Patterns of den occupation by the spotted hyaena (*Crocuta crocuta*)

Erin E. Boydston[1,*], Karen M. Kapheim[2] and Kay E. Holekamp[2]

[1]*US Geological Survey, Western Ecological Research Center, 160 N Stephanie Street, Henderson, NV 89074, U.S.A. and* [2]*Michigan State University, Department of Zoology, East Lansing, MI 48824-1115, U.S.A.*

Abstract

Spotted hyaenas utilize isolated natal dens (NDs) and communal dens (CDs) for rearing their cubs. Here we describe patterns of natal and CD occupation by hyaenas belonging to one well-studied clan in the Maasai Mara National Reserve during a 10-year period. Locations of 98 den sites that were used as natal or CDs by hyaenas in the study clan were digitized in a Geographic Information System, and the duration of use of each den site, frequency of re-use, and distances involved in den moves were quantified. Hyaenas moved their CD monthly on average. Most CD sites were occupied only once during the study, but several sites were used repeatedly. On rare occasions, the movement of hyaenas to a new den site could be attributed to a disturbance event at the CD, but factors regularly prompting hyaenas to move to new CD sites were unclear. High-ranking female hyaenas were more likely to rear their cubs from birth in a CD than low-ranking females. Low-ranking females almost always utilized isolated NDs for the first few weeks of a litter's development, and low-ranking females transferred their cubs over longer distances than did high-ranking females.

Key words: communal denning, den moves, hyaenas, Serengeti-Mara

Résumé

Des hyènes tachetées se servent des tanières isolées pour donner naissance et des tanières communales pour élever leurs petits. Dans cette étude nous décrivons les configurations d'occupation des tanières natales et communales appartenant à un clan d'hyènes très étudié dans la Réserve Nationale de Maasai Mara pendant une période de 10 ans. Les positions de 98 sites utilisés en tant que tanières natales ou communales par les hyènes dans le clan de l'étude furent numèrisées dans un Système d'Informations Géographiques, et la durée d'utilisation de chaque tanière, la fréquence de réutilisation, et les distances impliquées dans les déplacements entre tanières furent quantifiées. En moyenne, les hyènes se déplacèrent de leur tanière communale tous les mois. La plupart des sites de tanières communales furent occupés qu'une fois pendant la période de l'étude, mais plusieurs sites furent utilisès à de nombreuses reprises. Exceptionnellement, le déplacement pourrait être attribué à une perturbation de la tanière communale, mais les déterminants du déplacement régulier ne furent pas très clairs. Des hyènes femelles de haut rang furent plus susceptibles à élever leurs petits dans une tanière communale à partir de la naissance que les femelles d'un rang plus bas. Les femelles de bas rang se servaient presque toujours d'une tanière natale isolée pendant les premières semaines du développement de leur portée, et transféraient leurs petits sur les plus grandes distances que les femelles de haut rang.

Introduction

In the fission-fusion societies of spotted hyaenas (*Crocuta crocuta* Erxleben), dens serve important protective and social functions (Kruuk, 1972; Mills, 1983; East, Hofer & Turk, 1989; Cooper, 1993; Hofer & East, 1993c; Holekamp & Smale, 1998). The primary protective benefit of dens is that they shelter cubs, who usually spend their first 8–12 months of life at dens. Hyaena den holes have constricted entrances too narrow for adult hyaenas or other large carnivores to enter (Kruuk, 1972; Hofer & East, 1993c), and cubs can escape from approaching predators such as lions (*Panthera leo*) by fleeing underground (East *et al.*, 1989; Holekamp & Smale, 1998). Because many group members regularly visit dens, dens also function

*Correspondence: E-mail: eboydston@usgs.gov

importantly in the social development of cubs. Cubs form relationships with both peers and adults there, and dens also serve as meeting points for adults that otherwise spend much of their time alone (Holekamp, Boydston & Smale, 2000). Dens are common sites for the assembly of subgroups, such as hunting parties and territorial border patrols (Kruuk, 1972).

Cubs of spotted hyaenas, like those of brown (*Parayaena brunnea*) and striped hyaenas (*Hyaena hyaena*), live at dens longer than cubs of other carnivores (Owens & Owens, 1979; Mills, 1990; Wagner, in press). Two types of dens, natal and communal dens (CDs), have been described for spotted hyaenas (Kruuk, 1972; East *et al.*, 1989; Mills, 1990; Holekamp & Smale, 1998). Most *Crocuta* cubs start life at an isolated natal den (ND) used by only one mother for shelter of a litter consisting of one or two cubs (East *et al.*, 1989; Holekamp *et al.*, 1999). Hyaena NDs usually have only one or two underground entrances (East *et al.*, 1989) and are earthen dens originally excavated by aardvarks or warthogs, although hyaenas may modify the dens upon occupation (Kruuk, 1972). Neo-natal cubs spend much of their time inside the den, rarely emerging above ground unless their mothers are present (Kruuk, 1972; East *et al.*, 1989; Holekamp & Smale, 1998). Thus, during the first weeks of life, a cub interacts primarily with its mother and its littermate when one is present.

Within the territory of any hyaena social group, or 'clan' (Kruuk, 1972), there is usually one CD utilized concurrently by several litters ranging up to 15 months of age (Kruuk, 1972; Mills, 1990). CDs often have multiple entrances leading to a network of tunnels (Kruuk, 1972; Mills, 1990), and as with NDs, spotted hyaenas modify existing dens but do not excavate them (Kruuk, 1972). Mothers usually transfer their cubs to the clan's CD 1–5 weeks after birth (Kruuk, 1972; East *et al.*, 1989). With this move from the isolation of the ND, young cubs enter a complex new social environment in which they are exposed to hyaenas of various ages, social ranks, and relatedness. Mothers return often to the den to nurse their dependent offspring, and other adult females, adult males, and subadults also frequently visit the den. At the CD, young cubs begin to learn their social ranks in the clan's linear dominance hierarchy, and older clan members learn the identities and ranks of new cubs born into the clan (Holekamp & Smale, 1993; Smale, Frank & Holekamp, 1993; Holekamp & Smale, 1998; Engh *et al.*, 2000).

The move to the CD appears crucial for a cub's social integration into the clan, but first its mother must safely transfer the cub from the natal to the CD (East *et al.*, 1989; Holekamp *et al.*, 2000). Cubs are vulnerable to above-ground dangers during the move, when mothers shepherd or carefully carry them one at a time (East *et al.*, 1989; Holekamp & Smale, 1998). A shorter distance over which to move cubs between NDs and CDs might therefore be expected to decrease mortality risk during den moves, and females might benefit from using NDs located close to the CD. Because, regardless of their reproductive state, high-ranking females are more likely to occur in the vicinity of the clan's CD than are low-ranking females (Boydston *et al.*, 2003a), high-ranking females might occupy NDs closer to the CD than do low-ranking females.

Our objectives here were to describe patterns of CD use by hyaenas belonging to one well-studied clan during a 10-year period, and to examine locations of NDs relative to those of CDs. We present descriptions of CD locations, and also describe duration of den use, frequency of den re-use, and distances involved in den moves. We consider reasons why hyaenas might initiate CD moves, and specifically we examine the hypothesis that ectoparasite load at dens might prompt hyaenas to vacate dens. We then examine placement of NDs with respect to the CD to determine whether there is rank-related variation in the distances that females move their cubs when transferring them to the CD.

Materials and methods

The study clan, which usually contains 70–80 hyaenas, defends a territory encompassing 61 km^2 (Boydston, Morelli & Holekamp, 2001) in the Talek region of the Maasai Mara National Reserve, in the north-eastern part of the Serengeti-Mara ecosystem. This is an area of open rolling grassland interspersed with seasonal creek beds lined with bushes. Concentrations of resident ungulates graze this area year round, and these are joined for 3 or 4 months each year by large migratory herds of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) from the southern part of the Serengeti.

Each hyaena in the Talek clan was individually identified by its unique spots and other natural marks, and sexed 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 in dyadic agonistic interactions (Smale *et al.*, 1993). Maternal kin relationships were known for all natal Talek animals, as described previously (e.g.

Holekamp *et al.*, 1993). Talek females usually give birth to one or two cubs, and cubs reside at dens until about 8 months of age. Cub birth dates were estimated to ±7 days based on cub pelage, size, and other aspects of appearance when first seen above ground.

Between June 1988 and February 1998, observers monitored Talek hyaenas for 23–31 days per month, except during April 1991 when hyaenas were observed for only 14 days. Starting in 1990, approximately half the adult females in the clan wore radiocollars at any given time, and Talek hyaenas were tracked and observed daily between 05.30 hours and 09.00 hours and between 17.00 hours and 20.00 hours.

Here a single den included all the tunnel entrances that hyaenas were seen using for a continuous period of time within a 100 m diameter. Precise geographic locations of all dens occupied by Talek hyaenas were recorded in reference to landmarks or by latitude and longitude determined with a Magellan Meridian XL Global Positioning System (GPS) unit (Thales Navigation, Santa Clara, CA, USA). From aerial photographs (1:20,000 scale) of the study area, we generated a detailed digitized map of the north-eastern portion of the Maasai Mara National Reserve and geo-referenced this map to our GPS data. On this digital map, we placed locations of all dens.

A CD was identified as a den shared by two or more females for rearing cubs of ages up to 12 months. A CD was said to be 'active' or 'occupied' during the time that litters resided at the site, and a den was considered to be 'inactive' when cubs no longer resided there. We defined a ND as a den other than the active CD that was used by only one or two mothers for rearing neo-natal cubs. A ND used by two mothers was distinguished from a CD by the presence of only neo-natal cubs and by the concurrent use of a CD elsewhere in the territory by the Talek clan hyaenas, from which the ND was isolated. East *et al.* (1989) used the term 'birth den' to describe an isolated ND, but because some Talek cubs were born at CDs, we use the term 'birth den' more generally here to describe any den where a litter was believed to have been born, regardless of whether this den was an isolated ND or the clan's CD.

Litters were included in the study only if they were found at a ND within 30 days of birth or if observers saw them within 2 weeks of birth at the CD. The den where a litter was first observed was assumed to be its birth den. Based on observations of mothers at dens and other locations, and on observations of cubs, we determined the dates on which females moved their cubs in and out of dens. Researchers sometimes observed Talek hyaenas in the process of moving their cubs to a new den site, but most den moves were not directly observed and were known instead from finding hyaena mothers and den-dwelling cubs at a new site, and then verifying that there were no longer any cubs at the previous den. The move date was then recorded as the date half-way between the last sighting of a hyaena mother or her cubs at the old den and the first sighting of the mother or cubs at the new den. However, all dates of den moves were known within ±11 days. Using ArcView GIS (ESRI, Redlands, CA, USA) software, linear distances were measured between all birth dens and the current active CD, and between all consecutive den sites that a female used for rearing her litter until moving it to the CD.

In order to examine ectoparasites in hyaena dens, we collected dirt from the entrances to dens, from July 1997 to January 1998. Samples of 100–200 g dirt were collected when the ground was dry and when adult hyaenas were not present, usually at midday. Dirt was scraped into a clean plastic container from around the mouth of the den up to about a half meter into the den tunnel, and from different entrances if hyaenas were using more than one den entrance concurrently at a particular site. Dirt samples were weighed and sifted for ticks and any other invertebrates visible to the naked eye. Ticks were preserved in ethanol for identification. The number of ticks was recorded and expressed as the number per 100 g of dirt.

Statistics were calculated using SYSTAT 8.0 (Systat Software, Inc., Richmond, CA, USA). The number of ticks in active CDs and inactive CDs were not normally distributed, so we used the Mann–Whitney *U*-test to compare these. To examine variation in the number of ticks in relation to time elapsed since hyaenas had vacated dens, we used the Kruskal–Wallis nonparametric test statistic. Where social rank was the independent variable, we used Spearman's rank correlation coefficient for regression analyses to examine effects of rank on the dependent variables of distance moved and numbers of den moves. In these regression analyses, data for all litters were averaged for each individual in order to control for different numbers of litters produced per female. Mean values are presented ± SE.

Results

Communal dens

Talek hyaenas used a total of 57 different sites for communal denning between 1988 and 1998; some of these

sites were also used as NDs. An additional 41 den sites were used only as NDs and never as CDs. Den sites were distributed throughout most of the Talek clan territory (Fig. 1). Several dens were situated at the edge of the territory, but on average, CD sites were 1.3 ± 0.1 km (n = 57) and ND sites were 1.2 ± 0.1 km (n = 41) from the nearest edge of the territory. Areas where no den sites were located were generally areas of long grass where prey abundance was relatively low (Boydston *et al.*, 2003b). All dens were in earth; no calcrete den sites or caves occur within the Talek clan territory. Most (67%) den sites were situated within 0.25 km of a seasonal creek or river, while only 41% of the clan's territory fell within this distance of a water course.

Twenty-eight (49%) of the 57 different CD sites were used only once during the study period, and 29 of these sites (51%) were used repeatedly for communal denning (Fig. 2a). On average, hyaenas occupied a particular CD site for a continuous period of 31 ± 3 days (n = 132 periods of CD occupation). Twenty-two periods of CD occupation were very short, lasting a week or less before hyaenas moved to another den site. Only four of 132 periods of CD occupation lasted more than 4 months, with the longest period of continuous use of a CD site lasting 8.1 months (Fig. 2b). Den holes persisted for years, and Talek hyaenas reused 29 den sites with varying frequency. The average time elapsed between occupations of the same CD site was 13.4 ± 2.0 months (n = 73). The maximum period from the time that hyaenas vacated a den until they reoccupied that same CD site was 65 months, a den that was occupied in 1992 and next used in 1997. Two dens were used in both the first and last years of the study period, as well as several times in between. Despite the abundance of dens in the study site, only a few dens stood out as particularly popular sites for Talek clan CDs (Fig. 3), and these were occupied several times and for several months.

Den moves

Distances between CDs that were used consecutively were generally short, averaging only 1.5 ± 0.1 km (n = 131 den moves). Ten moves involved relocating 3–5 km from the previous CD. The maximum distance of a den move was 6.2 km, and no other den moves involved distances greater than 5 km. The timing of CD moves varied little from month to month (Fig. 4), with 5–12% of moves (n = 131) occurring in any given month of the year. Den moves occurred during months with and without rain (Fig. 4), and on one occasion during 1988–98 observers determined that a den move was prompted by flooding. Although den moves did not vary significantly with season, the months with the fewest den moves (February to April; Fig. 4) coincided with the

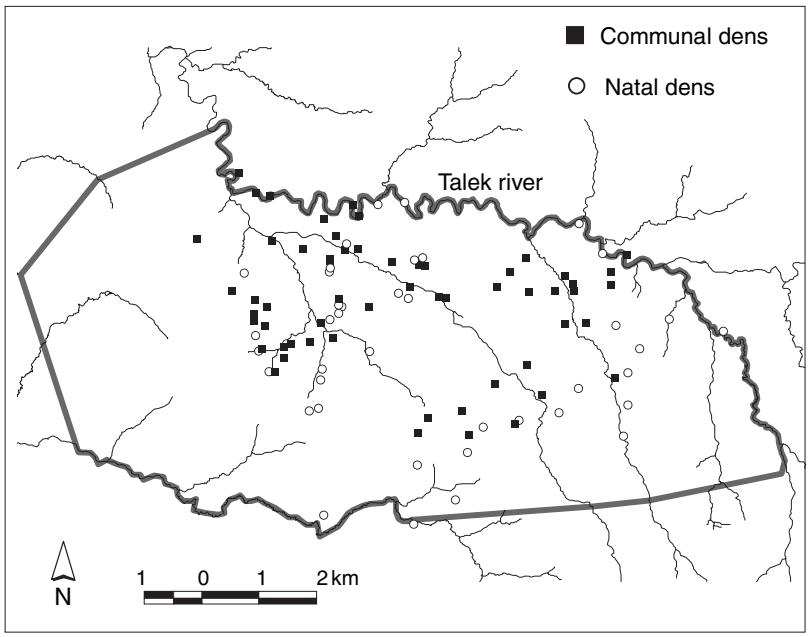

Fig 1 Locations of den sites used by Talek hyaenas as CDs (filled squares, n = 57) or sites used only as NDs (open circles, n = 41). Some CDs were also used as NDs. The bold line indicates the outline of the Talek clan territory.

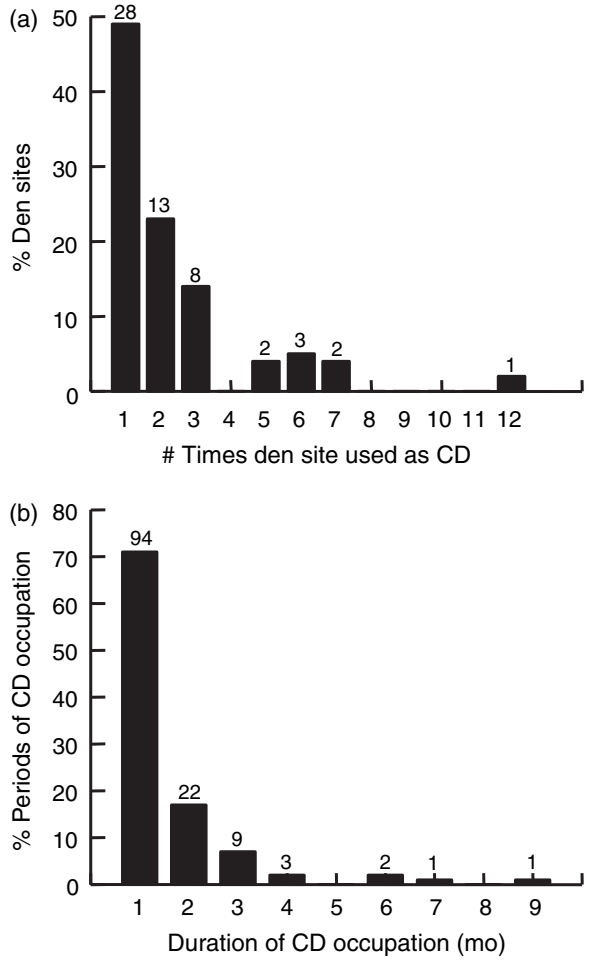

Fig 2 (a) Histogram showing number of times that Talek hyaenas occupied particular den sites as CDs. Sample sizes over bars indicate the number of den sites (n = 57 total den sites). (b) Histogram showing the length of time (month) that a given CD remained active for a continuous period. Sample sizes over bars indicate number of CD occupations (n = 132 periods of CD occupation). The *x*-axis indicates the maximum number of months that a den remained in continuous use. For example, nine sites were used as CDs for 2–3 months each

months during which Talek hyaenas experience an annual trough in the number of births (February to May; Holekamp *et al.*, 1999). Furthermore, November was the month with the most den moves (12%), and November was also the month with the highest mean number of births (Holekamp *et al.*, 1999). Female hyaenas were observed carrying or leading their den-dwelling cubs from one CD to another on fifteen occasions between 1989 and 1995. Some of these den moves occurred over the course of a few days with different groups of females moving their cubs at different times. In 73% of these moves, the highest ranking female with cubs at the den was among the first to move her cubs.

The number of ticks per 100 g of dirt collected from dens varied significantly with the length of time since hyaenas had vacated the dens (Kruskal–Wallis $H = 8.157$, $P = 0.043$, d.f. = 3; Fig. 5). Ticks seldom occurred at active hyaena dens (0.3 ± 0.3 ticks per $(100\ g)^{-1}$ dirt; n = 8; Fig. 5), whereas dens that hyaenas had vacated at least 1 month earlier had significantly more ticks (Mann–Whitney *U*-test = 40.5, $P = 0.013$, d.f. = 1). The average number of ticks found per 100 g soil for all dens formerly occupied by Talek hyaenas was 19.0 ± 8.5 ticks $(100\ g)^{-1}$ (n = 12). Three of the den sites were sampled after the den had been in use as a CD for at least 5 days, and these same dens were sampled again within 3 days of the hyaenas vacating them. Samples from two of those three dens contained no ticks at all, either before or after hyaenas moved out. The third den had no ticks after 11 days of occupation by hyaenas, but a day after hyaenas moved out, there were 16 ticks $(100\ g)^{-1}$. Thus, although in two cases den moves were apparently unrelated to tick density, in one case out of three, there was evidence suggesting that an increase in ectoparasite population density might have contributed to the initiation of a den move. Most ticks found in dens were soft-bodied ticks, *Ornithodorus moubata*, that were up to nearly 1 cm in body length. Ticks that could not be positively identified as *O. moubata* were found in only three samples. These other soft-bodied ticks were <1 mm in body length, were sometimes seen clinging to the ventral side of large *O. moubata*, and may have been larval stages of *O. moubata*. Although hard-bodied ticks are often found on immobilized Talek hyaenas, *O. moubata* have never been found on these hyaenas (K.E. Holekamp, unpubl. data). *Ornithodorus moubata* instead appear to specialize on warthogs as hosts (Walton, 1962). This suggests that infestations of these ticks were unlikely to have caused hyenas to change dens.

We observed fleas in only two of the sampled dens, neither of which was occupied by hyaenas at the time. One of these two dens had only a few fleas, but the other appeared to have hundreds hopping around on the substrate, and this also happened to be the den with the greatest density of ticks of all those sampled (113 ticks $(100\ g)^{-1}$ of dirt). At the time of sampling,

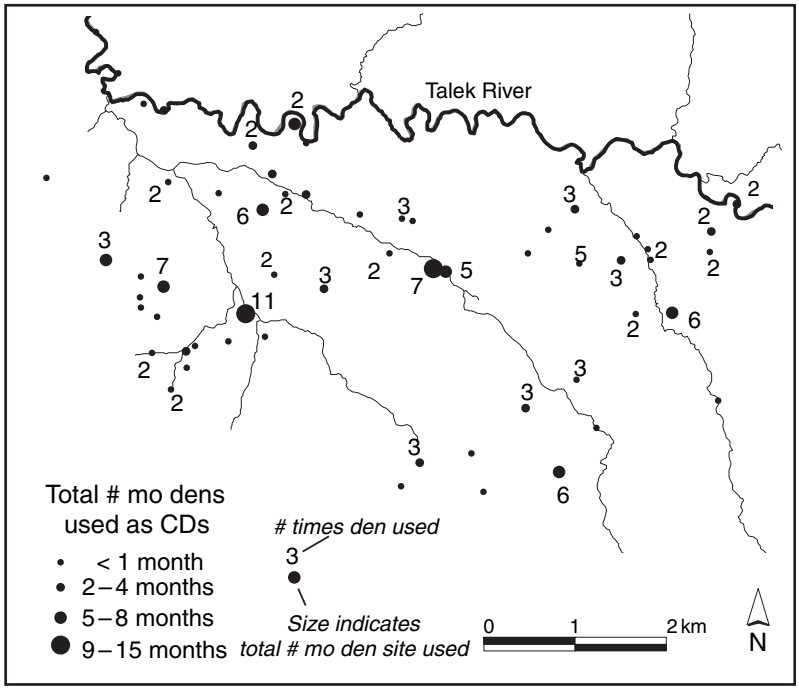

Fig 3 Map of 57 sites that were used for communal denning by Talek hyaenas between 1988 and 1998. The size of each dot reflects the total amount of time that a den was used during the entire study period. Numbers labelling dens indicate the number of times each site was reused as a communal den. Dens without number labels were used only once

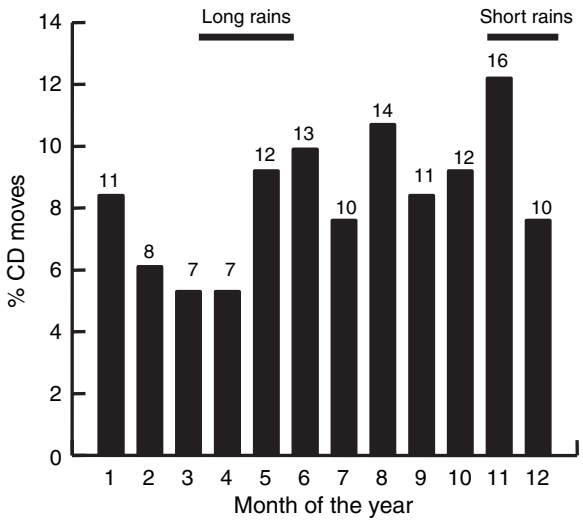

Fig 4 Histogram of the percent of CD moves that Talek hyaenas made during each month of the year (n = 131 moves). Horizontal lines indicate the months of the year when the rainy periods typically occur. Sample sizes over vertical bars indicate the number of moves during that month

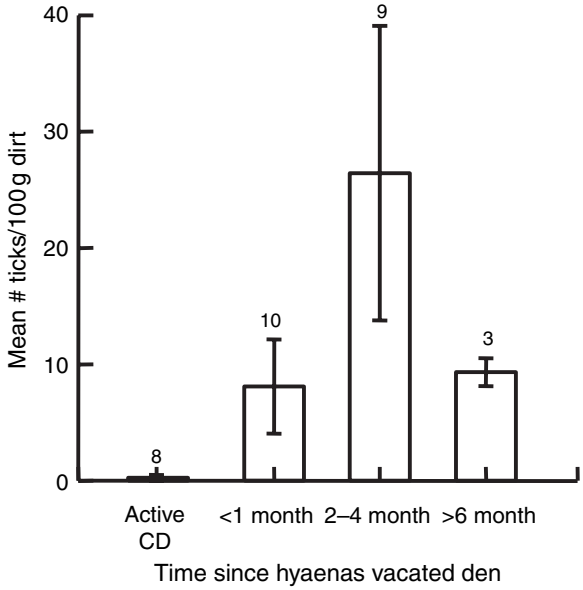

Fig 5 The mean number of ticks (with SE bars) per 100 g of dirt collected from dens varied with the length of time since hyaenas had vacated the dens. Sample sizes indicate number of dirt samples collected for each time period. A total of fourteen different den sites are represented here

some of the inactive hyaena dens were occupied by other animals, including warthogs and banded mongoose. However, some dens that were overgrown with vegetation around the holes and had spider webs across tunnel entrances were probably not in use by any mammals at the time of sampling.

Birth dens

Birth den locations were observed for 79 litters born to 39 different mothers (2.0 ± 0.3 litters per female). Sixteen litters (20%) were reared at the CD from birth, and 63 litters (80%) were born at isolated NDs. Of birth dens found by observers, 41 were used only as NDs and never as CDs during the study period (Fig. 1). There were few known cases of repeated use of ND sites (three of 41) in contrast to the frequent re-use of CDs.

Most NDs (89%) were occupied by only one mother at a time, but among the 63 litters born at NDs, there were three cases of pairs of females sharing NDs for rearing their litters. In one of the cases, the females were known to be sisters, but in the other two cases, the females were unrelated (K.E. Holekamp, unpubl. data).

Including 16 litters born at the CD, mothers selected birth dens that were situated an average of 1.7 ± 0.2 km (n = 39 mothers) from the active CD when cubs were born. This distance was correlated with social rank, and was greater for low-ranking females than for high-ranking females (Spearman's rank correlation $r_s = 0.32$, $P = 0.05$, n = 39). We measured the total cumulative distance that a female moved her cubs, before they arrived at the CD, for 37 of 39 mothers for which this information was available. Females moved their young cubs an average distance of 1.6 ± 0.2 km from birth until arrival at the CD, and the total distances over which mothers moved their cubs were greater for low-ranking than high-ranking females ($r_s = 0.41$, $P = 0.02$, n = 37; Fig. 6).

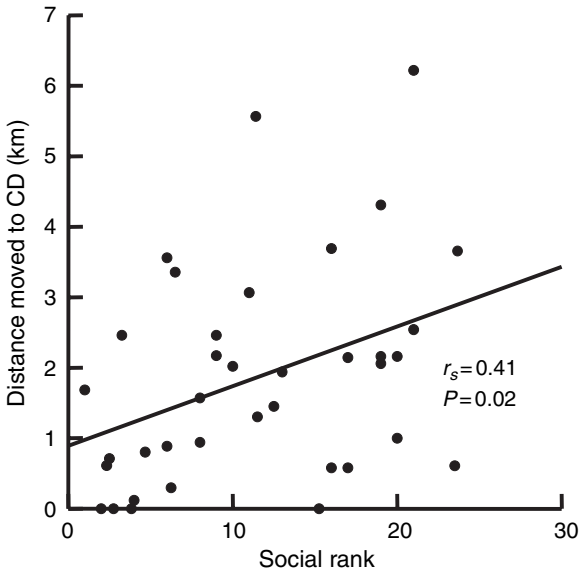

Fig 6 Distances that females moved their cubs from the birth den to the CD, averaged for all litters for each female

Discussion

Talek hyaenas occupied dens throughout much of their defended territory during the study period, although most dens were located near water sources. This was also true in the Kalahari where water is far less abundant than in the Serengeti ecosystem (Mills, 1990). Although there appeared to be an abundance of dens available for Talek hyaenas to use as NDs or CDs, many of which persisted in the environment for long periods of time, hyaenas repeatedly reused only a small subset of available dens. These preferred dens were usually close to other dens that hyaenas did not reuse, and presumably had certain characteristics other than their locations that made them particularly suitable for occupation.

There was great variation in the length of occupation of any given den for communal denning, ranging from a day to several months, and there was no strong seasonal pattern to the timing of CD moves. Spotted hyaenas in the Kalahari moved their CD on average every 45 days (Mills, 1990), and Talek hyaenas moved their CD approximately once a month, only slightly more often than did Kalahari hyaenas. Thus, despite enormous differences between the Serengeti-Mara and Kalahari ecosystems, including the sizes of hyaena clan territories (55–61 km^2 in the Serengeti-Mara, Hofer & East, 1993a; Boydston *et al.*, 2001; 1095 km^2 in the Kalahari, Mills, 1987), Talek hyaenas moved their CD only slightly more often than did Kalahari hyaenas. Talek clan den moves, both between NDs and from natal to CDs, were generally over distances shorter than 2 km. Kruuk (1972) observed seasonal differences in den placement for hyaenas in the Serengeti, and found that CDs in the dry season tended to be concentrated in the direction of migratory wildebeest herds. In the Serengeti, Hofer & East (1993a) documented a CD move of 25 km to an area far outside the clan's territory but close to the concentration of ungulates during that particular wet season. The hyaenas moved back to a den site within their territory after a couple months, when the migratory herds left the area. As seasonal and spatial variation in prey abundance and distribution are much more striking in the Serengeti than in the Mara, Serengeti hyaenas may be able to decrease their commuting distance to hunting grounds (Hofer & East, 1993a,b, 1993c) by

moving their dens closer to prey aggregations (Kruuk, 1972; Hofer & East, 1993a). In the Talek area where resident prey are relatively abundant and tend to concentrate year round in the center of the clan's territory (Boydston *et al.*, 2003b), seasonal movements of dens would be unlikely to increase hyaena foraging efficiency.

In most cases the proximate causes of den moves were unknown. In coyotes, reasons for most den moves were also unclear (Bekoff & Wells, 1982), but human disturbance was implicated in 20% of observed moves of coyote dens (Bekoff & Wells, 1982) and also caused wolves to abandon dens early (Ballard, Whitman & Gardner, 1987). Hyaena den moves sometimes clearly occur in response to disturbance by humans (Mills, 1990), but Talek hyaenas occasionally use den sites on which cattle and local herders can be found several hours each day (K.E. Holekamp, unpubl. data). Thus human activity does not necessarily cause den moves. We once apparently induced a den move by distributing vinegar and cayenne pepper around a den opening, but a second attempt to do this failed. Den moves by Talek hyaenas have apparently occurred in response to disturbances at the den induced by intruding lions or alien hyaenas, and also in response to the death of a cub at the den or flooding of the den. However, these events also occurred on other occasions when they were not immediately followed by den moves (K.E. Holekamp & L. Smale, unpubl. data). A build up of fleas may also cause spotted hyaenas to change dens (Mills, 1990), but data reported here on ticks indicated that ectoparasites do not appear to be an important causal agent involved in the initiation of most den moves by the Talek clan.

Although factors mediating the initiation of den moves remain poorly understood, it appears that higher-ranking females are more likely to lead den moves (present study, Holekamp *et al.*, 2000), and lower-ranking females may then need to move their cubs in order to keep them in contact with their peer cohort and to associate with the higher-ranking females (Holekamp *et al.*, 1997). As den moves often occur over a period of a few days, late-moving females may be moving to keep up with the clan rather than in response to the same factors that prompted the initiating females to move their cubs. Because den moves occurred less often during months with low birth rates and more often in months with higher birth rates (Holekamp *et al.*, 1999), the number of mothers using a den or the cohort size of den-dwelling cubs might be another factor influencing the probability that hyaenas will move their den. In any case, it appears that den moves may often result from decisions made by the highest-ranking female with den-dwelling cubs.

Although only a handful of den sites emerged as 'popular' CD locations for Talek hyaenas, many dens were used for NDs, transit stops, or short-term CDs. Talek hyaenas often made short hops to dens where they kept their cubs for only a few days. This indicates that the choice of new den placement may not be a coordinated decision made prior to moving. Perhaps hyaena mothers assess some aspects of dens after rather than before they move their cubs.

Most cubs were born at NDs that were within 2 km of the CD. Only 20% of litters studied here were reared from birth at the CD, and this percentage probably overestimated the number of litters born at the CD, as not all NDs were found. East *et al.* (1989) found that 30% of 20 litters in the Serengeti were born at the CD instead of isolated NDs, and so the pattern of ND use appears similar in the Mara and the Serengeti. Low-ranking females reared their cubs farther from the CD, moved them more often, and moved them over greater distances before reaching the CD than did high-ranking females. Although we could not associate cub mortality closely enough in time with den moves to examine rank effects of ND moves on cub survival, it may be that moving cubs over greater distances represents one factor contributing to the lower reproductive success of low-ranking females (Frank, Holekamp & Smale, 1995; Holekamp, Smale & Szykman, 1996).

Den moves occur frequently enough that most den-dwelling cubs probably experience many den moves, and virtually no cubs would fail to experience at least one den move before leaving the den altogether. Living at dens appears to be necessary for a cub's appropriate social development and integration into the clan, and den moves thus probably represent one of the costs of sociality in this gregarious carnivore. Living at different dens might help familiarize cubs with their clan's territory, and this potential benefit might compensate for some of the costs associated with changing dens.

An isolated ND may be more critical to the success of rearing cubs for low-ranking females than for high-ranking females (East *et al.*, 1989). Low-ranking females may benefit from reduced competition with conspecifics, or lower aggression, by having NDs that are more isolated at a time when cubs are particularly vulnerable. When their dens are situated farther from the CD, low-ranking females may experience less harassment from conspecifics. Females remain almost constantly at the den when they have

newborn cubs, and may not hunt for the first week after parturition (Henschel & Skinner, 1990). During this period, mothers also appear more reluctant to leave the den in the face of danger than they are at later stages of cub development. High-ranking females can successfully displace lower-ranking mothers from the CD entrance and therefore have unrestricted access to their cubs, which appears critical during the first weeks post-partum. Cubs of low-ranking females may even be temporarily trapped underground when a high-ranking female nurses her cubs in the den entrance and thus blocks the exit of other cubs. Thus the costs and benefits of den-sharing appear to vary with female social rank in this species.

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