Sex Differences in Territorial Behavior Exhibited by the Spotted Hyena (Hyaenidae, Crocuta crocuta)

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Abstract

Spotted hyenas (Crocuta crocuta) are gregarious carnivores that defend group territories against encroachment by neighboring conspecifics. Here we monitored the behavior of members of one clan of free-ranging spotted hyenas during border patrols, ‘wars’ with neighboring clans, and other interactions with alien intruders, to document differences between the sexes in territorial behavior in this species. We also examined the possibility that the probability or rate of attack on alien hyenas encountered within the clan’s territory would vary with the sex of the intruders. Initiation and leadership of most cooperative territorial behaviors were by adult female clan members, although border patrols were occasionally conducted by groups composed exclusively of resident males. The vast majority of alien intruders into the territory of the study clan were males. Resident females were more likely to attack intruding females than intruding males, but hourly rates of aggression directed by females towards aliens did not vary with intruder sex. Resident males were more likely than resident females to attack alien males, and resident males directed significantly higher hourly rates of aggression towards intruding males than females. Although female leadership in most cooperative territorial behaviors distinguishes spotted hyenas from many mammalian carnivores, other sex differences in the territorial behavior of spotted hyenas resemble those documented in other gregarious predators. Sex differences observed in hyena territoriality are consistent with the hypothesis that male and female clan members derive different selective benefits from advertisement and defense of group territories.

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Introduction


Investment in territorial behavior by individual members of animal groups should vary with the potential costs or benefits accruing to those individuals from advertisement and defense of the territory (e.g. Milinski & Parker 1991; Pusey & Packer 1997). Because strategies for maximizing reproductive success are sexually dimorphic in most animals (Darwin 1871; Bateman 1948; Trivers 1972; Emlen & Oring 1977; Clutton-Brock 1988), the costs and benefits of territorial behavior in mammalian carnivores should theoretically differ for males and females. These costs and benefits should also vary as a function of the sex of alien animals encountered within the home territory, and behavior consistent with these predictions has been observed to date in a number of carnivores. For example, lions, dwarf mongooses, suricates, and many mustelids defend their territories most vigorously against same-sex intruders (Powell 1979; Rood 1983; McComb et al. 1994; Grinnell et al. 1995; Heinsohn & Packer 1995; Doolan & Macdonald 1996). Among domestic dogs (*Canis domesticus*), group members are more aggressive towards strangers of the same sex than towards opposite-sex individuals (King 1954). Fights between opposite-sex pairs of brown hyenas from different social groups are rare, whereas same-sex fights are both more common and more intense (Mills 1983, 1990). Henschel & Skinner (1991) reported that female spotted hyenas in their study population in southern Africa engaged more frequently in territorial scent-marking than did males, and that females invested more time in territorial activities than did males. Our broad objective here was to replicate and extend these findings in a population of spotted hyenas in eastern Africa.

Spotted hyenas live in complex stable social groups called clans (Kruuk 1972). Each clan contains multiple adult females, their offspring, and one to several resident immigrant adult males. Female hyenas generally spend their entire lives in their natal clans, while all males disperse shortly after puberty (Henschel & Skinner 1987; Smale et al. 1997; Holekamp & Smale 1998a). Males that successfully immigrate are subordinate to all natal females and their offspring in the new clan (Tilson & Hamilton 1984; Smale et al. 1993). Thus, adult females are socially
dominant to adult immigrant males, and immigrant males invariably defer to all natal animals during competition over food (Holekamp & Smale 1998a).

Although all adult female clan members breed, the reproductive success of female Crocuta varies directly with their priority of access to food (Frank et al. 1995; Frank 1986b; Holekamp et al. 1996, 1999). In eastern Africa, the diet of spotted hyenas consists mainly of medium and large-bodied ungulates that they hunt themselves (Kruuk 1972). Hyenas usually hunt within the boundaries of their clan territories, and defense of territory borders is often associated with competition over food (Kruuk 1972; Henschel & Skinner 1991). The reproductive success of male Crocuta is most strongly affected by whether or not males can manage to join new clans after dispersing from their natal groups, and by the duration of their tenure in those new clans (Engh et al., unpubl. data). These different determinants of reproductive success in males and females should generate corresponding sex differences with respect to the perception of potential threats to critical resources, to the value hyenas of each sex assign to the group territory, and hence, to the risks which males and females are willing to take in its defense.

Our specific goals here were to document the territorial behavior exhibited by members of one large clan of spotted hyenas, examine leadership roles during group interactions with alien hyenas, and compare hourly rates at which resident females and immigrant males engaged in territorial marking and aggressive behavior toward intruders. The forms of territorial behavior we monitored included patrols along territorial borders, clashes or ‘wars’ between neighboring clans, and other encounters between resident and alien hyenas within the territory of the study clan. We hypothesized that because female hyenas are philopatric and require exclusive access to food available within the territory, they should stand to lose more than males from alien intrusions into their territory (e.g. Henschel & Skinner 1991; Heinsohn & Packer 1995). We therefore expected that female Crocuta would engage more frequently than males in territorial marking and defense and that they would take more risks when confronting intruders. We further expected resident females to behave more aggressively than resident immigrant males towards intruders, particularly alien female intruders who would not show male-like deference to resident females during competition for access to food resources critical for successful reproduction. Because resident males should attempt to maximize their own mating opportunities, we hypothesized that they would play a larger role than females in defending the clan’s territory against intruding males, who might attempt to join the clan and thus compete with resident males for access to females.

**Methods**

**Study Population**

The study animals comprised one large clan of spotted hyenas inhabiting the Talek region of the Masai Mara National Reserve, Kenya. This area is
characterized by open rolling grassland broken by seasonal creek beds, and it is grazed all year round by large concentrations of several different ungulate species (Frank 1986a). Between 25 May 1988 and 25 May 1998, observers monitored Talek hyenas on 3120 d. Each Talek hyena was individually identified by its unique spots and other natural marks, and sexed based on the dimorphic glans morphology of the erect phallus (Frank et al. 1990). Reproductive states of Talek females were known, and ages of all hyenas born in the study clan since 1988 were known to within ± 7 d, as described previously (Holekamp & Smale 1993; Holekamp et al. 1996). Natal animals were considered to be adults at 3 yr of age, and younger animals were considered to be sub-adults. All hyenas born in Talek were considered to be resident animals, as were those adult males who had emigrated from other clans but who had been present in the Talek area and tolerated by residents there for at least 30 d. Although sub-adults occasionally participated in territorial behaviors, we focused here exclusively on behavior exhibited by resident adult females and resident immigrant males. Adult natal males rarely participated in territorial activities, so all adult males used in all data analyses below were immigrants. All adult hyenas observed in the Talek area that had never previously been seen there were called ‘alien intruders’.

Behavioral Observations

Most behavioral data were collected between 05:30 h and 09:00 h, and between 17:00 h and 19:30 h, but these were supplemented with observations made near midday and at night using night vision binoculars. On any given day of observation, either one or two research vehicles were deployed in the Talek area and environs, with one or two observers per vehicle. Throughout the study period, each time we came across one or more hyenas separated from other hyenas by at least 200 m, we initiated an observation session. The observation session ended when we left that individual or group. The duration of observation sessions ranged from 5 min to several hours. During every observation session, all aggressive, appeasement, and scent-marking behaviors (Kruuk 1972) were recorded as critical incidents (all-occurrence sampling, Altmann 1974). All clan wars, other appearances of alien hyenas in the Talek area, and interactions between Talek hyenas and intruders were also recorded.

When groups of intruders are detected near territorial boundaries, resident hyenas may initiate a cooperative attack to expel them (Kruuk 1972; Hofer & East 1993a, b; Holekamp et al. 1993). These clan wars are characterized by coordinated rushes and attacks by both sets of participants, as well as by frequent recruitment vocalizations to call allies to the scene (e.g. Kruuk 1972; East & Hofer 1991). Although actual physical contact between opponents is rare during clan wars, serious injury or death sometimes results from severe biting (Van Lawick & Van Lawick-Goodall 1971; Kruuk 1972; Henschel & Skinner 1991). Clan wars here were identified, and distinguished from other encounters with alien hyenas, when multiple rushes and attacks were exhibited by both sets of participants. Whenever permitted by observation conditions during clan wars, we recorded the
identities of all individual Talek hyenas participating. We also recorded the identities of Talek hyenas in the front lines of an attack as well as those in the rear. We divided participating Talek hyenas into those seen in a front line in at least one attack per clan war and those never observed in a front line at all during a particular clan war.

Similarly, we recorded information on participation and group leadership during each border patrol observed. During a border patrol, several hyenas maintain body postures indicating great excitement as they move along, or to, a territorial boundary, where they engage in high rates of scent-marking behavior and socially facilitated defecation in ‘latrine’ areas (Kruuk 1972; Mills 1984; Henschel & Skinner 1991; Sillero-Zubiri & Gottelli 1992). Here the leader of a border patrol was defined simply as the individual at the front of a moving queue of hyenas. Multiple individuals were often observed in the lead during a single border patrol. We divided participating hyenas into those seen in the lead at least once and those never observed to lead at all during a particular border patrol. Records from border patrols also included information on whether or not each participating hyena engaged at least once in scent-marking via deposition of ‘paste’ from anal scent glands (called ‘pasting’ by Kruuk 1972) or defecation in latrine areas along borders of the Talek clan’s territory. A latrine can be identified by the presence of several piles of feces deposited by multiple hyenas at the same spot. Hyena feces often turn white after drying, making latrines conspicuous for many weeks after deposition (Kruuk 1972). Here we calculated the proportion of individuals of each sex present at each border patrol that either scent-marked or defecated at least once before the group began to disband. Furthermore, in a subset of observed border patrols, we were able to record all occurrences of pasting behavior by all participating hyenas, so that we could compare individual pasting rates for male and female participants.

In addition to large groups of intruders found near territorial boundaries during clan wars, lone alien hyenas or small groups of aliens may occur deep within another clan’s territory. We recorded all behavioral interactions between Talek hyenas and intruders during every observation session in which at least one intruder and one Talek resident were present simultaneously. In these observation sessions, it was usually possible to record identities of all Talek hyenas present. Observation sessions in which Talek residents encountered aliens were included in analyses of aggression only when all Talek hyenas present could be identified, and also when all alien hyenas present could be sexed.

In each session where resident and alien hyenas were present concurrently, we assumed there was the potential for each resident to direct aggression towards each alien. These opportunities for aggression were called encounters. The total number of encounters per session was calculated as the product of the number of Talek residents present multiplied by the number of alien hyenas present in that session. Thus a session in which five Talek hyenas met up with two aliens resulted in 10 encounters, each of which might possibly have involved aggression. When both aliens and residents occurred together, for each Talek hyena present we calculated the hourly rate at which it directed aggression towards aliens of each
sex. To correct for the number of potential alien targets, hourly aggression rates were divided by the number of male or female aliens present. Aggressive behaviors directed at aliens were called attacks and included threats, displacements, chases, and bites (Kruuk 1972). Submissive behaviors included flattening the ears back against the head, head-bobbing, backing away or retreating, grinning, and giggling (Kruuk 1972). Submissive behavior not preceded by aggressive behavior emitted by another hyena was called ‘unsolicited appeasement’.

Spatial Data and Statistical Analyses

Precise geographic locations of all territorial behaviors and all encounters with intruders were recorded by reference to landmarks or by latitude and longitude determined with a Magellan Meridian XL Global Positioning System (GPS) unit. From aerial photographs (1:20000 scale) of the study area, we generated a detailed digitized map of the north-eastern portion of the Masai Mara National Reserve and geo-referenced this map to our GPS data. On this digital map, we placed locations of all clan wars and group scent-marking sites and defined the borders of the Talek clan’s territory as the lines best incorporating these points. Thirteen adult Talek females wearing radio-collars were tracked multiple times each week during 1996–1998, and their locations were also plotted on the digitized map. Approximate boundaries of territories occupied by neighboring clans, other than boundaries shared with the Talek clan territory, were determined by recording locations of clan wars elicited by the sound playbacks conducted by Ogutu & Dublin (1998).

χ²-tests were used to compare participation in border patrols and clan wars by resident males and females. We also used χ²-tests to compare the proportions of encounters in which resident animals either attacked intruders or exhibited no aggression towards them. Hourly rates of dyadic aggression against aliens of each sex were calculated for all Talek hyenas. Aggression rate data were not normally distributed, so these were analyzed with the Kruskal–Wallis test for variance among groups and the Dunn’s test for multiple comparisons. Differences between groups were considered significant when p < 0.05.

Results

During the study period, we observed Talek hyenas engage in 31 clan wars and 35 border patrols involving intensive scent-marking via pasting or socially facilitated defecation at latrine sites (Fig. 1a). Borders of the area marked and defended by the Talek clan, as inferred from the data in Fig. 1(a), are drawn in Fig. 1(b), along with locations of 133 interactions between Talek hyenas and aliens that could not be classified as clan wars, and 160 sightings of aliens alone. The Talek River, which formed the northern boundary of the Masai Mara National Reserve in this area, also formed the northern border of the Talek clan’s territory. A tributary of the Talek River formed much of the eastern border, and a large seasonal water course called Ol Keju Rongai formed much of the southern
border of the Talek territory. The western border was not marked by a water course. The area advertised and defended by the Talek clan thus covered approximately 61 km². On average, \( 94.4 \pm 1.9\% \) of all 3130 sites at which 13 radio-collared Talek females were found during 1996–1998 fell within the Talek clan territorial boundaries (Fig. 1c). Finally, territories of neighboring hyena clans bordered the territory of the Talek clan in all compass directions, and clan wars were observed between Talek hyenas and members of all neighboring clans (Fig. 1d).

In nine clan wars, we were able to record the identities of all participants as well as all occurrences of agonistic behaviors, and we were also able to ascertain which individuals were in the front lines of each attack. Both adult females and males participated in all nine of these clan wars. Of all Talek females in these clan wars, 38 (75\%) were observed at least once in the front line of an attack, whereas only 10 of 27 (37\%) adult males were observed in front lines. Thus females were significantly more likely to lead attacks than were males \((\chi^2 = 10.28; \text{df} = 1; p < 0.01; \text{Fig. 2})\). Of all adult females participating in clan wars, 36\% were pregnant, 58\% were lactating, and 6\% were neither pregnant nor lactating.
In the 23 border patrols for which we knew the identities of all Talek hyenas participating, only adult females participated in three patrols, only adult males participated in two patrols, and 18 patrols involved participants of both sexes. All mixed-sex border patrols were always led by females. Of all females that participated in border patrols, 40 (42%) were observed in the lead at least once during a border patrol, whereas only seven (15%) of 47 male participants were seen leading a patrol. Thus, as with clan wars, border patrols were significantly more likely to be led by females than by males ($\chi^2 = 10.42; \text{df} = 1; p < 0.01$; Fig. 2). There were no sex differences in the proportions of individuals present during border patrols who either pasted along the way ($\chi^2 = 0.42; \text{df} = 1; p > 0.10$) or defecated in latrine areas ($\chi^2 = 0.70; \text{df} = 1; p > 0.10$). However, females tended to paste during border patrols at slightly higher hourly rates than did males ($t = -1.95; \text{df} = 11; p = 0.07$; Fig. 3).

Excluding clan wars, we found 458 alien hyenas in the Talek territory during 293 different observation sessions. The mean intruder group size was 1.6 ± 0.1 individuals (n = 293). Talek hyenas were present with aliens in only 133 of those 293 observation sessions (Fig. 1b). Thus Talek hyenas may have detected fewer than half of all known intrusions by one or more aliens. The mean intruder group size when aliens were detected by Talek residents was 1.4 ± 0.1 individuals (n = 133; Fig. 4). An ungulate carcass was present during 42 sessions with intruders, and no food was present during 91 sessions. All Talek hyenas were individually identified and sexes of all aliens were determined in 107 of 133 sessions with intruders, totaling 46.5 observation hours. Only 13% of sexed alien intruders were females. Intruder groups contained only males in 93 sessions, only females in 10 sessions, and mixed-sex groups in four sessions. During these 107
sessions, we recorded 384 encounters between individual Talek adults and aliens, including 202 encounters involving 55 resident females, and 182 encounters involving 47 resident immigrant males.

Talek residents attacked aliens, or aliens directed unsolicited appeasement behavior towards residents, in 68 sessions. In 34 sessions, neither residents nor

Fig. 3: Rates of pasting behavior during border patrols exhibited by resident Talek males and females. Sample sizes indicate numbers of border patrols.

Fig. 4: Sizes of 293 alien groups observed within the Talek clan territory. Alien hyenas met Talek hyenas in 133 cases. Numbers of groups are indicated above bars.

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intruders showed aggression or submission. In five additional sessions, Talek hyenas exhibited submissive behavior to aliens, but showed no aggression, nor did aliens show submission to residents. In each of these five sessions, only one resident hyena was present (four Talek males; one Talek female), and in four cases that individual was outnumbered by aliens.

Resident Talek females were significantly more likely to attack alien females than alien males \( \chi^2 = 11.42; \text{df} = 1; \ p < 0.001; \) Fig. 5). Although resident females appeared more likely than resident males to attack intruding females, this difference was not statistically significant \( \chi^2 = 2.91; \text{df} = 1; \ p = 0.088 \). Similarly, although resident males appeared somewhat more likely to attack alien males than alien females, this difference was not statistically significant \( \chi^2 = 0.735; \text{df} = 1; \ p > 0.10 \). Resident males were significantly more likely than resident females to attack alien males \( \chi^2 = 9.25; \text{df} = 1; \ p < 0.005 \).

The mean hourly rates of aggression directed by individual Talek hyenas towards aliens are shown in Fig. 6. The individuals exhibiting the lowest rates of aggression were resident Talek males confronting alien females. The rates of aggression varied among groups (Kruskal–Wallis test statistic = 7.816; df = 3; \( p = 0.05 \); Fig. 6) and were significantly higher when resident immigrant males encountered alien males than when they encountered alien females (Dunn’s test statistic Q = 5.64; \( p < 0.01 \); Fig. 6). In contrast, rates of aggression directed by Talek females towards aliens did not vary with intruder sex (Dunn’s test statistic Q = 0.171; \( p > 0.05 \); Fig. 6). There was no significant difference between attack rates of resident females and resident males directed towards alien males (Dunn’s test statistic Q = 1.586; \( p > 0.05 \); Fig. 6). However, resident females attacked

![Bar chart showing aggression rates](image)

**Fig. 5:** Percent of resident Talek males and females that attacked alien males or females at least once during an encounter. Sample sizes indicate total number of encounters (resident–alien pairs).
alien females at higher rates than did resident males (Dunn’s test statistic $Q = 5.033; p < 0.01; \text{Fig. 6}).$

**Discussion**

**Intrusion Pressure and Defense of Borders**

The territorial behavior exhibited by spotted hyenas varies among study populations. Vigorous and frequent territorial behavior in *Crocuta* appears to occur where hyena intrusion pressure is intense or when specific carcasses are contested (Kruuk 1972; Henschel & Skinner 1991). In areas characterized by very low hyena density, clans occupy exclusive ranges but there is little evidence of intrusion pressure or contested carcasses in border areas, and both clan wars and border patrols tend to be rare (Tilson & Henschel 1986). Frank (1986a, b) monitored the Talek clan from 1979 to 1983 but observed only three clan wars and rarely saw border patrols or found latrines. Frank concluded that Mara hyena clans occupy ranges with diffuse limits separated by wide areas of ‘no-man’s-land.’ By contrast, our 1988–1998 data suggest that the boundaries of the Talek territory are well-defined (Fig. 1), that the areas Frank (1986a, b) described as no-man’s-land are occupied by members of neighboring clans, and that territories of Mara hyenas form an uninterrupted mosaic in suitable habitat as do those of *Crocuta* inhabiting other areas of eastern Africa (Kruuk 1972; Hofer & East 1993a). The differences between our results and those obtained by Frank (1986a, b) can probably best be explained by differential observation.
efforts: Frank and his assistants observed Talek hyenas for 517 d whereas we watched them for 3120 d. The rates at which clan wars were seen in both studies were in fact quite similar when corrected for the total time spent observing Talek hyenas.

In the current study, alien hyenas were observed frequently in the Talek area, and intruders generally met hostile receptions from the Talek residents detecting their presence. Most of the alien hyenas that could be sexed in the Talek territory were males, a finding consistent with the earlier observation that Talek males, but not females, regularly make exploratory excursions into the territories of neighboring clans in preparation for dispersal (Smale et al. 1997; Holekamp & Smale 1998a). If males originating in neighboring clans behave like Talek males, then many male intruders in the current study were probably visiting Talek to assess prospects for immigration into the study clan. Only 13% of the alien intruders into the Talek territory were females, which stands in marked contrast to the finding by Henschel & Skinner (1991), that 71–89% of intrusions into their clan in southern Africa involved females. Although female Crocuta have occasionally been known to emigrate from their natal clans, successful female immigration into an existing clan has never been observed. Instead, dispersing females either form a new clan or lead nomadic lives (Mills 1990; Holekamp et al. 1993). Thus, heavy intrusion pressure from females in some populations is more likely to be associated with foraging than with dispersal (e.g. Hofer & East 1993b), and in the Talek area, xenophobic behavior towards aliens may help minimize intrusion pressure by foragers from neighboring clans.

Sexually Dimorphic Territorial Behavior

We observed marked differences between adult immigrant male and adult female hyenas with respect to leadership during cooperative territorial activities, marking of territorial boundaries, and aggression toward intruders. Females were more likely than males to lead border patrols and clan wars, and resident females tended to scent-mark along territorial boundaries at higher hourly rates than did adult males. Thus our results support and extend the earlier findings of Henschel & Skinner (1991), who found that resident females scent-marked more frequently than males and invested more time in territorial activities than did males. Our leadership data also suggest that female Crocuta are willing to assume more risks than males during territorial defense. Interestingly, the fact that Talek border patrol groups sometimes contained only resident males demonstrates that group territorial defense is not strictly the domain of females. Nevertheless, the fact that most cooperative territorial activities are led by female spotted hyenas sets this species apart from wolves, jackals, dingos, and other gregarious canids in which males generally take the lead in territorial defense (reviewed in Holekamp et al. 2000).

The sexually dimorphic territorial behavior of Talek hyenas was not limited to leadership, but also expressed itself in probabilities and rates of attack that varied based on the sex of the resident and that of the intruder. During encounters
between residents and aliens inside the Talek territory, residents were more likely to attack same-sex than opposite-sex intruders. Furthermore, although hourly rates of female aggression did not vary significantly with intruder sex, resident males directed higher hourly rates of aggression towards alien males than towards alien females. Thus, spotted hyenas exhibit sexually dimorphic territorial behavior conforming to predictions of game theoretical models suggesting that individual group members should engage in territorial defense in proportion to both their need for resources available in the defended space and the severity of the threat to those resources posed by specific types of intruders (e.g. Hammerstein 1981; Temeles 1989, 1990). In this regard, spotted hyenas also resemble lions, canids and other carnivores (McComb et al. 1994; Grinnell et al. 1995; Heinsohn et al. 1996).

**Sex-Specific Selection Pressures**

The sexually dimorphic territorial behavior observed in the present study suggests that ultimate explanations for territoriality may differ for male and female Crocuta, as they do in lions (Packer et al. 1990; Grinnell et al. 1995; Heinsohn & Packer 1995). Possible explanations for territorial behavior in hyenas include defense of resources such as food or potential mates (e.g. Kruuk & Macdonald 1985) and offspring defense (e.g. Wolff & Peterson 1998). Because resident immigrant male hyenas that have not yet fathered any cubs in Talek may attack alien male intruders (Smale et al. 1997; Engh et al., unpubl. data), the offspring defense hypothesis seems a less likely explanation for male territoriality than does resource defense. Furthermore, access to females limits male reproductive success in this species (Engh et al., unpubl. data), and the fact that rates of aggression by resident males were significantly higher when they encountered alien males than females (Fig. 6) suggests that the most likely explanation for male aggression towards male intruders is defense of potential mates.

Females are the limiting sex in this species, so female territoriality is more likely to be explained by hypotheses suggesting the defense of offspring or food resources than one suggesting the defense of mates. Wolff & Peterson (1998) proposed that female territoriality against other females evolved to protect immobile altricial young from female infanticide. Because hyenas’ cubs reside at dens until 8–12 mo of age (Hofer & East 1993c; Holekamp & Smale 1998b), female territoriality might promote defense of immobile young. Infanticide has been documented by conspecifics of both sexes in Crocuta (e.g. Kruuk 1972; Hofer & East 1995), and offspring defense has been shown to be a powerful selective force promoting group living in other carnivores (Owens & Owens 1984; Packer & Pusey 1984; Packer et al. 1990; Pusey & Packer 1994), so similar selective forces may have shaped territorial behavior by female Crocuta.

In lions, infanticide by adult males accounts for 27% of all cub mortality in the first year of life (Pusey & Packer 1994). Lions and spotted hyenas occur sympatriically in many African ecosystems, utilize virtually identical food
resources, and both live in multi-male, multi-female groups with fission–fusion structures and male-biased dispersal (Packer 1986; Pusey & Packer 1987; Packer et al. 1990; Grinnell et al. 1995). Female lions are most gregarious when they have dependent young and they cooperatively defend young against infanticidal males (Packer et al. 1990; Pusey & Packer 1994). Male lions are approximately 50% larger than females, and this extreme sexual dimorphism probably prevents lone females from confronting males with aggressive defense of young.

In contrast to lions, male spotted hyenas are roughly 10% smaller than females (Matthews 1939; Kruuk 1972; Mills 1990). Thus, although infanticidal behavior may be directed at hyena cubs by conspecifics of either sex (Hofer & East 1995), lone female hyenas can effectively defend their offspring against either male or female intruders detected near their cubs. We have never observed a clan war near a den. Females participate in territorial defense regardless of their reproductive state, and to date only resident Talek hyenas have been observed directing aggressive behavior (including infanticidal aggression) towards cubs of Talek females. Thus it seems unlikely that female Crocuta cooperatively defend their group territories exclusively to protect their offspring from conspecific attack, although this may certainly be a beneficial consequence of territorial behavior.

Serengeti hyenas ignore intruders in transit through their territories, but attack commuters feeding at kills and engage in wars with neighbouring clans (Hofer & East 1993b). In the present study we found that Talek females attack with equal frequency all intruders posing a potential threat to the food supply within their territory. Females may be more likely to attack intruding females than males because the former potentially represent a more severe long-term threat to the food supply. That is, if resident animals reveal any weakness in their territorial defense, alien females may recruit allies in their home clans and attempt to take over the area, as has been observed during clan fission events by Mills (1990) and Holekamp et al. (1993). The defense of food resources has previously been proposed as the primary function of territoriality in spotted hyenas (Kruuk 1972; Henschel & Skinner 1991). Indeed, it appears that natural selection has favored female Crocuta to maintain boundaries of a territory supporting enough herbivore prey to feed themselves and their young throughout the year.

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