ANIMAL BEHAVIOUR, 2008, *76*, 619–636
doi:10.1016/j.anbehav.2008.05.001

Social and ecological determinants of fission–fusion dynamics in the spotted hyaena

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*(Received 25 September 2007; initial acceptance 12 December 2007;
final acceptance 20 February 2008; published online 16 June 2008; MS. number: A10865R)*

Theory predicts that individuals living in fission–fusion societies, in which group members frequently change subgroups, should modify grouping patterns in response to varying social and environmental conditions. Spotted hyaenas, *Crocuta crocuta*, are long-lived carnivores that reside in permanent social groups called clans. Clans are complex, fission–fusion societies in which individual members travel, rest and forage in subgroups that frequently change composition. We studied two clans in Kenya to provide the first detailed description of fission–fusion dynamics in this species. Because social and ecological circumstances can influence the cohesiveness of animal societies, we evaluated the extent to which specific circumstances promote the formation of subgroups of various sizes. We found that cooperative defence of shared resources during interclan competition and protection from lions were cohesive forces that promoted formation of large subgroups. We also tested hypotheses suggesting factors limiting subgroup size. Mothers with small cubs avoided conspecifics, thereby reducing infanticide risk. Victims of aggression either reconciled fights or separated from former opponents to reduce the immediate costs of escalated aggression in the absence of food. As predicted by the ecological constraints hypothesis, hyaenas adjusted their grouping patterns over both short and long time scales in response to feeding competition. *Crocuta* were most gregarious during periods of abundant prey, joined clanmates at ephemeral kills in numbers that correlated with the energetic value of the prey and gained the most energy when foraging alone because cooperative hunting attracted numerous competitors. Overall, our findings indicate that resource limitation constrains grouping in this species.

Keywords: competition; conflict resolution; cooperative hunting; *Crocuta crocuta*; ecological constraints; group living; social rank

Most mammalian carnivores are solitary, spending their lives alone except when breeding (Gittleman 1989). Among the roughly 20% of carnivore species that are at least somewhat gregarious, a few species live in groups that are highly cohesive, such as wild dogs (*Lycaon pictus*) and various species of mongooses. However, like elephants (*Loxodonta* spp.), cetaceans (e.g. bottlenose dolphins, *Tursiops truncatus*) and certain primates, most gregarious carnivores live in groups commonly referred to as fission–fusion (FF) societies. FF societies are stable social units in which individual group members are often found alone or in small subgroups and in which subgroup size and composition change frequently over time. In the FF societies of hamadryas (*Papio hamadryas*), gelada baboons (*Theropithecus gelada*) and elephants, stable subgroups that contain multiple individuals join (fusion) and break away from (fission) other stable subgroups belonging to the larger social unit (Kummer 1971; Wittemyer et al. 2005). By contrast, the FF societies of gregarious carnivores are typically individual-based (Rodseth et al. 1991) such that individual group members are commonly found alone and individually make decisions to join or leave subgroups (Gittleman 1989).

Gregarious carnivores living in FF societies typically know each other as individuals and defend a common territory, but all group members rarely occur together

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0003–3472/08/$34.00/0

concurrently (reviewed by Holekamp et al. 2000). Although group members seldom exhibit signs of distress when separating from groupmates, they typically engage in reunion displays upon subgroup fusion (Holekamp et al. 2000). Terrestrial carnivores that live in societies with these characteristics include lions (*Panthera leo*), coatis (*Nasua* spp.), European badgers (*Meles meles*), dingoes (*Canis lupus dingo*), coyotes (*Canis latrans*), dholes (*Cuon alpinus*), kinkajous (*Potos avus*), brown hyaenas (*Parahyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*).

Spotted hyaenas are long-lived carnivores that reside in permanent social groups, called clans, in which individual members travel, rest and forage in subgroups (Kruuk 1972; Mills 1990) that change membership multiple times per day (Kolowski et al. 2007). Virtually all males permanently disperse from their natal clans after puberty, whereas females are philopatric (Mills 1990; Smale et al. 1997; East & Hofer 2001). Clans contain one to several matrilines of adult females and their offspring, as well as multiple adult immigrant males. Individuals choose to join subgroups containing particular clan members, and they vary in the extent to which they associate with conspecifics (Szykman et al. 2001; Smith et al. 2007). Hyaenas associate most often with kin (Holekamp et al. 1997a; Wahaj et al. 2004). Among nonkin, hyaenas prefer to join subgroups containing potential mates (Szykman et al. 2001) and same-sexed social companions who are higher ranking than, but close in rank to, themselves (Smith et al. 2007). Although up to 80 individuals may belong to a single clan concurrently (Kruuk 1972; Mills 1990; Henschel & Skinner 1991), all clan members are rarely, if ever, found together in one place (Holekamp et al. 2000). Here we provide the first detailed description of FF dynamics in the spotted hyaena. Because social and ecological circumstances can promote or constrain the cohesiveness of animal societies (Chapman 1990; Wrangham et al. 1993; Chapman et al. 1995), we first evaluated the extent to which specific circumstances promote the formation of hyaena subgroups of various sizes and the tendency for individual hyaenas to be found alone or with conspecifics. We then tested three hypotheses suggesting factors limiting subgroup size in this species.

First, the infant safety hypothesis (Otali & Gilchrist 2006) predicts that reproduction is a disruptive force in FF societies in which offspring are vulnerable to infanticide, the direct killing of infants by older conspecifics. Because adult *Crocuta* are known to commit infanticide (Kruuk 1972; East & Hofer 2002; White 2005), we tested two predictions derived from this hypothesis. Mammalian offspring are especially vulnerable to infanticide immediately after parturition (Agrell et al. 1998), so we expected adult females to spend the most time away from other conspecifics during early lactation. We also expected young hyaenas to be found most often with their mothers during early life history stages, in which young are most vulnerable to infanticide.

Second, the dispersive conflict resolution hypothesis (Schino 2000) proposes that costs associated with physical combat, such as energy expenditure and risk of injury or death, limit gregariousness among animals living in FF societies. *Crocuta* frequently direct aggression towards clanmates to establish and maintain rank relationships even in the absence of food (Kruuk 1972; Smale et al. 1993). Because *Crocuta* are well armed with massive teeth and jaws, victims of aggression risk injury resulting from continued or escalated fighting during within-group conflicts (Kruuk 1972). Thus, individuals might reduce the short-term costs of conflict by relying on dispersive mechanisms to avoid or resolve fights. If this is the case, then hyaenas should leave subgroups more often after receiving aggression than when conspecifics direct no aggression towards them. Furthermore, hyaenas sometimes resolve conflicts by engaging in conciliatory behaviours such as greetings and/or nonaggressive approaches (Hofer & East 2000; Wahaj et al. 2001). If reconciliation promotes social cohesion in this species, then targets of aggression should remain in subgroups more often when they reconcile with former opponents than when no reconciliation occurs.

Finally, the ecological constraints hypothesis (Chapman et al. 1995) posits that resource competition, as affected by both short-term and seasonal fluctuations in resource availability, limits subgroup size among animals that otherwise benefit from grouping. This hypothesis explains FF dynamics in a number of nonhuman primates, but should also theoretically be able to explain grouping patterns in a broad range of gregarious taxa, including spotted hyaenas. *Crocuta* benefit from grouping because multiple, often unrelated (Van Horn et al. 2004), clan members cooperate to obtain and defend resources from kleptoparasitism by neighbouring hyaena clans or lions and to protect clanmates from direct killing by lions (Kruuk 1972; Henschel & Skinner 1991; Boydston et al. 2001). Nevertheless, hyaenas compete intensely with groupmates for limited food, comprising mainly ungulate prey they have killed themselves (Kruuk 1972; Tilson & Hamilton 1984; Frank 1986; Engh et al. 2000). Ungulate carcasses represent energy-rich food patches that are both ephemeral and usurpable, and an individual's priority of access to food is determined by its social rank (Tilson & Hamilton 1984; Frank 1986; Engh et al. 2000). If the ecological constraints hypothesis is correct, then given their reduced priority of access to resources, low-ranking hyaenas should spend more time alone than high-ranking hyaenas. We also expected heterogeneity in the foraging environment to influence grouping patterns (Ramos-Fernandez et al. 2006). If feeding competition in particular constrains subgroup size, then hyaenas should congregate at food patches in numbers proportional to the amount of energy contained within patches, and they should spend relatively more time with conspecifics than alone when prey are superabundant. Furthermore, low-ranking hyaenas should be particularly vulnerable to costs associated with feeding in large subgroups. To test this prediction, we replicated earlier work (Frank 1986) by inquiring whether social rank determines feeding success in adult female *Crocuta* and extended it by examining how a female's relative rank within her current subgroup influences her ability to feed. Finally, although energy gain increases with group size in some carnivores living in cohesive societies (e.g. wild dogs; Creel & Creel 1995; Creel 1997), the ecological constraints hypothesis predicts that per capita energy intake and the proportion of time individuals spend feeding should decline with increasing subgroup size among spotted hyaenas.

METHODS

Study Populations

We monitored two large *Crocuta* clans inhabiting the Masai Mara National Reserve, Kenya. From July 1988 through December 2004, we monitored hyaenas in the Talek clan. From August 2002 to March 2004, we also studied the Mara River clan, located 8 km west of Talek, in an area with habitat types and prey abundance that did not differ significantly from those in the Talek area (Kolowski et al. 2007). We identified individuals in both clans by their unique spots. From 1988 to 1999, the Talek clan defended a stable group territory covering an area of 62 km^2 (Boydston et al. 2001). Starting in 2000, the original Talek clan permanently split to form two new clans, Talek East and Talek West, defending adjacent territories of 19 and 28 km^2, respectively (Kolowski et al. 2007). Members of the Mara River clan defended a territory of 31 km^2. Subjects in the current study were members of the original Talek, the Talek West and the Mara River clans.

Resident ungulates grazing year round in the study areas include Thomson's gazelle (*Gazella thomsonii*, average body mass 25 kg), impala (*Aepyceros melampus*, 53 kg) and topi (*Damaliscus korrigum*, 119 kg). Large migratory herds of wildebeest (*Connochaetes taurinus*, 132 kg) and zebra (*Equus burchelli*, 235 kg) join resident ungulates annually between June and September; the superabundance of prey during these months relaxes feeding competition among hyaenas (Holekamp et al. 1993, 1996). The *Crocuta* in our study areas hunt all of these species and occasionally also scavenge carcasses of adult giraffe (*Giraffa camelopardalis*, 935 kg) and elephants (3550 kg). Mean masses reported here are from Kingdon (1997) and Oindo (2002).

Here we estimated (to ±7 days) the ages of cubs upon first observing them above ground (Holekamp et al. 1996). We sexed hyaenas based on the morphology of the erect phallus (Frank et al. 1990). Adult females bear young in isolated natal dens and transfer them to a communal den when the cubs are 2 to 5 weeks of age (Kruuk 1972; East et al. 1989). There is no allonursing or communal care of young in this species (Mills 1985). We considered cubs to be independent of dens when we found them more than 200 m from the current communal den on at least four consecutive occasions; this occurred when cubs were around 9 months of age (Boydston et al. 2005). On average, den-independent cubs nurse from their mothers until they are 14 months of age (Holekamp et al. 1996). Here we assigned weaning dates (to ±10 days) based on observed weaning conflicts and the cessation of nursing (Holekamp et al. 1996). We considered natal animals older than 24 months to be reproductively mature adults (Glickman et al. 1992).

We ranked adults in a linear dominance hierarchy, based on outcomes of dyadic agonistic interactions (Holekamp & Smale 1993; Smale et al. 1993). All adult female spotted hyaenas breed, but high-ranking females enjoy greater reproductive success than do low-ranking females (Frank et al. 1995; Holekamp et al. 1996; Hofer & East 2003). All adult females are dominant to all immigrant males. Here we ranked immigrant males and adult females in separate hierarchies, with 1 being the highest possible rank in each. We assigned relative ranks to adult females at each kill based on their positions within the dominance hierarchy relative to those of the other females present at that kill.

Behavioural Data Collection

We used two general methods to collect behavioural data: long-term focal animal 'follows' and short-term observation 'sessions'. From 2002 to 2004, we conducted focal follows on 19 adults (11 females, 8 males) fitted with radiocollars (Telonics, Inc., Mesa, Arizona). Focal animals were members of either the Talek West clan ($N = 9$) or the Mara River clan ($N = 10$). Focal animals spanned a wide range of social ranks. Follows were focal animal samples (Altmann 1974) with continuous recording of behaviour, lasting from 2 to 15 h. Using methods described by Kolowski et al. (2007), we conducted follows at all times of day and night with the aid of night-vision binoculars and infrared spotlights. In addition to continuous monitoring of behaviour, every 10 min we recorded the total number of hyaenas present in the subgroup of the focal hyaena. We recorded the identity of every hyaena in the subgroup whenever possible. Subgroups comprised one or more hyaenas separated from other hyaenas by at least 200 m. The 19 hyaenas followed were in view of observers, on average, for 98 ± 0.56% of follow minutes ($N = 100$ follow segments). We terminated a follow when the focal animal remained out of sight for more than 30 min.

We were unable to follow hyaenas for complete 24-h periods due to constraints imposed by terrain and vegetation. Instead, we documented the 24-h pattern of social activity for each individual hyaena by observing it during shorter follow segments that together generated a composite 24-h cycle. We attempted to complete this cycle as quickly as possible after its onset, with the average time necessary for completion being 31 days. All analyses below requiring equal sampling throughout the 24-h period use only data from composite 24-h cycles. However, other analyses use all recorded follow segments, 21% of which did not contribute to a composite 24-h cycle (e.g. due to hyaena death or collar failure before cycle completion). In all analyses based on follows, the sampling unit was the individual hyaena. Averaged estimates represent any individual observed during more than one composite follow. Because females with den-dwelling cubs spend much of their time at the communal den (Holekamp et al. 1996), where subgroup size is often large, we followed only females without den-dwelling cubs to allow for appropriate comparisons between the sexes.

Fluidity is a measure of how often subgroup composition changes over time (Kummer 1971). To describe the size and fluidity of subgroups here, we averaged subgroup size, subgroup duration and minimum number of changes in subgroup size during each composite follow across all focal animals. In addition, we calculated the mean number of different clan members encountered per hour and the total numbers of clan members encountered by focal animals during follow segments conducted between 1800 and 0900 hours. We used individual follow segments for these calculations because accurate estimation of these two variables required the use of continuous monitoring. We focused exclusively on the 1800–0900 hour period here because Mara hyaenas spend most of their daylight hours lying in cool, shaded spots and move very little (Kolowski et al. 2007).

Our second method of data collection was based on short-term observation sessions involving members of the Talek and Talek West clans. We collected these data daily around dawn and dusk, between 0530 and 0900 hours and between 1700 and 2000 hours, respectively, throughout our 16-year study. We initiated a session each time we encountered one or more hyaenas separated from others by at least 200 m. Sessions ranged in duration from 5 min to several hours and ended when we left an individual or subgroup. Every 15–20 min throughout each session, we conducted a scan in which we recorded the identity and activity of every hyaena present. We also recorded the geographic location, relative to known landmarks, at which subgroups were found, subgroup size (total number of hyaenas observed in the session), the primary activity in which hyaenas present were engaged, and whether food, alien hyaenas or lions were also present. In 2003 and 2004, we recorded subgroup locations using GPS units. From GPS data, we calculated distances between successive observation sessions occurring within the same morning or evening sampling period to estimate distances among subgroups in our study area.

Tendency to Be Alone

Based on session data, we evaluated how the tendency to be alone varied across the life span by calculating the percentage of sessions in which natal males and females were found alone during each of the following life history stages: (1) natal den; (2) communal den; (3) den-independent but still nursing; (4) weaned but prereproductive; (5) reproductively mature adult. To calculate the percentage of observations alone, we divided the number of sessions in which an individual was found alone by the total number of sessions in which we observed that individual during a particular life history stage, and then multiplied by 100. We used this same method to calculate the percentage of sessions in which we found immigrant males alone. We also assessed the relationship between an adult's intrasexual social rank and its tendency to be alone. For reasons detailed elsewhere (Holekamp et al. 1997a; Smith et al. 2007), we calculated an overall mean proportion of observations alone for each intrasexual rank position by summing proportions across all individuals holding that rank during the study and divided this value by the total number of individuals holding that rank position. We limited analyses based on rank to years (July 1988 to July 1989, 1991 to 1999, and 2002 to 2004) in which rank relationships were known to be stable.

Social and Ecological Influences on Subgroup Size

We assigned each session to one of nine behavioural contexts (Table 1) to evaluate the extent to which specific circumstances influence subgroup size and the tendency for individuals to be found alone or with conspecifics. To compare conflicts with lions or alien hyaenas to situations in which lions or aliens were present but no conflict occurred, we also assigned sessions in which lions and aliens were present, but no between-group fighting occurred, to their own 'nonconflict' contexts. Conflicts occurred if we observed at least one agonistic interaction between our study animals and lions or alien hyaenas. We assigned conflict sessions occurring at kills only to the conflict context. The 'other' category (Table 1) provided a 'baseline'

Table 1. Behavioural contexts

Behavioural context	Social and ecological circumstance
Hunting	One or more resident hyaenas chased a selected prey animal for at least 50 m, regardless of the outcome of the hunting attempt[1,2]*
Natal den	One or more resident hyaenas observed at an isolated den used by only one mother for shelter of a single litter until her cubs reached 2 to 5 weeks of age; no food present[1,3,4]*
Kill	One or more resident hyaenas observed feeding on at least one fresh ungulate carcass[1,2,3]; no hunting observed*
Courtship/ mating	Immigrant male(s) engaged in mating tactics such as shadowing, defending, harassing or mounting a sexually mature female[1,5,6]; no food present*
Communal den	One or more resident hyaenas observed at a den or den complex used concurrently by several litters ranging up to 12 months of age[1,3,7,8]; no food present*
Border patrol	Resident hyaenas engaged in high rates of scent-marking and socially facilitated defecation along territory boundaries[1,9]; no food present*
Clan war	Agonistic interactions observed between resident and alien hyaenas at territory boundaries[1,9,10]; no lions present
Conflict with lion(s)	Agonistic interactions observed between resident hyaenas and at least one lion[1,11,12], regardless of location or other activity
Other	One or more resident hyaena(s) travelling or resting when no food present; none of the contexts above applied*

Each session was assigned to one of the behavioural contexts.
(1) Kruuk (1972); (2) Holekamp et al. (1997b); (3) Mills (1990); (4) East et al. (1989); (5) East et al. (2003); (6) Szykman et al. (2007); (7) White (2007); (8) Boydston et al. (2005); (9) Boydston et al. (2001); (10) East & Hofer (1991); (11) Cooper (1991); (12) Höner et al. (2005).
*Context assigned only when both lions and alien hyaenas were absent.

measure of social activity for *Crocuta* because neither resources (e.g. food or mates) nor threats (e.g. natural enemies or competitors) that might attract or repel conspecifics were present during these sessions. We considered subgroup sizes that differed from baseline to represent the formation of smaller or larger subgroups. To ensure consistency in data collection across years, we limited our analyses to sessions in which hyaenas were located without the aid of radio telemetry because radiocollars were not used in Talek until 1991.

Tests of Hypotheses Suggesting Forces Limiting Subgroup Size

Infant safety hypothesis

We compared the tendency for adult females to be alone, or with only their dependent offspring, across reproductive states; we considered offspring to be dependent until they were weaned. We divided the lactation interval into two parts: the first 2 weeks of lactation ('early lactation') and the remainder of the lactation interval ('late lactation'). We then assigned each female in each session to one of the following reproductive states: the first, second, or third trimester of pregnancy; early lactation; or late lactation. We divided the total number of sessions during which a female in a particular reproductive state was found alone, or with only her dependent offspring, by the total number of sessions in which we observed that adult female in that reproductive state, and multiplied by 100. Next, we evaluated the relative impacts of reproductive state and prey abundance on the tendency for adult females to be alone or with only their dependent offspring. Focusing here on the subset of females observed at three or more observation sessions across all five reproductive states, we compared female behaviour between months when migratory prey were present and absent. Finally, focusing on offspring, we evaluated how the tendency to be with one's mother varied across the life span by calculating the percentage of sessions each hyaena spent with its mother during each life history stage.

Dispersive conflict resolution hypothesis

From 1988 to 2001, we conducted 30-min focal animal 'surveys' on natal animals of both sexes that were no longer living at dens to evaluate the effect of within-group conflict on subgroup cohesion. During surveys in which the focal animal was the target of at least one dyadic aggression (e.g. lunge, snap, bite, chase, displace, push, stand over and intentional movement to bite), we recorded whether focal animals engaged in conciliatory behaviours in response to aggression within 15 min after each fight. We ended all surveys when the focal animal moved at least 200 m away from its subgroup or 15 min passed after the fight started, whichever occurred first. We then compared the tendency for a focal animal to leave its subgroup between surveys in which it received aggression (but did not reconcile) and surveys in which that same animal received no aggression. We also compared the tendency for a victim of aggression to remain within its current subgroup between surveys in which it initiated a conciliatory interaction with a former opponent and surveys in which it failed to reconcile its fights with that same opponent. We required that sessions containing matched surveys occur within 45 days of one another, that they contain similar numbers (±4) of individuals and that either both occur at kills or both occur away from kills. Due to small sample size, surveys assigned to other behavioural contexts were excluded (Table 1).

Ecological constraints hypothesis

We estimated local abundance of prey and assessed the extent to which this influenced the tendency for hyaenas to be with conspecifics (versus alone) and to hunt with particular numbers of conspecifics. To do this, we performed biweekly counts between 0800 and 1000 hours of all prey animals found within 100 m of two 4-km transect lines in different parts of the Talek area and averaged biweekly counts to determine mean monthly prey counts. We also inquired whether the mass of the ungulate carcass available in each kill session predicted the numbers of hyaenas present. Here we focused only on sessions in which the prey species was known or in which only 'scraps' (e.g. scattered bones, horns and/or small pieces of skin) were present that contained little nutritional or energetic value. We used mean mass values for each prey species (Kingdon 1997; Oindo 2002) to estimate food amounts available at kill sessions. Following Henschel & Tilson (1988), we assumed scraps weighed 2 kg.

Because hunting success is significantly higher when hyaenas hunt in groups than when they hunt alone (Holekamp et al. 1997b), we also asked whether hunting and feeding subgroup sizes were related. We did this to evaluate the relative costs and benefits associated with feeding or hunting with conspecifics. The addition of a second hunter increases hunting success by 19%, but the addition of subsequent hunters does not significantly increase hunting success further (Holekamp et al. 1997b). Therefore, we compared numbers of new arrivals and total competitors present 5, 10 and 15 min after solo hunters or pairs of hunters successfully captured prey. To control for effects of prey size, we limited this analysis to matched sessions in which solo hunters and pairs of hunters acquired ungulates of similar size. Lone hyaenas regularly kill antelope as large as wildebeest or topi in this population (Holekamp et al. 1997b).

We inquired about the effects of intraspecific competition on feeding success using two types of data from adult females. We first assessed how per capita energy gain varied among females as a function of subgroup size. We also asked how the proportion of scans in which females fed varied as function of subgroup size and social rank. Using methods developed by Creel & Creel (2002), we determined the energetic value of each prey animal consumed by each hyaena subgroup of known size based on the species, sex and age class of that prey animal. Here we used only sessions in which the amount of food (e.g. proportions of flesh, viscera and skin) consumed by known individuals was visually quantifiable. We considered amounts to be quantifiable only when our field notes indicated exact changes in the amount of food (e.g. forelimbs, hindlimbs, pelvis, lumbar spine, ribcage, neck and head) consumed over time. These amounts corresponded directly to published data on the masses of East African prey (Sachs 1967; Blumenschine & Caro 1986). We subtracted the amount of edible biomass present at the end of the session or when no meat remained on the carcass, whichever occurred first, from that present when the food was first acquired or when the session began if we arrived on the scene after the prey animal had been captured.

We standardized subgroups containing hyaenas of various ages by calculating rates of energy gain by juveniles relative to those of adult females, as has been done for other carnivores (Packer et al. 1990; Mills & Biggs 1993; Baird & Dill 1996). Frank (1986) found that cubs less than 5 months of age and immigrant males rarely feed at kills with adult females. Therefore, we ignored food intake by animals in the former two categories in our calculations. We assumed that individuals 6 to 24 months of age consumed only half as much food mass per unit time as did adult females (Frank 1986). When changes in feeding subgroup sizes occurred, we calculated a weighted average of the number of adults present as {$\sum$ (no. of minutes each subgroup size lasted) × [(no. of adult females in each subgroup) + (0.5 × no. of subadults present in each subgroup)]}/(no. of minutes each session lasted). We calculated per capita energy intake per minute by dividing the number of kilojoules the entire subgroup consumed by the number of adult females present and the number of minutes in which feeding was observed. Kolowski et al. (2007) found that adult females in the Masai Mara spend, on average, 9.2 min feeding at fresh kills during each 24-h period. Therefore, we multiplied energy intake per minute for each session by 9.2 min to convert to daily rates, allowing for comparison with values reported elsewhere.

Within each scan made at each kill session, we quantified the proportion of the adult females present that were actually feeding from the carcass and asked whether this proportion varied as a function of the number of adult females present. In each kill session between 1988 and 1999 at which neither alien hyaenas nor lions were present, we averaged the proportion of adult females feeding over all scans within each session and multiplied this value by 100. Because food is unequally divided among adult females (Frank 1986), we also assessed how the proportion of time adult females fed at kills varied with their absolute social rank within the clan and with their relative rank within their current subgroups. This was based on the number of scans in which each adult female fed at kills, divided by the number of scans in which that female was present at kills while she held a particular rank position, and then multiplied by 100. Here again, we used values averaged over all individuals that held each particular rank position.

Statistical Analyses

We employed nonparametric statistics throughout most of this study due to low sample sizes, the inability to transform nonnormally distributed data or both. We used the Mann–Whitney U test to compare means between two independent samples and Kruskal–Wallis ANOVA to compare means among multiple groups. We used the Wilcoxon signed-rank test and Friedman ANOVA for repeated measures to compare the means of two or more than two dependent groups, respectively. We calculated correlation coefficients, Spearman's r, to examine correlational relationships. We compared the effects of multiple independent variables using analysis of covariance (ANCOVA) on log-transformed, normally distributed data. We report partial eta-squared values as measures of effect size. We performed all statistical tests using Statistica 6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.). We used only two-tailed tests and considered differences to be statistically significant at $\alpha < 0.05$. We corrected for multiple testing using the sequential Bonferroni adjustment (Rice 1989). We report P values in their adjusted form and critical values following Mundry & Fischer (1998). Wherever appropriate, we report means ± standard error (SE).

RESULTS

Fluidity, Duration and Size of Subgroups

During long-term focal follows, we monitored the behaviour of 19 hyaenas for a total of 624 h and completed composite 24-h follow cycles for 16 hyaenas ($N = 5$ males, $N = 11$ females). Of those hyaenas, we followed six for two complete cycles. Variation in subgroup size experienced by one typical adult female spotted hyaena during her two composite long-term follows is shown in Fig. 1. Hyaenas

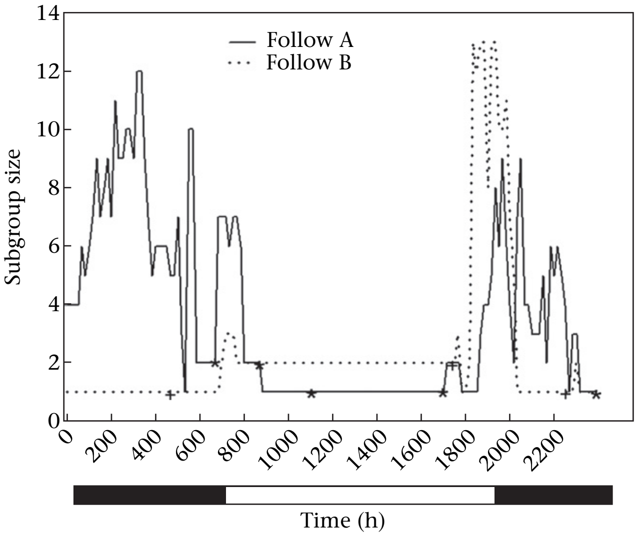

Figure 1. Variation in subgroup size experienced by one adult female spotted hyaena during two long-term follows, A and B, conducted at different times. Follow A consisted of five segments lasting an average of 4.8 h each. Follow B consisted of three segments lasting an average of 8.0 h each. Breaks between continuous follow segments are indicated by asterisks (follow A) and plus signs (follow B). Plotted values include the focal animal and represent subgroup size recorded every 10 min; a subgroup size of 1 indicates the focal animal was alone. Shaded and open bars indicate hours of darkness and daylight, respectively.

Table 2. Mean ± SE subgroup sizes and estimates of fluidity for males ($N = 5$) and females ($N = 11$) based on entire 24-h composite follows

	Females	Males	*U* statistic	*P* value
Subgroup size	3.9±0.6	3.1±0.3	24.0	0.692
No. subgroup size Δ*s*	26.7±3.3	23.5±3.3	20.5	0.427
Subgroup duration (min)	54.3±7.4	60.7±10.1	18.0	0.282
% Time spent alone	27.2±7.2	35.1±10.7	24.0	0.692

from both Talek West and Mara River clans encountered similar numbers of different conspecifics during each hour followed (1.7 ± 0.3 and 1.7 ± 0.2 individuals/h, respectively; Mann–Whitney *U* test: $U = 38.0$, $P = 0.825$). Because we detected no significant differences for this or any other variable, based on clan membership, we pooled follow data from both clans (Mann–Whitney *U* test: $U \geq 0.20$ and $P > 0.20$ for all variables). We detected no sex differences in any measure calculated from follow data (Mann–Whitney *U* test: $U \geq 18.0$ and $P \geq 0.28$ in all cases; Table 2).

Although clan sizes ranged from 47 to 55 for Talek West and from 28 to 41 for Mara River during the period in which we conducted long-term follows, subgroup size averaged only 3.6 ± 0.4 individuals over all 24-h composite follows. The largest subgroup size recorded during any of the follows was 23 hyaenas (44% of the clan), during a conflict with lions. Subgroup size was highly fluid such that focal hyaenas, on average, experienced a minimum of 25.7 ± 2.5 changes in subgroup size during a 24-h period. Subgroup sizes experienced by each focal individual varied dramatically both within and between days (e.g. Fig. 1). The maximum number of observed changes in subgroup size during a 24-h period was 48. During follows, subgroup compositions lasted for an average of 56.3 ± 5.9 min, and adults spent approximately one-third (29.6 ± 5.8%) of their time alone. On average, adults ($N = 19$) encountered a minimum of 8.2 ± 0.7 other clan members (19.7 ± 1.6% of the entire clan) within a single follow segment during the active period; these segments lasted an average of 5.4 ± 0.4 h. Thus, each hyaena encountered roughly 1.5 new conspecifics per hour during the active period.

Observation session data generated patterns that were generally consistent with data from long-term follows. On average, the distance between subgroups at two different observation sessions occurring sequentially within the same morning or evening sampling period was 1.11 ± 0.03 km ($N = 1291$ distances; ranging from 201 m to 9.8 km). Mean subgroup size was 3.70 ± 0.02 hyaenas ($N = 34\,848$ sessions). Modal subgroup size, however, was only one hyaena, and almost half of our observation sessions (45.3%) involved lone hyaenas (Fig. 2). Excluding transient males (immigrants remaining in the clan for less than 6 months), our clan in the Talek area contained 39 to 74 members, and the mean size of the clan during the entire study was 57 ± 3 hyaenas, based on monthly population estimates. Subgroups ranged in size from 1 to 39 individuals (Fig. 2) and were always less than current clan sizes. For example, when we observed 39 hyaenas together, the current clan size was 67 individuals. We never observed the entire clan together concurrently during a single session. The frequency with which we encountered subgroups of specific sizes decreased as subgroup size increased (Spearman rank correlation: $r_S = -0.997$, $P < 0.00001$, $N = 39$ sizes, Fig. 2).

Variation in the Tendency to Be Alone

The tendency for hyaenas to be alone increased significantly with each successive life history stage (Kruskal–

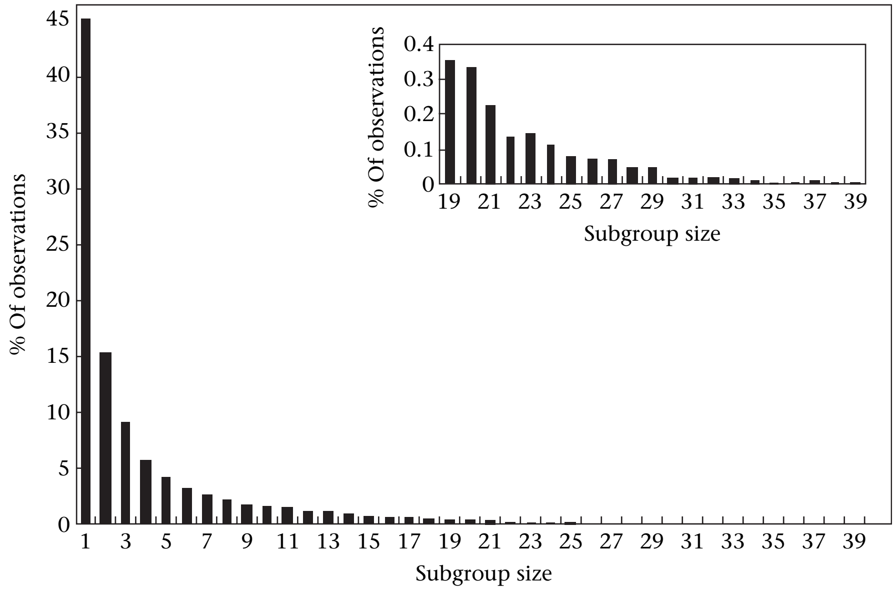

Figure 2. Frequency distribution of subgroup sizes in which we found members of the Talek clan throughout our longitudinal study ($N = 34\,848$ observation sessions). The inset shows a magnified view of the frequency of subgroup sizes ranging from 19 to 39.

Wallis test: $H_{4,695} = 421.3$, $P < 0.00001$; Fig. 3a). Cubs were alone significantly more often at communal than at natal dens (Mann–Whitney *U* test: $Z = -2.62$, $P < 0.009$). Cubs independent of the communal den were alone more often than were those still residing at the communal den, but less often than weaned, prereproductive animals ($Z = -11.1$ and -8.29, respectively, $P < 0.00001$ for both). We detected no sex differences in the proportion of sessions spent alone within any life history stage before adulthood (Mann–Whitney *U* test: $Z_1 = 0.00$, $Z_2 = -0.60$, $Z_3 = -1.59$, $Z_4 = -0.73$, $P \geq 0.56$ in all cases, Fig. 3a). However, reproductively mature natal males were significantly more likely to be alone than were either adult females ($Z = -3.31$, $P = 0.006$) or weaned, prereproductive natal males ($Z = -2.99$, $P = 0.014$). By contrast, adult females were no more likely to be alone than were weaned, prereproductive females ($Z = -1.13$, $P = 0.52$). On average, immigrant males ($N = 67$) were found alone during a significantly greater proportion of their sessions (21.2 ± 1.5%) than were adult females ($N = 84$, 15.8 ± 1.3%, Mann–Whitney *U* test: $Z = 3.21$, $P = 0.001$). Within each sex, low-ranking adults were also found alone significantly more often than were high-ranking individuals (Spearman rank correlation: $r_S = 0.77$ and 0.85, $N = 24$ and 18 rank positions, for adult females and immigrant males, respectively, $P < 0.00001$ for both; Fig. 3b).

Social and Ecological Influences on Subgroup Size

The total numbers of hyaenas present during sessions varied significantly with the context in which the hyaenas

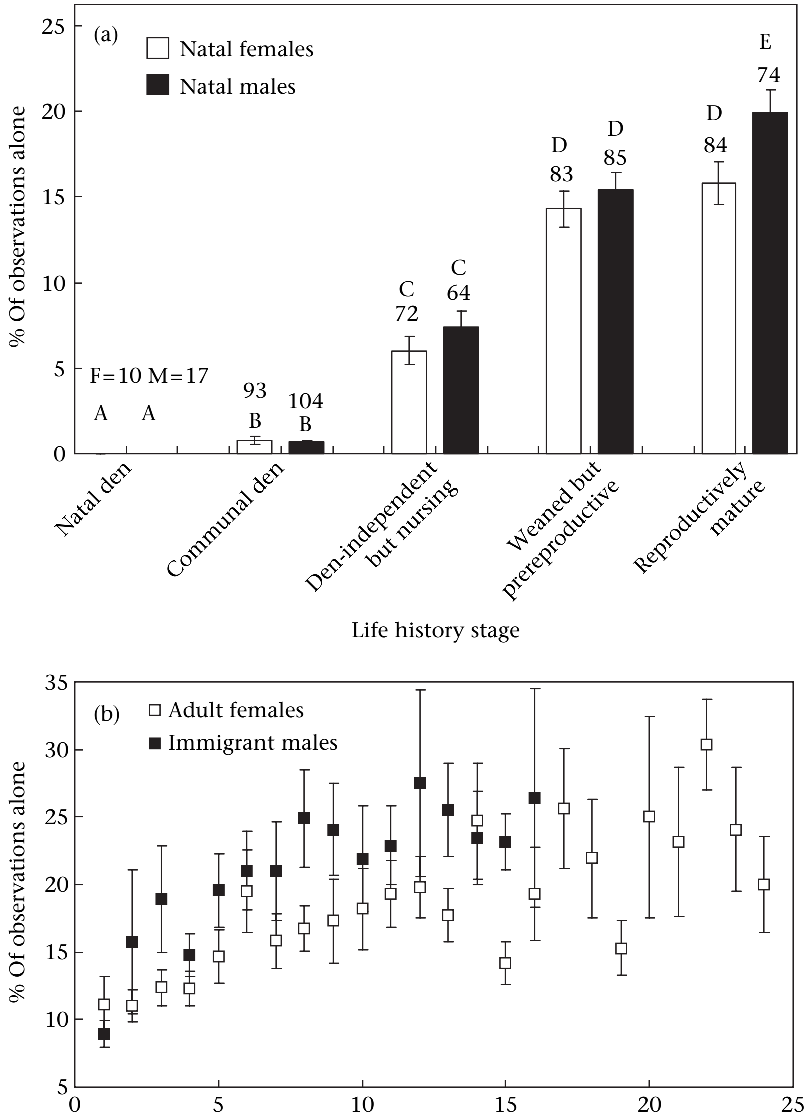

Figure 3. Mean ± SE percentage of observation sessions in which (a) natal animals were found alone during each life history stage and (b) adult females ($N = 45$) and immigrant males ($N = 40$) were found alone as a function of intrasexual social rank. By convention, the highest possible rank is 1. Sample sizes in (a) shown above each bar represent numbers of individuals. Different letters above bars indicate statistically significant differences after correcting for multiple testing.

were observed (Kruskal–Wallis test: $H_{8,34\,847} = 11\,030.49$, $P < 0.0001$, Fig. 4). During baseline sessions, mean subgroup size was only 2.2 ± 0.2 hyaenas. Hunting subgroups were significantly smaller than baseline (Mann–Whitney U test: $Z = 5.00$ and $P = 0.0002$), indicating that hyaenas typically leave subgroups to hunt alone or with a single companion. In fact, solo hunters and pairs of hunters conducted 87.3% of 393 hunts observed here. Subgroups observed at natal dens were also generally small, but did not differ significantly from baseline ($Z = 0.12$, $P = 0.91$). Courtship interactions, communal dens, kills, border patrols, conflicts with lions and clan wars attracted significantly larger numbers of individuals than did baseline sessions ($Z = -34.08$, -87.59, -47.74, -8.92, -9.92, -6.08, respectively, $P < 0.0002$ in all cases, Fig. 4). Hyaenas were observed with conspecifics in 81.5% of sessions in which lions were present but no interspecific agonistic interactions were observed; mean subgroup size here (8.6 ± 0.4, $N = 390$ sessions) was significantly smaller than in sessions in which agonistic interactions occurred between lions and hyaenas ($Z = 4.06$, $P < 0.0001$). Mean subgroup size in sessions in which alien hyaenas were present, but no clan wars occurred, was 5.0 ± 0.5 hyaenas ($N = 101$ sessions), a value significantly lower than that observed during clan wars ($Z = -4.87$, $P < 0.0001$). Overall, both intra- and interspecific between-group conflicts promoted the formation of large subgroups.

Testing the Infant Safety Hypothesis

In general, the tendency for adult females to be alone or only with their dependent offspring varied significantly among reproductive states (Friedman's ANOVA: $F_{4,38} = 66.4$, $P < 0.00001$, Fig. 5a). Females were seen alone or with only their dependent offspring significantly more often during late pregnancy and early lactation than during any of the other phases of the reproductive cycle (Wilcoxon signed-ranks tests: $Z \geq 3.24$ and $P \leq 0.016$ in all cases). As predicted by the infant safety hypothesis, females were seen alone with their dependent offspring significantly more often during early lactation than during other reproductive states ($Z = 4.87$, $P = 0.0001$). However, the increasing tendency for females to be found alone as pregnancy progressed (Fig. 5a) was not predicted by the infant safety hypothesis.

Our model containing the subset of females ($N = 16$) observed across all reproductive states during both months of prey scarcity and months of abundance, with social rank as a covariate ($F_{1,149} = 3.685$, partial $\eta^2 = 0.024$, $P = 0.057$), explained a significant amount of variation ($r^2 = 0.316$) in the tendency for females to be alone or with only their dependent offspring (ANCOVA: $F_{10,149} = 6.879$, $P < 0.00001$). As before (Fig. 5a), the tendency for females to be alone, or with only dependent offspring, varied significantly among reproductive states ($F_{4,149} = 15.089$, partial $\eta^2 = 0.288$, $P < 0.00001$). Prey abundance, however, did not significantly predict this aspect of female behaviour ($F_{1,149} = 0.028$, partial $\eta^2 = 0.0001$, $P = 0.867$) nor did it interact with the effect of reproductive state ($F_{4,149} = 1.181$, partial $\eta^2 = 0.031$, $P = 0.321$). These results indicate that social rank and reproductive state are better predictors of a female's tendency to be alone, or with only dependent offspring, than is local prey abundance.

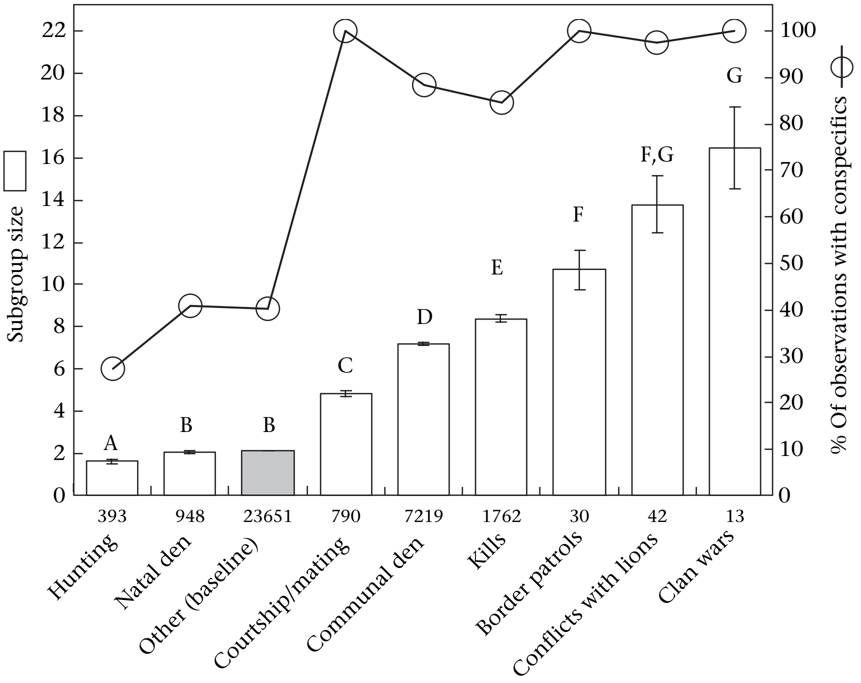

Figure 4. Mean ± SE subgroup size and proportion of observations in which *Crocuta* were found in subgroups containing more than one individual as functions of the context in which groups formed. Sample sizes, shown below each bar, represent numbers of observation sessions assigned to each context. Different letters indicate statistically significant differences between contexts after correcting for multiple testing. The shaded bar represents the baseline value of subgroup size occurring in 'other' sessions, against which other groups were compared.

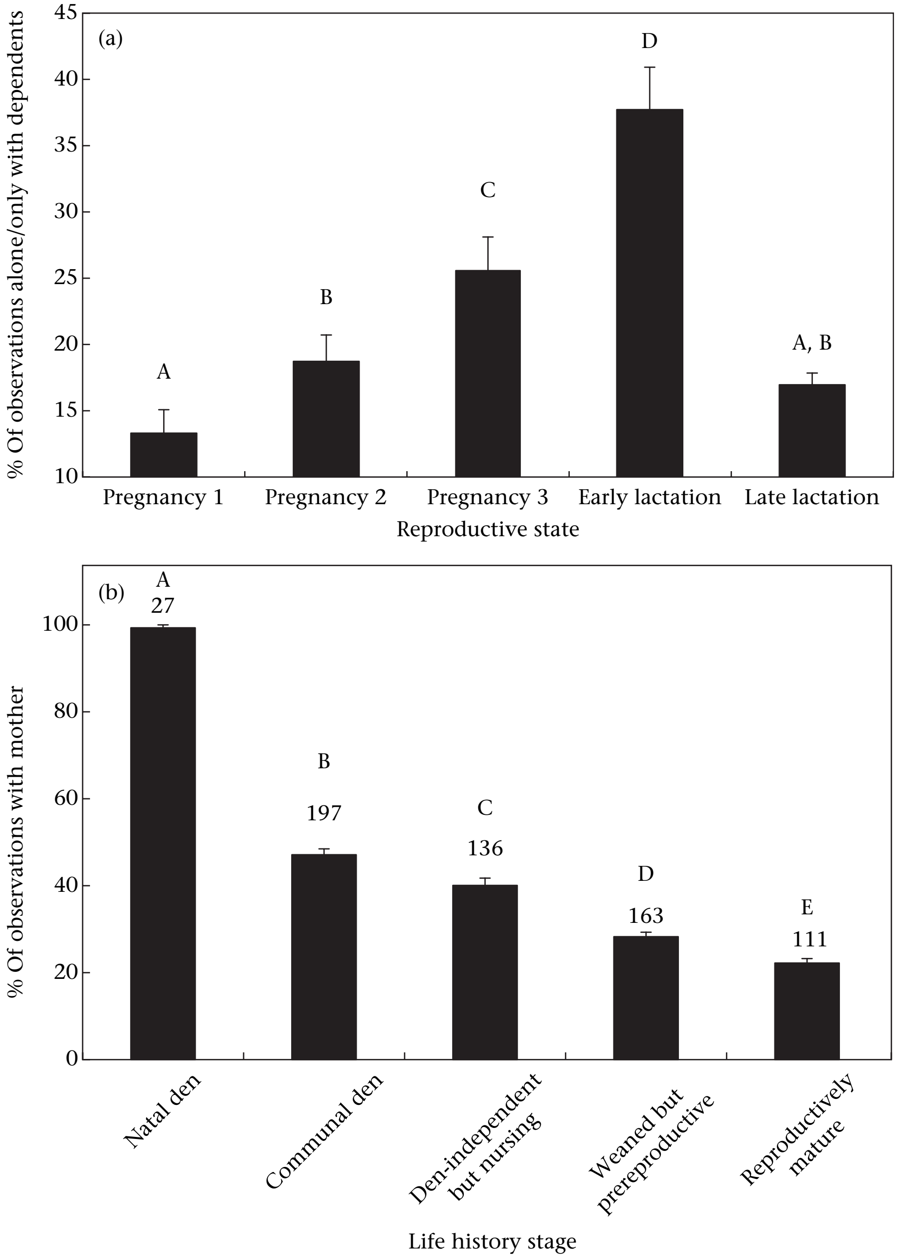

Figure 5. Mean ± SE percentage of observations in which (a) adult females ($N = 38$) were found alone or with only their dependent offspring as a function of the female's reproductive state and (b) natal animals were found with their mother during each life history stage. Sample sizes, shown above each bar in (b), represent numbers of individuals observed in each life history stage. Different letters indicate statistically significant differences between categories after correcting for multiple testing.

Mothers were most likely to be present with their offspring during the life history stages in which their offspring were most vulnerable to infanticidal conspecifics. Mothers and infants spent progressively smaller proportions of their time together as offspring matured (Kruskal–Wallis test: $H_{4,633} = 237.3$, $P < 0.0001$; Fig. 5b). We observed mothers and cubs together more often at the natal den than at communal dens (Mann–Whitney U test: $Z = -8.35$, $P < 0.0001$) because newborn cubs rarely appeared above ground when their mothers were absent. We observed mothers and cubs together more often when cubs resided at communal dens than when cubs were den-independent but still nursing or weaned but prepubertal ($Z = -4.00$ and 5.52, respectively, $P < 0.001$ for both). We also saw mothers and offspring together more often when offspring were weaned but prepubertal than when offspring were reproductively mature ($Z = 3.67$, $P = 0.001$). We found no sex differences in this measure within any life history stage ($Z_1 = -0.43$, $Z_2 = 0.15$, $Z_3 = 1.36$, $Z_4 = 1.58$, $Z_5 = -0.71$, $P \geq 0.575$ for all).

Testing the Dispersive Conflict Resolution Hypothesis

Overall, we conducted a total of 211 focal animal surveys, 162 of which were in the absence of food and

49 of which were at kill scenes, in which clan members directed aggression towards 68 different focal animals in the absence of lions, aliens and courtship/mating. Within a single survey, a particular animal never responded to aggression by both reconciling with a former opponent and departing from its current subgroup. In response to aggression, focal hyaenas left their current subgroup after 19.8% of fights away from kills and 2.2% of fights at kills ($N = 33$ fights involving 21 focal animals). We never observed focal animals reconciling at kills, but they did reconcile with former opponents after 11.7% of fights away from kills ($N = 19$ fights involving 17 focal animals).

We completed 145 pairs of matched surveys, occurring within 13 ± 1 days of one another, in which the same animal was present with conspecifics and received aggression in one survey but not the other. None of these fights were reconciled. Matched surveys differed in subgroup sizes by only 0.9 ± 0.1 hyaena. In the absence of food, as predicted by the dispersive conflict resolution hypothesis, the probability of immediate departure from the scenes was significantly higher when focal animals received aggression ($23.8 \pm 5.2\%$) than when they did not ($2.2 \pm 1.0\%$; Wilcoxon signed-ranks test: $Z = 3.68$, $P = 0.0002$, $N = 47$ focal animals). However, victims of aggression were significantly less likely to depart from their current subgroups at kills than from subgroups in which no food was present (Mann–Whitney U test: $Z = -2.20$, $P = 0.028$, $N = 20$ and 47 focal animals, respectively). Victims of aggression virtually always remained in feeding subgroups; focal animals were no more likely to depart from feeding subgroups after receiving aggression ($5.0 \pm 5.0\%$) than when they did not receive aggression ($5.0 \pm 5.0\%$, $N = 20$ focal animals). Our sample did not permit us to run a Wilcoxon signed-ranks test on these data because only two focal animals differed in their responses between matched surveys at kills.

We completed 13 matched surveys during which the same victim of aggression responded by initiating a conciliatory interaction with its former opponent during one survey but failed to do so during the other. These matched surveys were collected away from food within 20 ± 5 days of one another, and pairs of surveys differed in subgroup sizes by only 1.4 ± 0.3 hyaenas. As predicted by this hypothesis, reconciliation promoted subgroup cohesion. The tendency for focal animals to remain in subgroups following fights was significantly greater when victims of aggression reconciled with former opponents ($100 \pm 0\%$; no departures) than when they did not ($61.5 \pm 14.0\%$; Wilcoxon signed-ranks test: $T = 0$, $P = 0.043$, $N = 13$ focal animals).

Testing the Ecological Constraints Hypothesis

Consistent with the ecological constraints hypothesis, *Crocuta* adjusted grouping patterns to match seasonal variation in local prey abundance and the energy available at food sources. *Crocuta* were significantly more likely to be found with conspecifics during months when migratory prey were present ($N = 60$ months) than when migratory prey were absent ($N = 122$, Mann–Whitney U test: $Z = -3.36$, $P < 0.0001$, Fig. 6a). Variation in hunting subgroup size could not explain this seasonal change in the tendency to be with conspecifics because mean numbers of individuals found hunting together did not differ significantly between months in which migratory prey were present and those in which ungulate prey were absent ($N = 393$ hunting subgroups, Mann–Whitney U test: $Z = -0.38$, $P = 0.703$). Overall numbers of hyaenas present at kills increased with the mass of the prey carcass available within each session, even at scavenged carcasses such as adult giraffe and elephants (Spearman rank correlation: $r_S = 0.98$, $N = 8$ prey types, $P < 0.0001$, Fig. 6b).

The total numbers of competitors present at kills increased significantly over time within 15 min after successful hunts ended (Friedman's ANOVA: $F_{2,18} = 11.27$, $P = 0.0001$, Fig. 7), but only when multiple hyaenas made kills. During the first 5 min, on average, two more competitors arrived at kills made by pairs compared to kills made by solo hunters (Wilcoxon signed-ranks test:

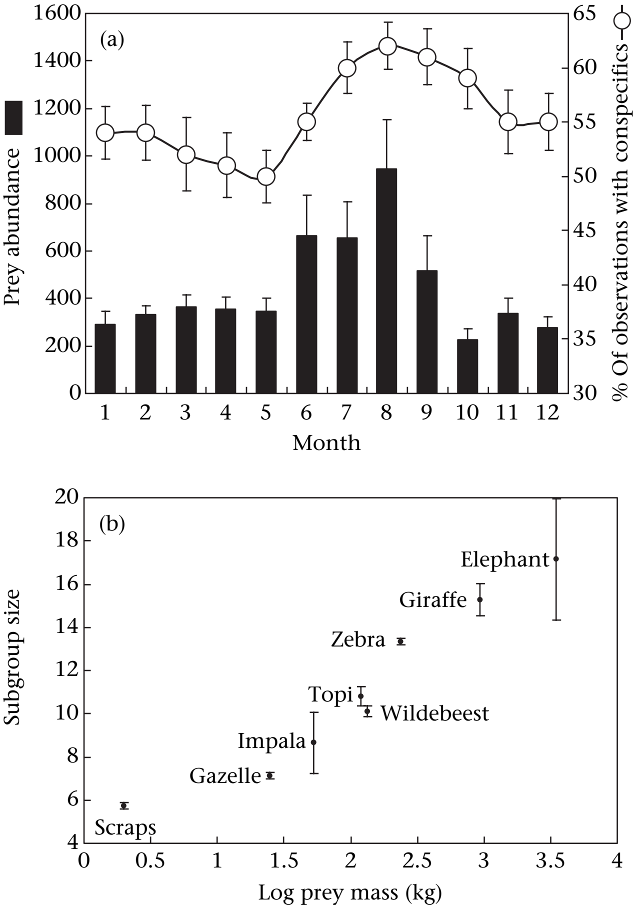

Figure 6. (a) Monthly mean ± SE numbers of prey animals counted each month during biweekly ungulate censuses and percentage of observation sessions in which *Crocuta* were found in subgroups containing more than one individual. (b) Mean ± SE subgroup size as a function of prey mass (logs of values reported by Kingdon 1997 and Oindo 2002) available at sessions with scraps ($N = 1315$) or fresh kills. Sample sizes for kills were Thomson's gazelle, $N = 382$; impala, $N = 53$; wildebeest, $N = 706$; topi, $N = 108$; zebra, $N = 193$; giraffe, $N = 29$; and elephant, $N = 13$.

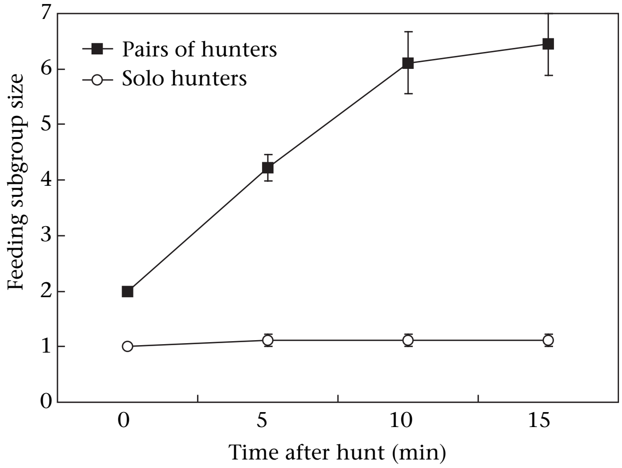

Figure 7. Feeding subgroup size during the first 15 min after solo hunters or pairs of hunters killed ungulates of similar size ($N = 9$ matched pairs of hunts).

$T = -1.50$, $P = 0.035$). On average, 10 min after prey capture, more than six competitors were present at kills made by two hunters, whereas lone hunters virtually always continued to feed alone ($T = -1.00$, $P = 0.028$). Very few new conspecifics arrived at any of the kills sampled here more than 10 min after prey capture.

Crocuta consumed quantifiable amounts of fresh biomass at 41 different kill sessions lasting an average of 26 ± 3 min each (range 6 to 98 min). On average, each adult female consumed 44 161 ± 6737 kJ (6.4 ± 1.0 kg) in a single day. However, per capita energy intake was highly variable at fresh ungulate carcasses and decreased significantly as the number of adult females present increased (Spearman rank correlation: $r_S = -0.63$, $P < 0.0001$, Fig. 8a). The lowest rate of per capita energy gain (527 kJ/hyaena/day) was experienced by 5.5 hyaenas feeding on a single juvenile Thomson's gazelle, whereas the highest rate (202 509 kJ/hyaena/day) occurred when a hyaena fed alone on an adult wildebeest.

The proportion of scans in which adult females were able to feed at kills also declined significantly as the number of adult female competitors increased (Spearman rank correlation: $r_S = -0.62$, $P < 0.00001$, $N = 426$ sessions, Fig. 8b). On average, high-ranking females were significantly more likely to feed at kills than were low-ranking females ($r_S = -0.60$, $P = 0.002$, $N = 24$ rank positions, Fig. 9a). Females outranking others within their current subgroup also gained better access to kills than did those with low relative ranks ($r_S = -0.70$, $P = 0.006$, $N = 14$ relative ranks, Fig. 9b).

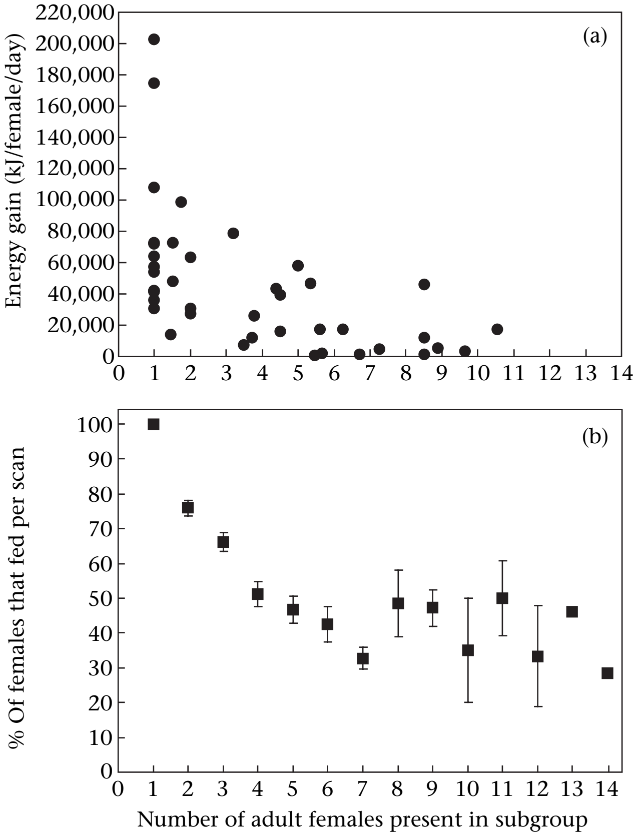

Figure 8. (a) Per capita daily energy gain as a function of the number of adult females present at fresh ungulate kills ($N = 41$). (b) Mean ± SE percentage of adult females observed feeding per scan as a function of the number of adult females present within each subgroup at kills ($N = 426$ sessions).

DISCUSSION

Fluidity of Spotted Hyaena Societies

Spotted hyaena clans are dynamic, fluid societies in which subgroup composition changes frequently over time. Although Mara hyaenas spent the majority of their time with conspecifics, our data demonstrate that *Crocuta* clans are atomistic, individual-based societies (Rodseth et al. 1991). The mean subgroup size for hyaenas ($\bar{X} = 4$) was similar to that reported for other species living in individual-based FF societies, including lions ($\bar{X} = 2$ to 5; Packer et al. 1990), chimpanzees (*Pan troglodytes*, $\bar{X} = 7$ to 9; Symington 1990), spider monkeys (*Ateles geoffroyi*, $\bar{X} = 4$; Symington 1990) and bottlenose dolphins in Western Australia ($\bar{X} = 4$ and 6; Connor et al. 1999) and Sarasota, Florida, U.S.A. ($\bar{X} = 5$; Irvine et al. 1981), but not those in Doubtful Sound, New Zealand ($\bar{X} = 17$; Connor et al. 1999; Lusseau et al. 2003). Subgroups lasted longer for hyaenas ($\bar{X} = 56$ min) than for chimpanzees ($\bar{X} = 25$ min; Lehmann & Boesch 2004), but were shorter than those observed for Doubtful Sound dolphins ($\bar{X} > 24$ h; Lusseau et al. 2003) or lions ($\bar{X} = 48$ to 75 h; Packer et al. 1990). Mara hyaenas spent roughly the same amount of time alone ($\bar{X} = 30\%$) as did spider monkeys ($\bar{X} = 13$ to 37%) or chimpanzees ($\bar{X} = 14$ to 65%; reviewed by Symington 1990), but more time alone than Doubtful Sound dolphins ($\bar{X} < 1\%$; Lusseau et al. 2003) or lions ($\bar{X} = 10$ to 15%; Packer et al. 1990).

Variables Promoting Subgroup Fission and Fusion

Life history stage, sex, social rank and current activity all influenced the likelihood of finding hyaenas of both

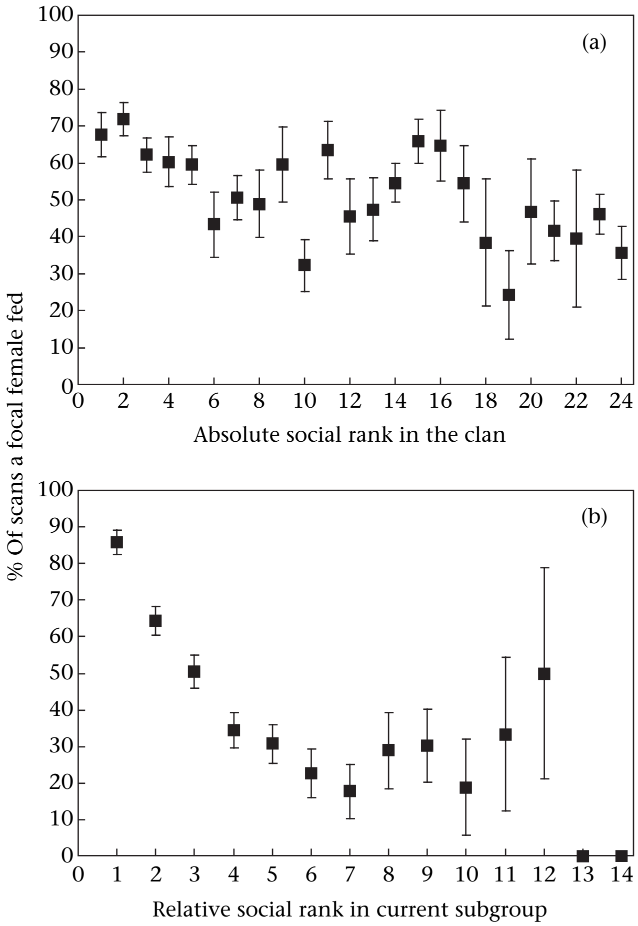

Figure 9. Mean ± SE percentage of scans in which focal females were observed feeding at kills while holding (a) an absolute social rank position within the clan ($N = 24$ absolute ranks) or (b) a relative social rank position within the current subgroup ($N = 14$ relative ranks).

sexes alone, as did reproductive state among adult females. Spotted hyaenas tended to occur in larger subgroups when they were active than during hours when they were resting. Intriguingly, this pattern appears to differ from those of certain other mammalian carnivores, including both brown and striped (*Hyaena hyaena*) hyaenas and European badgers (Mills 1990; Woodroffe & Macdonald 1993; Wagner 2006), which are all usually found in larger subgroups when resting than when active. Also, adult spotted hyaenas spent more time alone than did younger individuals. Adult males were generally alone more often than adult females, but adult females with neonatal cubs were away from other clan members most often.

Our current finding that, within each sex, low-ranking hyaenas were alone more frequently than high-ranking individuals supplements previous research indicating that low-ranking adults spend more time farther from the den (Boydston et al. 2003) and associate less often with same-sex conspecifics (Holekamp et al. 1997a; Smith et al. 2007) than do high-ranking animals. Rank-related variation in subgroup composition contributes to these patterns. Hyaenas generally prefer to associate with members of their own matriline, and high-ranking matrilines contain more individuals than do low-ranking matrilines (Holekamp et al. 1997a; Van Horn et al. 2004; Wahaj et al. 2004). Among nonkin, hyaenas actively join subgroups containing social companions ranking higher than themselves; this gains them social and feeding tolerance from the dominant animals with which they associate most often (Smith et al. 2007).

Our finding that multiple animals ($\overline{X} = 5$ hyaenas) congregate during courtship and mating is consistent with previous work showing that numbers of males observed with females increase as females approach oestrus (East et al. 2003; Szykman et al. 2007). Given the importance of the communal den as a focal point for social activity (Boydston et al. 2005; White 2007), including cooperative and affiliative behaviours among kin (Smale et al. 1993; Engh et al. 2000; Wahaj et al. 2004), we were not surprised to find large subgroups ($\overline{X} = 7$ hyaenas) at these locations.

Overall, our data suggest that cooperative defence of shared resources during between-group competition (e.g. clan wars, lion–hyaena interactions) is a strong cohesive force in hyaena societies, promoting the formation of large subgroups. Most interestingly, we found that large numbers of hyaenas ($\overline{X} = 11$ to 17) joined forces during intra- and interspecific between-group conflicts. Clan members gathered during cooperative marking and defence of territory boundaries, during defence of carcasses from either alien hyaenas or lions and in response to predation attempts by lions.

Crocuta can successfully defend food from lions only when the ratio of hyaenas to lions is high (e.g. 4:1 when adult male lions are absent; Kruuk 1972; Cooper 1991). Because lions are three to five times larger than hyaenas, the resource holding power of a single lion exceeds that of a single hyaena (Kruuk 1972; Cooper 1991; Höner et al. 2002). In addition to being their direct competitors, lions also represent a leading mortality source for spotted hyaenas (Kruuk 1972; Mills 1990; Watts 2007). Therefore, individual hyaenas cannot effectively compete with lions for possession of a carcass or defend themselves from predation by lions without aid from conspecifics. Effective maintenance of group territories also requires that individuals from multiple matrilines, with low mean relatedness (Van Horn et al. 2004), join forces during cooperative defence against neighbouring hyaena clans. Loss of a clan war can result in substantial reduction in the area of a clan's territory, and repeated losses can further result in overall loss of the territory to a neighbouring clan (K. E. Holekamp, unpublished data). Cooperative defence of territories appears to offer a similarly important advantage during intraspecific between-group conflicts in a variety of other carnivores such as dwarf mongooses (*Helogale parvula*), meerkats (*Suricata suricatta*), and Ethiopian wolves (*Canis simensis*, reviewed by Creel & Macdonald 1995), with the larger of two groups typically winning disputes.

Factors Limiting Subgroup Size

Our data were consistent with all three of the hypotheses suggesting factors limiting subgroup size in spotted hyaenas. First, as predicted by the infant safety hypothesis (Otali & Gilchrist 2006), adult females spent the most time alone with dependent offspring during early lactation, when they stayed near isolated natal dens. Mother–cub associations were especially close at the natal den and declined as cubs matured. Similarly, lion and chimpanzee mothers are also most solitary during early lactation (Packer et al. 1990; Symington 1990; Otali & Gilchrist 2006). In fact, lionesses keep cubs hidden in thick vegetation for the entire first month of life. Like lions (Packer et al. 1990), female hyaenas were also frequently found alone during late pregnancy, a finding not predicted by the infant safety hypothesis. Reproductive suppression associated with attacks by conspecifics is unlikely to explain this pattern because female mammals are less physiologically vulnerable to pregnancy loss resulting from attacks during late than during early pregnancy (Wasser & Barash 1983). However, females late in pregnancy may be least constrained by demands of prior offspring and therefore prefer to forage alone to maximize energy intake in preparation for the substantial energetic demands imposed on them by neonatal cubs.

The immediate threat of aggression disrupted subgroups in the absence of food, a finding consistent with predictions of the dispersive conflict resolution hypothesis (Schino 2000). In contrast, victims of aggression rarely reconciled at, nor departed from, feeding subgroups. This suggests that, whereas hyaenas sometimes retreat a few steps away from food in response to receiving aggression (Kruuk 1972; Frank 1986), individuals rarely leave feeding subgroups when food of high quality is present. Away from kills, however, targets of aggression always remained in subgroups after reconciling fights with former opponents, and targeted hyaenas frequently left their subgroups if fights were not reconciled. These data suggest that reconciliation promotes social cohesion by reducing the potential for escalated aggression among individuals that remain in their current subgroups. In the absence of conciliatory interactions, subgroup fission reduced the risk of continued conflict and the potentially lethal consequences of escalated aggression. In captivity, hyaenas fight intensively and severely wound groupmates when denied opportunities to depart (Jacobi 1975). However, within-group conflict rarely leads to mortality of adult hyaenas in natural populations (Kruuk 1972). Therefore, the ability of *Crocuta* to resolve conflicts by separating from former opponents appears to provide a second mechanism, along with reconciliation (Hofer & East 2000; Wahaj et al. 2001), by which hyaenas reduce the immediate costs of intragroup conflict.

Finally, our results were consistent with all predictions of the ecological constraints hypothesis (Chapman et al. 1995). This hypothesis was able to explain grouping patterns of all animals in the population, not just those of reproductive females or hyaenas recently attacked, over multiple time scales. Our data show that feeding competition constrains grouping behaviour in the short term at kills and in the long term during periods of food scarcity lasting several months. Our findings, together with data from previous studies (Frank 1986; Holekamp et al. 1996; Höner et al. 2005), imply that ecological constraints operate at virtually all times in the lives of spotted hyaenas. It appears that the only situations that can trump the disruptive force of feeding competition in hyaena societies are those occurring when females have highly vulnerable offspring.

As in other animal societies characterized by FF dynamics (Kummer 1971; Chapman et al. 1995; van Schaik 1999; Lusseau et al. 2004; Lehmann et al. 2007; Aureli et al., in press), the flexible FF structure of *Crocuta* clans permits individuals to adjust grouping patterns in response to fluctuations in local resource abundance. In Tanzania and Namibia, hyaenas redistribute themselves from less profitable areas to more profitable areas in response to long-term changes in prey abundance (Trinkel et al. 2004; Höner et al. 2005). Similarly, *Crocuta* in our study were most gregarious when ecological constraints were relaxed during periods when prey, particularly large-bodied ungulates, were abundant. Because hunting subgroup size did not vary seasonally, the benefits of cooperative hunting could not explain this variation in gregariousness. Instead, this dynamic pattern may be driven by increased within-group aggression at kills during the extended period each year in Talek when prey are scarce (Holekamp et al. 1993).

Over shorter time scales, we showed that hyaenas quickly congregated at kills in numbers correlated with the size and energetic value of captured prey. As predicted by the ecological constraints hypothesis, reduced feeding competition permitted the formation of larger subgroups and greater per capita food intake at large compared to small carcasses. The relative costs of joining feeding groups varied with rank such that low-ranking hyaenas, which enjoyed little resource holding power, were least likely to feed in large subgroups. Our data are consistent with earlier research showing that priority of access to food is determined by rank in this species (Tilson & Hamilton 1984; Frank 1986). In addition, here we show for the first time that an individual's relative rank within its current subgroup directly predicts its immediate rate of food consumption, which likely influences staying and leaving decisions in feeding subgroups. Our work, therefore, extends previous findings indicating that low-ranking individuals hunt significantly more often and in smaller subgroups than do high-ranking hyaenas (Holekamp et al. 1997b). More generally, our data support the hypothesis that resource limitation constrains subgroup size.

On average, adult females consumed 44 161 ± 6737 kJ (6.4 kg) per hyaena per day. This mean daily energy intake value is within the range of values reported for wild spotted hyaenas elsewhere in Africa: 2.5 kg (Kruuk 1972), 3.6 kg (Henschel & Skinner 1990), 3.8 kg (Green et al. 1984), 6.2 kg (Mills 1990), 7.4 kg (Whateley 1980), and 9 kg (Gasaway et al. 1991). They also match the value reported for hungry captive hyaenas housed in a group of five individuals (4 kg per hyaena; Henschel & Tilson 1988); here Mara hyaenas in subgroup sizes of 4.5 to 5.5 each consumed 27 865 ± 7674 kJ (4.1 kg) per hyaena per day.

A number of authors (e.g. Kruuk 1972; Tilson & Hamilton 1984) have suggested that group living evolved in *Crocuta* to facilitate cooperative hunting of large ungulates. Many carnivores, including wild dogs, jackals

(*Canis* spp.), coyotes and lions (reviewed by Creel & Macdonald 1995), gain some advantages from cooperative hunting. Similarly, *Crocuta* enjoy increased hunting success and capture a larger array of prey species when hunting in groups than when hunting alone (Kruuk 1972; Holekamp et al. 1997b). However, our current results, like those from earlier work (Holekamp et al. 1997b), suggest hyaenas typically hunt either alone or in pairs, such that the average subgroup size during hunting is significantly smaller than the mean subgroup size documented in any other context.

We suggest that *Crocuta* often hunt alone because individuals who leave their groupmates to hunt are likely to be able to feed from any carcass they acquire for at least a few minutes before other competitors arrive. Here we found that Mara hyaenas often fed alone before additional competitors arrived after prey capture. Hyaenas are able to detect sounds associated with kills from at least 2.4 km away (Mills 1989). Noise generated by pairs of hunters competing over kills (e.g. giggles in response to aggression) attracts additional competitors to kills made by groups; by contrast, hyaenas feed silently when alone. Spotted hyaenas can ingest meat and bone at a rate of 1.3 kg/min (Kruuk 1972) and lone hunters in our study typically enjoyed much longer periods of solitary feeding than did hyaenas hunting in groups. Each lone hunter should be able to ingest approximately 6.5 kg of food during only the first 5 min after making a kill. This amount is as much or more than the average adult spotted hyaena consumes in a 24-h period in many parts of Africa (Kruuk 1972; Green et al. 1984; Henschel & Skinner 1990).

Although group hunters are 19% more likely than solo hunters to succeed in capturing prey, even the addition of a second hunter dramatically increases ensuing subgroup size. Here, on average, within 10 min of prey capture, over six hyaenas competed for kills made by pairs of hunters, whereas solo hunters almost always still fed alone. We found that hyaenas fed nearly the entire time they were alone at fresh kills, but hyaenas in subgroups of six at kills spent less than half their time (43%) feeding. Moreover, per capita energy gain declined rapidly with increasing subgroup size such that the majority of individuals feeding in large subgroups consumed very little food. Taken together, these results suggest that hyaenas hunting alone enjoy more time feeding, and thus consume more food mass, than individuals hunting with conspecifics. Overall, the initial benefits of increased hunting success are more than offset by the costs of increased competition in the larger subgroups that form after group hunts. Rather than functioning as a cohesive force in *Crocuta* societies, our data suggest that hunting actually promotes subgroup fission. In this regard spotted hyaenas differ from societies of wild dogs (Creel 1997), but are similar to those of many other gregarious carnivores [e.g. coatis (Gompper 1996), European badgers (Kruuk & Parish 1982), brown and striped hyaenas (Kruuk 1976; Mills 1990; Wagner 2006) and kinkajous (Kays & Gittleman 2001)] in which individuals reduce feeding competition by leaving groupmates to forage alone or in small subgroups.

Conclusions

Unlike animals living in cohesive social groups, individuals living in FF societies are able to make decisions without the consensus of the entire group (Conradt & Roper 2005). Our current study demonstrates that *Crocuta* choose to associate with particular numbers of conspecifics based upon their own current state and in response to fluctuations in the local resource base. Although our data are consistent with predictions of all three of the hypotheses we tested here, only the ecological constraints hypothesis can explain variation in grouping patterns involving all clan members over both short and long time scales.

Extant spotted hyaenas apparently descended within the past 900 000 years from a carrion-feeding ancestor with a solitary lifestyle much like that of the modern striped hyaena (Lewis & Werdelin 2000). Our data suggest that selection favouring cooperative hunting did not shape gregariousness during the evolution of this species. However, the ability to capture a larger array of prey animals more successfully might have emerged as a secondary consequence of group living favoured by other selection pressures. In many different species, flexible FF lifestyles limit the costs of group living while allowing group members to aggregate when the benefits of sociality are high or the costs of grouping are low (Wrangham et al. 1993; Chapman et al. 1995). Here we found that within-group competition tended to drive individuals apart, whereas intra- and interspecific between-group competition was a strong cohesive force within *Crocuta* clans. Our data, therefore, suggest that group living might have evolved in spotted hyaenas to permit cooperation among conspecifics during defence of shared resources, including both space and food. However, constraints imposed by limited food resources might account for retention of the tendency for *Crocuta* to spend large amounts of time alone, rather than the evolution of a more cohesive social structure.

Acknowledgments

We thank the Office of the President of Kenya and the Kenyan Ministry of Education, Science and Technology for permission to conduct this research. We also thank the Kenya Wildlife Service, the Narok County Council, and the Senior Warden of the Masai Mara National Reserve for their cooperation. Our research, described in Animal Research Protocol AUF 05/05-064-00, was approved most recently on 24 April 2007 by the Institutional Animal Care and Use Committee at Michigan State University (MSU) and complies with Kenyan law. T. Getty, A. McAdam, W. Pangle, G. Ramos-Fernandez and L. Smale provided useful comments on a previous version of the manuscript. We thank L. Smale for her role in data collection and the following individuals for their assistance in the field: C. Beaudoin, N. E. Berry, E. E. Boydston, S. M. Cooper, S. M. Dloniak, M. Durham, A. L. Engh, J. Friedman, P. Garrett, I. Graham, M. Gibbons, T. H. Harty, K. M. Kapheim, C. I. Katona, K. Nelson, G. Ording, W. Pangle, M. Szykman, J. B. Tanner, K. R. Theis, K. Weibel, H. E. Watts, S. A. Wahaj and B. White. We thank

P. S. Bills for assistance in extracting data from archived field notes. Our work was supported by NSF Grants IBN9630667, IBN9906445, IBN0113170, IBN0343381 and IOB0618022 to K.E.H., fellowships from MSU to J.M.K. and J.E.S., an MSU Fowler Endowed Scholarship to K.E.G., and a Scholar Award from P.E.O. Sisterhood International to J.E.S.

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