution (UD) was also calculated for each collared hyena (Worton, 1989; Powell, 2000) with 95 % probability for each year of age in which that individual was relocated at least 30 times.

Monitoring dispersal behaviour

It was possible to document age of dispersal in 44 natal Talek males born between 1985 and 1998, 17 of which wore radio-collars, and 27 of which did not. With 1 exception, radio-collared hyenas were considered to have dispersed when they were repeatedly and exclusively tracked to locations outside the defended boundaries of the Talek clan's territory for a period of at least 6 months. The 1 exception was a male who died in his new area after only being gone from Talek for 3 months. Smale, Nunes *et al*. (1997) used radio-telemetry data to demonstrate that dispersing male hyenas undertake several exploratory forays outside their natal clan's territory before emigrating. Therefore, adult natal males not fitted with radio-collars were considered to have dispersed only if they had engaged in a series of such excursions before their disappearance from the Talek clan, if they were in good health when last seen, and if they were last seen in the Talek territory when they were older than 24 months of age. If these 3 conditions were met, the estimated age of dispersal for an uncollared male was the age at which he was last seen in the Talek territory before his first absence from Talek of at least 6 months. These were considered reasonable criteria because some of these uncollared males were later observed at varying distances from Talek during call-in experiments performed in the mid-1990s (Ogutu & Dublin, 1998, 2002).

It was possible to determine the location of the new clans into which 14 radio-collared Talek hyenas immigrated. A collared hyena was considered to be a resident immigrant in his new clan after dispersal if he remained there at least 6 months (with the 1 exception mentioned in the previous paragraph). The number of territories a dispersing Talek male traversed before settling was calculated based on knowledge of the approximate locations of territorial boundaries of other hyena clans in the reserve acquired from opportunistic observations of clan wars, boundary latrines, use of communal dens (Boydston, Morelli *et al*., 2001; Van Horn, Engh *et al*., 2004), and also from events observed during the call-in experiments mentioned above.

Statistical analyses

Dependent variables included distance to the den or to the centre of the Talek territory, age (months) at dispersal, number of territories moved at dispersal, and area of 95 % UDs for each collared individual during each year of age. UD area data were log-transformed for statistical analysis. Independent variables were sex, age (months or years), and

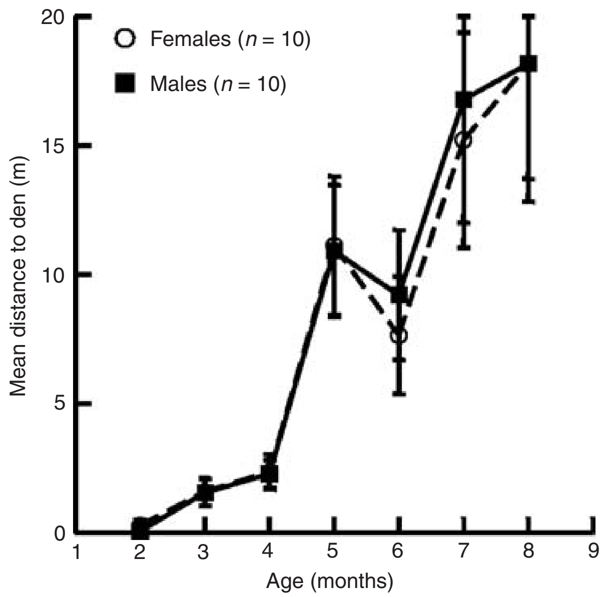

Fig. 1. Mean distance from the communal den at which den-dwelling male (solid lines; solid squares) and female (dashed lines; open circles) *Crocuta crocuta* cubs were observed. Bars, SE of mean distance. Observations: female cubs, 13 ± 4 per month; male cubs 14 ± 5 per month; total observations, 2278.

social rank. In examining effects of age, sex, and rank on spatial measures obtained from individual hyenas, general linear models were used for analysing categorical and continuous independent variables. To compare measures recorded for males and females at particular ages, *t*-tests with Bonferroni corrections for multiple tests were used. Because some individuals were seen more frequently than others, mean distances at which individuals were found each month from either the territory centre or communal den were used in analyses to control for unequal numbers of observations per individual. All statistical analyses were performed using SYSTAT software. Mean values are presented $\pm$ SE.

RESULTS

Patterns of space use before dispersal

In an ANCOVA examining the effects of sex, age (2–8 months), and rank, mean distances at which den-dependent cubs were observed from the communal den during scan samples varied significantly only with age ($F_{1,136} = 70.32$, $P < 0.001$; Fig. 1). There were no significant interaction effects among the independent variables. The maximum distance at which these cubs were observed from the den during focal animal samples also increased significantly with age ($F_{1,124} = 16.11$, $P < 0.001$). There were no sex differences in measures of either mean distance ($F_{1,136} = 0.06$, $P = 0.807$; Fig. 1) or maximum distance from the communal den ($F_{1,124} = 0.05$, $P = 0.823$). Neither mean ($F_{1,136} = 0.07$, $P = 0.786$) nor maximum distance from the communal den ($F_{1,124} = 0.02$, $P = 0.876$) varied significantly with maternal rank.

On average, the 22 cubs from the 11 mixed-sex twin litters gained independence from the communal den at 8.9 ± 0.3 months, and there was no sex difference in the age of independence (paired *t*-test, $t = 0.935$, $P = 0.37$). Locations at which the 22 cubs were found were recorded starting at 9 months of age, which was considered as the age of den independence for this cohort. These litters were first examined for sex differences in space use after den independence by comparing males and females within litters only for the time during which both the male and female cub were alive and present in the Talek clan. For eight of the 11 litters, both the male and female cubs survived for at least 7 months after becoming independent of the den. Distances at which these 16 cubs were found from the communal den until death, dispersal, or 36 months of age revealed no differences between male and female littermates even after they became independent of the communal den (Fig. 2). Littermates continued to show strikingly similar patterns of space use even after weaning (Fig. 2), when the pair ceased sharing the common food source of mother's milk as a possible incentive for remaining in close proximity to one another.

The patterns observed in Fig. 2 suggested that perhaps littermates were more likely than randomly selected cubs to occur together in the same places within the territory of the Talek clan. Therefore, the same 11 litters were next examined for sex differences using all surviving cubs to 36 months of age, regardless of whether or not both littermates survived. When all cubs at all possible ages from these litters were included in the sample, an ANCOVA examining the effects of age and sex on distance to the communal den revealed a significant interaction between age and sex ($F_{1,333} = 2.671$, $P = 0.012$; Fig. 3). Age had a highly significant effect on distance at which animals were found from the clan's communal den ($F_{1,333} = 13.938$, $P < 0.001$; Fig. 3) but sex alone did not ($F_{1,333} = 2.284$, $P = 0.103$; Fig. 3). In an ANCOVA examining the effects of age and sex on distance to the centre of the territory among 22 hyenas up to 36 months of age, age was a significant factor ($F_{1,333} = 4.664$, $P = 0.032$), but sex was not significant ($F_{1,333} = 2.527$, $P = 0.113$). However, the interaction between age and sex was significant ($F_{1,333} = 5.000$, $P = 0.026$).

Post-hoc tests with Bonferroni corrections for multiple comparisons were made on the results from the preceding ANCOVAs to identify the specific ages at which males and females differed with respect to their distances from the communal den and the centre of the territory. There were no significant sex differences in distances from the communal den before animals reached age 30 months, but at ages 30, 32, 33, and 36 months, males were found significantly farther from the communal den than were females. Post-hoc tests also revealed a sex difference in distance from the centre of the territory first at age 32 months and subsequently at ages 33, 34, and 36 months. During the first several months after cubs

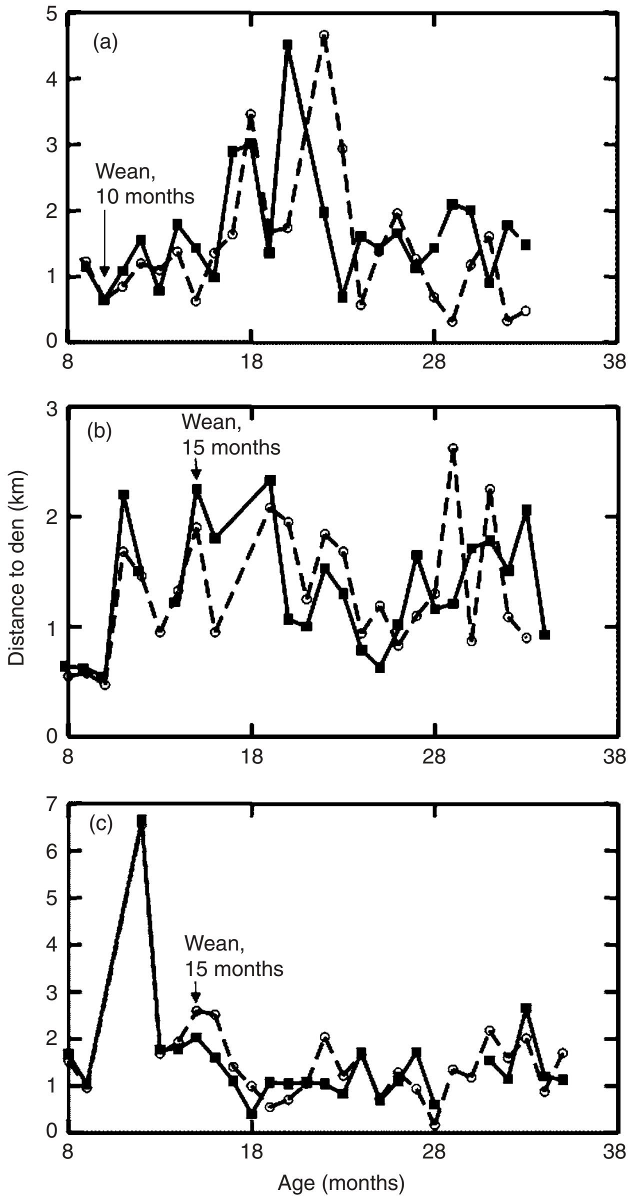

Fig. 2. Mean distances from the Talek communal den at which three pairs of mixed-sex *Crocuta crocuta* littermates were found between gaining independence from the communal den and 36 months of age. Dashed lines with open circles, females; solid lines with filled squares, males; arrows, weaning ages. Maternal ranks of the litters shown here are: (a) 1; (b) 5; (c) 12.

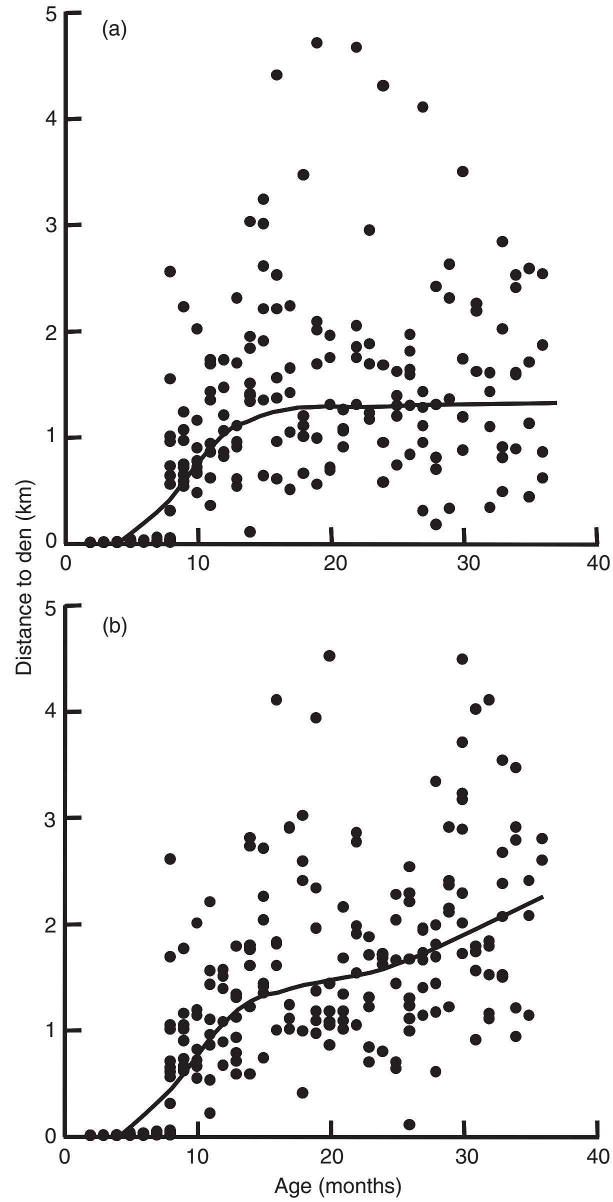

Fig. 3. Mean distances from the Talek communal den at which *Crocuta crocuta* were found between the time they left the communal den and either death, disappearance, or 36 months of age, whichever came first: (a) females ($n = 11$); (b) male ($n = 11$). Each point represents the mean distance based on all observations of one cub during a single month. Lowess curves are smoothed through the data.

became independent of the communal den, males and females did not differ in the distances at which they were found from the den. These data suggest that a sex difference in space use began to emerge around 30 months of age. This difference may have resulted from movements by males toward the periphery of the natal territory (Smale, Nunes *et al.*, 1997), and forays into the territories of neighbouring clans that males often took before permanently leaving Talek (Fig. 4). Interestingly, the patterns of space use among females as measured by their distance to the den seemed to change little after *c.* 16 months (Fig. 3a). By contrast, patterns of male space use continued to change, and distances from the den at which males were found continued to increase with age until they reached 36 months of age, died, or dispersed. For both males and females, individual variation was readily apparent in mean monthly distances to the den after den independence (Fig. 3).

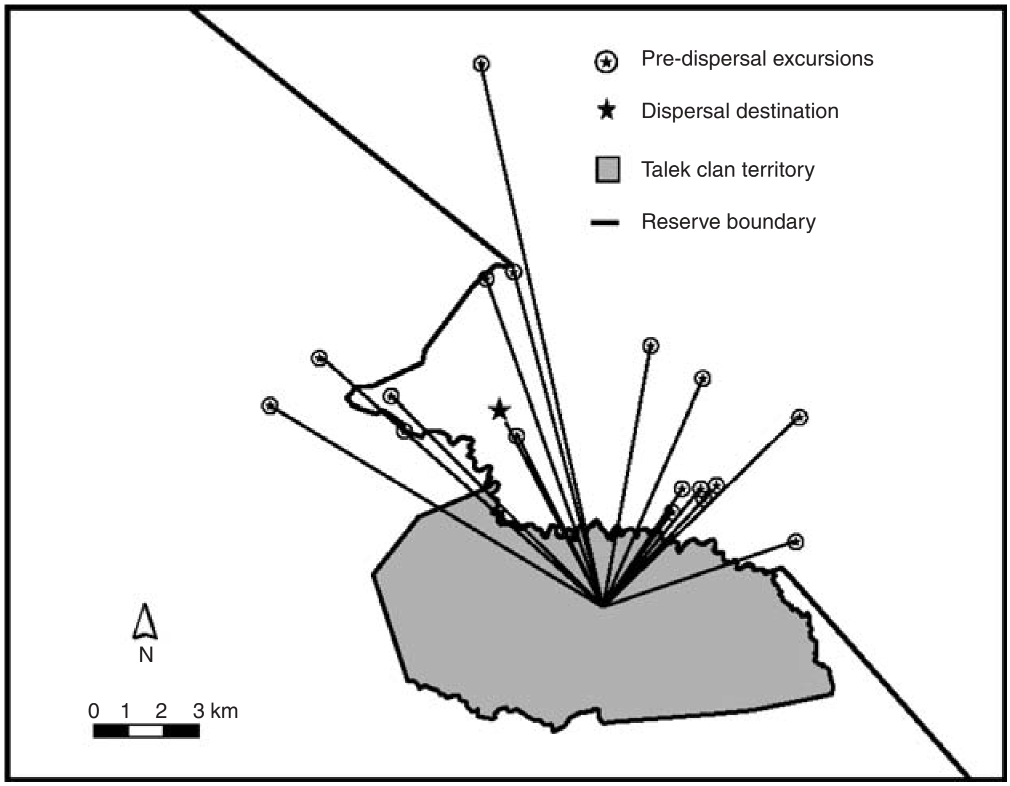

Fig. 4. A typical series of exploratory excursions made by one Talek natal male *Crocuta crocuta* before he dispersed. Circled points, furthest distances from the centre of the Talek clan's territory at which this male was found on 17 exploratory excursions he took before permanently leaving Talek at dispersal (indicated by solid star). He was observed inside the Talek territory between all consecutive sightings outside the Talek territory. Heavy line, northern boundary of the Masai Mara National Reserve, Kenya; shaded area, territory defended by the Talek clan (Boydston, Morelli *et al.*, 2001).

Patterns of space use during and after dispersal

A representative series of pre-dispersal exploratory excursions made by one radio-collared Talek natal male before dispersal is depicted in Fig. 4. This male made 17 forays outside his natal territory before he left permanently. The average maximum distance from the centre of the Talek clan territory on which this male was observed during these forays was 3.9 ± 0.7 km, and the mean duration of these excursions was 17.0 ± 8.2 days. These 17 excursions took the male into the territories of at least four new clans.

All surviving natal Talek males dispersed by 69 months of age (mean age $= 43.2 \pm 1.6$, $n = 44$; Fig. 5). Age at dispersal did not vary significantly with the maternal rank of natal males ($F_{1,42} = 0.067$, $P = 0.433$). After dispersal, collared Talek natal males were found on average 6.8 ± 0.3 km ($n = 14$ males) from the centre of the Talek clan territory whereas before dispersal these same males were found only 2.7 ± 0.2 km from the centre. Thus as expected, natal males were found significantly farther from the centre of the Talek clan territory after than before they dispersed (*t*-test, $t = 11.89$, $P < 0.001$, $n = 14$). Of 14 collared Talek males known to settle for at least 6 months in the territory of a new clan after dispersing, six joined one of the clans defending territories that abutted the Talek clan's territory, and six others dispersed only one territory further (Fig. 6). The maximum number of territories traversed by dispersing Talek males was four. Although collared females occasionally made brief forays into neighbouring territories (also see Boydston, Kapheim *et al.*, 2003), none of them dispersed.

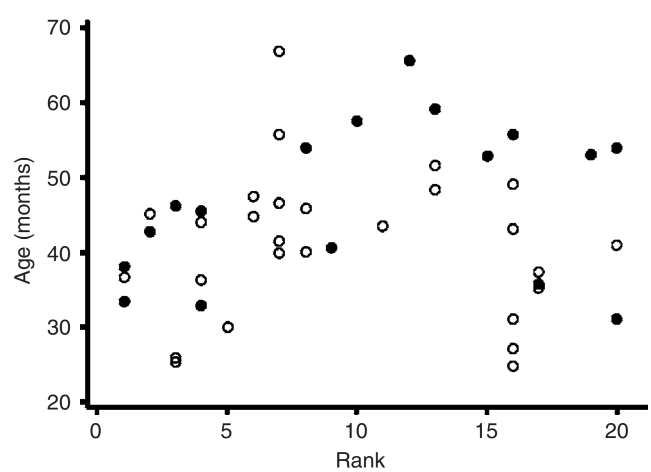

Fig. 5. Age at emigration of each of 44 natal Talek male *Crocuta crocuta*, 17 of which wore radio-collars (filled circles) and 27 of which did not (open circles).

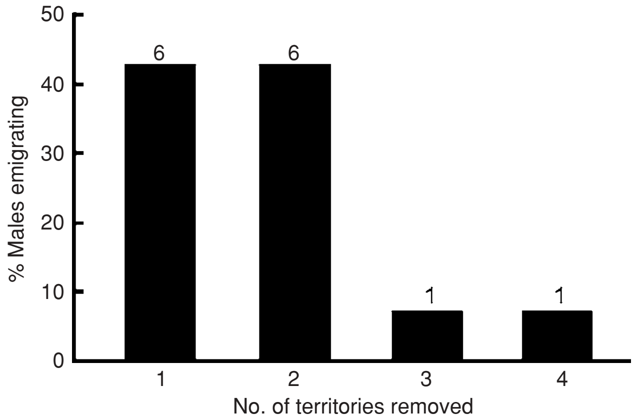

Fig. 6. Number of territories away from Talek moved at dispersal by 14 radio-collared natal male *Crocuta crocuta*. Males removed only one territory settled in territories adjacent to that of the Talek clan.

The sex difference in patterns of space use that emerged in spotted hyenas during their third year of life persisted throughout the remainder of the life span (Fig. 7). The oldest known Talek female lived to 17 years; this female died a few hundred metres from her birthplace. The oldest known Talek natal male lived at least to 14 years; he was last seen 40 km from his birthplace, having engaged in secondary as well as natal dispersal (Van Horn, McElhinney & Holekamp, 2003). In an ANOVA examining the effects of age and sex on mean distance from the centre of the territory each year for hyena ages 1–9 years old (Fig. 7a), age ($F_{8,130} = 8.69$, $P < 0.001$) and sex ($F_{1,130} = 58.44$, $P < 0.001$) were both significant, as was their interaction ($F_{8,130} = 5.44$, $P < 0.001$). Bonferroni-corrected post-hoc tests yielded significant sex differences with respect to distance from the centre of the territory at ages 5 and 6 years. In an ANOVA examining the effects of age and sex on home-range size, age ($F_{8,120} = 21.81$, $P < 0.001$), sex ($F_{1,120} = 23.83$, $P < 0.001$), and their interaction ($F_{8,120} = 2.28$, $P = 0.026$) were also all significant, but Bonferroni-corrected post-hoc tests did not reveal specific ages at which the sizes of male and female home ranges differed. From Fig. 7(a) it is apparent that natal Talek males did not shift their patterns of space use nearer to the Talek clan territory as they aged. Instead, throughout the remainder of the life span, males continued to be found three to four times farther from the centre of the Talek territory than did females. Similarly, starting in the third year of life, male home ranges tended to be larger than those of Talek females (Fig. 7b), although few UD data were available for Talek natal males older than 6 years.

DISCUSSION

As they grow up in their natal clans, young *Crocuta* first experience a spatial world that is very tightly restricted to the immediate vicinity of the current den. Starting in the third month of life, however, the spatial world of each hyena cub expands rapidly as it matures. Distances at which cubs were observed from the communal den increased significantly with age from 2 to 8 months of life. Similarly, distances that coyote pups *Canis latrans* moved from their dens increased linearly with age to 7 months of age (Harrison, Harrison & O'Donoghue, 1991). Movements that took den-dwelling hyena cubs relatively far from the den entrance were generally brief excursions on which they were usually accompanied by their mothers.

As occurs in many gregarious mammals (Greenwood, 1980; Mills, 1990; Smale, Nunes *et al*., 1997), most spotted hyena males, but very few females, disperse from their natal groups (Henschel & Skinner, 1987; Holekamp & Smale, 1998*a*,*b*). Surprisingly, in our study, however, sex differences in patterns of space use did not begin to emerge until late in the third year of life. Although striking early sex differences in some social behaviours are evident in young spotted hyenas living at communal dens (Smale, Frank *et al*., 1993; Holekamp & Smale, 1998*a*), no sex differences were found in the distances at which males and females were observed from the den entrance during the first 8 months of life. Much of a cub's time above ground at the communal den is spent socializing with other clan members (Holekamp & Smale, 1998*a*), and the distribution of conspecifics around the den probably influences the movements of cubs. Distances travelled from the den entrance during this period are also undoubtedly affected by the limited locomotor abilities of cubs and the time needed to escape from potential danger. During the period of den dependence, cubs are quick to flee into the den when frightened (Holekamp & Smale, 1998*a*), so they may generally remain close to the den both because they are still unfamiliar with the larger spatial world, and also for quick access to a safe underground haven. Neither patterns of social interaction nor use of the den for safety, however, would be expected to affect the space use of males and females differently during this period. To the contrary, selection pressures on the space use patterns of male and female cubs while living at the communal den should theoretically be quite similar, and this may explain the similarity in their use of space.

After Talek cubs became independent of the communal den, they began travelling around the clan's territory, initially with their mothers and later with other conspecifics or on their own. A cub's average distance to the den increased 10 times at den independence, but sex differences in patterns of space use did not emerge at this time. Interestingly, sex differences in these patterns did not emerge suddenly at weaning. Although variation among litters in the distances at which littermates were found from the den was observed, males and females within litters exhibited remarkably similar patterns of space use during this phase of development. It seems that our inability to detect any sex difference within matched pairs of siblings before 36 months was because littermates associate more closely than do random pairs of mixed-sex cubs. This most probably occurs because siblings can benefit by assisting each other in vigilance against predators, and in cooperative acquisition and defence of

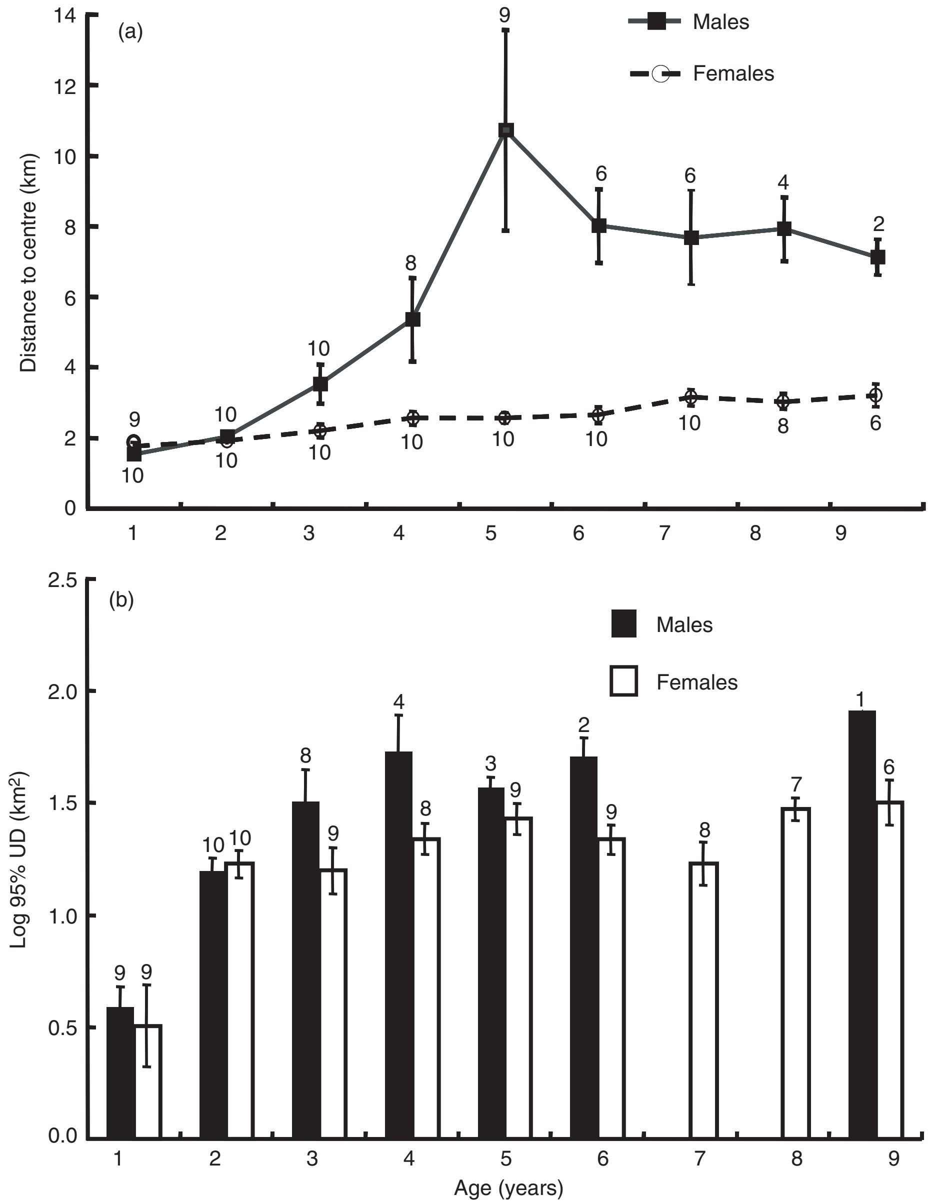

Fig. 7. (a) Mean distance from the geographic centre of the Talek clan territory at which 10 natal *Crocuta crocuta* of each sex were found as a function of age. (b) Log 95 % fixed kernel utilization distribution (UD) for these same animals, all of whom were collared in their third year. Of the original 20 hyenas, only those for which at least 30 locations were available per year are included in each bar.

food (Smale, Holekamp *et al*., 1995; Holekamp, Cooper *et al*., 1997; Wahaj *et al*., 2004) during this challenging period between weaning and the age at which they attain adult hunting proficiency (Holekamp, Smale, Berg *et al*., 1997).

Earlier data documenting periods during which natal animals of each sex were absent from the Talek clan territory (Smale, Nunes *et al*., 1997; Holekamp & Smale, 1998*a*) suggested that a sex difference in space use might emerge among hyenas as young as 24 months. That is, males are absent relatively frequently while females are seldom absent from the natal territory during the third year of life (Smale, Nunes *et al*., 1997). Our current data indicate that the absences of males from the natal area can be accounted for by brief exploratory excursions made by young adults into neighbouring territories. Male *Crocuta* go through puberty at *c*. 2 years of age (Glickman *et al*., 1992). Thus ontogenetic emergence of a sex difference in space use seems to be associated with reproductive maturity of males, and by 36 months of age the sex difference in space use is quite distinct.

Although patterns of space use have been shown to vary among individual adult female *Crocuta* with social rank and reproductive state (Boydston, Kapheim *et al*., 2003), our study shows that the annual average distance at which females were found from the communal den did not change with age once females became independent of the communal den. By contrast, young male hyenas were found at increasingly greater distances from the den, and they typically engaged in a number of exploratory excursions that took them into the territories defended by multiple neighbouring hyena clans. Similar exploratory forays by males have also been documented in red foxes *Vulpes vulpes* (Woollard & Harris, 1990), dwarf mongooses *Helogale parvula* (Rood, 1987), and other carnivores (Waser, 1996). In contrast to male lions inhabiting the Serengeti plains (*Panthera leo*, Pusey & Packer, 1987*b*), however, dispersing male hyenas do not seem to become nomadic after leaving the natal clan. Instead, via a series of exploratory excursions, individual male hyenas seem to assess the potential for successful immigration into surrounding clans without leaving the natal group.

Mean dispersal ages have been reported for several mammalian carnivores (e.g. *Nasua narica*, Gompper, 1997; *Panthera leo*, Funston *et al.*, 2003), including spotted hyenas (Van Horn, McElhinney *et al.*, 2003), but data documenting ontogenetic emergence of sex differences in patterns of space use in these animals are exceedingly rare (Waser, 1996; Funston *et al.*, 2003). By contrast, sex differences in adult home-range size have been well-documented in these animals. Adult home-range sizes vary with sex in most mammalian carnivores, with males using larger areas than females (e.g. Sandell, 1989; Caro, 1994; Stander *et al.*, 1997; Nielsen & Woolf, 2001). Similarly, among Talek hyenas, males occupied larger home ranges than did females, with this sex difference first becoming apparent during the third year of life (Fig. 7b). It is not yet clear why males might need larger home ranges than females in this species. Perhaps the low priority of access to kills available to male hyenas (Kruuk, 1972) forces them into a wider array of habitats while foraging than is required for females. Alternatively, since it is known that a substantial proportion of immigrant males engage in secondary dispersal in this species (Van Horn, McElhinney *et al.*, 2003), males may wander more widely than females in search of new habitat in which competition for access to oestrous females is reduced.

Dispersing Talek males moved far shorter distances than they were physically capable of travelling, and these distances were quite short relative to the long distances that hyenas elsewhere in this ecosystem are known to commute routinely for food. Hofer & East (1993*a*,*b*) found that spotted hyenas residing in the Serengeti National Park, Tanzania, routinely commute an average distance of 40 km from their communal dens to feed on migratory antelope, and that Serengeti hyenas may travel up to 80 km from the den during a single foraging trip. By contrast, dispersing male hyenas from the Talek clan typically settled 8–10 km from the centre of their natal territory, suggesting that travel distance during dispersal is not constrained by physical limitations. Similarly, among male badgers *Meles meles*, wolves *Canis lupus*, coatis *Nasua narica*, and dwarf mongooses *Helogale parvula*, successful dispersers often settle in social groups immediately adjacent to their natal groups (Waser, 1996; Gompper, Gittleman & Wayne, 1998).

All Talek males inevitably dispersed, but East & Hofer (2001) found in their Serengeti *Crocuta* population that four of 128 (3%) natal males never dispersed. This suggests that dispersal opportunities may be more limited for hyenas in the Serengeti than in the Mara. Prey are seasonally very scarce in Serengeti, and mean clan size there is smaller than in our study area (Hofer & East, 1993*a*), so habitat saturation may be more common in Serengeti, and male philopatry occasionally favoured there (e.g. Mumme, 1997).

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