Rare Male Aggression Directed Toward Females in a Female-Dominated Society: Baiting Behavior in the Spotted Hyena

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Spotted hyenas (*Crocuta crocuta*) are gregarious carnivores. The females are socially dominant to males, and adult males rarely direct aggression toward adult females. This study analyzed all cases in which adult immigrant males behaved aggressively toward adult females in a large population of free-living hyenas in Kenya, observed for 11 years. Our goals were to describe the conditions under which male attacks on females occur, and address possible adaptive functions. Most aggression directed by adult immigrant males against females occurred when coalitions of two or more males attacked a single adult female, who typically responded by defending herself and fighting back. Male aggression against females frequently occurred at sites of ungulate kills, but males never behaved aggressively toward females over food, and all male attacks on females were unprovoked. Although no mounting or other copulatory behaviors ever occurred during or immediately after an attack, the number of male attacks on females peaked around the time of conception. Daily rates at which males attacked females did not vary with female social rank. However, daily attack rates did vary significantly with female reproductive state, and the highest rates of male attack on females were observed during the two stages of the reproductive cycle during which females were most likely to conceive litters. The adaptive significance of male aggression against females in this species remains unknown, but a tight association between male attacks on females and a female's time of conception provides strong evidence of some role for male aggression in hyena sexual behavior. In particular, our data are consistent with hypotheses suggesting that male aggression toward females in this species either serves to inform females about male fitness or represents sexual harassment. Aggr. Behav. 29:457–474, 2003. © 2003 Wiley-Liss, Inc.

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INTRODUCTION

Aggression directed by males toward conspecific females occurs in a wide range of animal taxa [birds: McKinney et al., 1983; mammals: Smuts and Smuts, 1993; insects: Stone, 1995].

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Male mammals have been observed to behave aggressively towards females in a variety of contexts. For example, male olive baboons (*Papio cynocephalus*) attack females during feeding competition, in defense of a close female associate or her offspring, and during disputes with other males [Smuts, 1985]. In addition, male aggression toward females often occurs in a sexual context [reviewed in Clutton-Brock and Parker, 1995]. Male mammals in species ranging from feral horses (*Equus caballus*) to hamadryas baboons (*Papio hamadryas*) chase and bite females to keep females in their groups and to discourage females from associating with rival males [Linklater et al., 1999; Stammback, 1987]. In other baboons and some macaque species, males behave aggressively toward females to punish persistent refusal to mate [Smuts, 1987]. In some species, males may physically force females to copulate with them, as observed in orangutans [*Pongo pygmaeus*: Mitani, 1985]. All of the species mentioned above exhibit strong sexual dimorphism in morphology and behavior. That is, males are larger and better armed than females, and males dominate females. Here we document male aggression against females in the spotted hyena, a species in which females exceed males in body size by approximately 10%, and in which females are socially dominant to males [Kruuk, 1972].

Spotted hyenas are gregarious carnivores that live in social groups called clans. Each clan contains one to several matrilines of adult females and their offspring, as well as one to several immigrant adult males. Clans are rigidly structured by hierarchical rank relationships [Frank, 1986b; Holekamp and Smale, 1990, 1993; Kruuk, 1972; Mills, 1990; Tilson and Hamilton, 1984;], and an individual's social rank determines its priority of access to food and other resources [Frank, 1986b; Kruuk, 1972; Tilson and Hamilton, 1984]. Adult females are socially dominant to all adult males not born in the clan [Kruuk, 1972; Smale et al., 1993].

In addition to discerning that female *Crocuta* are socially dominant to males, Kruuk [1972] observed that the only circumstances under which adult male hyenas behave aggressively toward adult females involve what he called ''baiting'' behavior. During baiting, the female hyena sits or lies in a crouched position with her ears flattened back against her head and her teeth bared, while multiple males surround her with their ears cocked forward and their elevated tails bristled. The males often rush at the female, and attempt to sniff or bite her, and she sometimes sustains serious wounds from their attacks [Kruuk, 1972]. The female defends herself, often lunging at one or more of the participating males, and she may inflict serious wounds on them. Kruuk [1972] was uncertain about the adaptive significance of this odd behavior pattern, but he doubted that baiting was related to sexual behavior, during which males show fear and behave in extremely submissive ways toward females.

Here we present data suggesting that this rare male aggression directed toward females is tightly coupled to female reproductive state in spotted hyenas. First we compare rates at which intrasexual and intersexual aggression occur among free-living *Crocuta*. We then examine the circumstances under which male hyenas behave aggressively toward females, and consider the possible proximate causes and adaptive function of male aggression directed toward females in this species. We address four hypotheses that suggest possible adaptive functions of female-directed male attacks. We test predictions of these alternative hypotheses to inquire whether male hyenas attack females to displace females from desired resources, to test female receptivity, to coerce females into estrus, or to demonstrate some aspect of male fitness to prospective mates. Female hyenas are philopatric, but all males disperse to new clans sometime after reaching reproductive maturity at age two [Smale et al., 1997]. Although adult natal males occasionally participate with immigrant males in coalitionary aggression directed at females, such participation is rare [Holekamp and Smale, 1998]. We therefore focus exclusively on aggressive interactions between immigrant males and adult females.

METHODS

Subject Animals and Study Area

This study was conducted in the Talek area of the Masai Mara National Reserve, in southwest Kenya. This is an area of open, rolling grasslands grazed year round by large concentrations of several different ungulate species. The subject population was one large *Crocuta* clan inhabiting a home range of approximately 65 km^2 [Boydston et al., 2001; Frank, 1986a] and was monitored continuously from June 1988 through August 1999. We identified all hyenas in the Talek study clan individually by their unique spot patterns, and we determined their sex from the dimorphic glans morphology of the erect phallus [Frank et al., 1990]. Mother-offspring relations were established on the basis of regular nursing associations. We photographed immigrant males immediately upon their first sighting in the Talek area. A male's tenure in the study clan at the time when he performed a behavior of interest was calculated by subtracting his date of arrival from the date on which that behavior was observed.

Behavioral Observations

Throughout the study period, we recorded all approaches, appeasements, and aggressive behaviors among hyenas as critical incidents [all-occurrence sampling of Altmann, 1974]. We recorded an approach when one individual moved to within 1 m of another individual. Appeasement behaviors included head bob, carpal crawl, giggle, squeal, back off, and assumption of the body posture in which the ears are flattened back against the head, the tail is tucked between the legs, the body is lowered and bent, and the head is down. Listed in order of increasing intensity, aggressive behaviors included displace, intention movement to bite, push, stand over, lunge, rush, snap, chase, and bite [Holekamp and Smale, 1990]. Any interaction between two or more hyenas in which we observed one or more of these individual acts of aggression was called an aggressive interaction, or attack. We calculated "baiting rates" as the number of attacks by males against females per unit time. For some analyses we divided acts of aggression into "low intensity" and "high intensity" categories. The former included displace, intention movement to bite, push, stand over, and lunge. The latter included rush, snap, chase, and bite. If an aggressive interaction involved only one aggressor and one recipient, we called it a dyadic interaction. By contrast, a coalitionary interaction involved two or more aggressors attacking a single target animal.

We assigned each aggressive interaction a location, the physical locality where the interaction took place, and a context, the social situation immediately preceding the attack. Locations included "dens," "kills," and "other" places away from dens or food. We observed aggressive interactions among adult hyenas in the following five contexts: during competition over food, in defense of cubs, when one hyena was pestering (e.g., persistent sniffing, etc.) another, during displacement aggression, and in situations where none of these other possibilities applied, such that the aggression appeared to be entirely unprovoked.

We calculated daily rates at which adult hyenas of each sex emitted and received aggression for a portion of the study period, between June 1988 and May 1995. For this analysis, we divided the number of aggressive interactions involving each individual as either attacker or target by the total number of hours each individual was observed during that period, and then multiplied this number by 24. In a separate analysis, we calculated the percent of attacks emitted and received by adults of each sex that occurred in coalitions by summing the number

of attacks occurring in coalition, dividing by the total number of attacks, then multiplying this value by 100.

We determined intrasexual social ranks of individuals in the clan's dominance hierarchy from outcomes of several thousand dyadic agonistic interactions during which one individual exhibited appeasement to the other, whether or not the appeasement was elicited by aggression from the social partner, as described by Holekamp and Smale [1990] and Smale et al. [1993]. By convention, the highest-ranking (alpha) individual was assigned a rank position of one. To evaluate frequency of male aggression towards other males as a function of social rank category, we calculated rates of male attacks on other males during an 8.6–month period for which the male hierarchy was completely stable. When contrasting rates of male aggressive behavior directed at other males or at females, we divided male social ranks into three equal rank categories: high, middle, and low.

For each aggressive interaction in which one or more males attacked a female, we recorded the identity and social rank of the female target and of each attacking male. For each attack, we also recorded, whenever possible, the particular acts of aggressive behaviors emitted by each individual male, the female's responses to each individual male (classified simply as aggressive or non-aggressive), and the location, context, and duration (in minutes) of each attack.

We determined whether rate or intensity of male aggression varied with female reproductive condition. To do this, for the date on which each intrasexual aggressive interaction was observed, we assigned each female to one of the six reproductive states described below. If we were uncertain about a female's reproductive condition when she was the target of male aggression, then that interaction was excluded from relevant analyses. We defined the six reproductive states as follows:

Nulliparous (N). Here females were older than 24 months, but had not yet conceived their first litter. The youngest age at which female *Crocuta* in this population first conceived was 25.4 months, and females were observed to copulate as early as 24.2 months of age [pers. obs.]. Age at first parturition can readily be established in this species because the female bears an enlarged clitoris (the pseudopenis) which tears when her first litter is born [Frank and Glickman, 1994], and heals leaving a large patch of pink scar tissue on its posterior surface. The condition of this surface was carefully monitored in all nulliparous females older than 2 years, during the phallic erections commonly exhibited when hyenas greet each other [East et al., 1993; Kruuk, 1972]. Thus, even when a female's first litter was lost before her cubs first appeared above ground, it was possible to reliably determine when (to within 10 days) she had delivered her first litter.

Pregnant (P). The duration of pregnancy in *Crocuta* is 110 ± 1 days [Kruuk, 1972; Schneider, 1926; M.L. Weldele, pers. comm.]. We assigned birth dates to litters by estimating cub ages when we first observed cubs above ground at natal or communal dens. Cub ages could be estimated to ± 7 days based on their pelage, size, and other aspects of their appearance and behavior. We calculated conception dates by subtracting 110 days from estimated birth dates, thus resulting in conception dates that were accurate to ± 8 days. Although most female hyenas wean one litter weeks or months before conceiving another, females of all social ranks have occasionally conceived while still nursing a previous litter [Holekamp et al., 1996]. Females known to be pregnant while still lactating were assigned a reproductive state of 'P'.

Lactating (L1, L2, L3). The lactation interval began with the birth of a litter and ended with its weaning. Weaning conflicts and cessation of nursing indicated when cubs were

weaned. Weaning conflicts between cubs and their mothers are easily observed in this species due to the characteristic begging behavior and loud whining exhibited by cubs at this time. We recorded all weaning conflicts in field notes as critical incidents [Altmann, 1974]. In determining weaning dates, we searched all field notes for observations of nursing behavior when mother and cub were found together. If mother and cub were not found together frequently after the last observed nursing bout, we identified the weaning date as being midway between the last nursing bout and the next sighting of mother and cub together without nursing. However, we only used intervals of 20 days or less in this analysis, so all weaning dates used here were accurate to within $\pm$ 10 days. Lactation periods vary in length among Talek females from 7 to 21 months [Holekamp et al., 1996; Holekamp and Smale, 2000]. Therefore, to compare rates and intensities of male aggression among females with different lactation period lengths, we divided the total period of lactation into three periods of equal length (represented as L1, L2, and L3) for each female.

Other (O). Females assigned to this condition had weaned one litter but had not yet conceived their next litter. Little is known about the reproductive cycle of the spotted hyena. Matthews [1939] and Lindeque [1981] suggested that estrous cycles in this species recur every 14 days, but there are no apparent external morphological indicators of estrus in female spotted hyenas, and copulations are rarely observed.

For each female in each reproductive state, we calculated a daily rate of male aggression toward that female using the formula: (number of male attacks directed at each female per reproductive state/total number of hours the female was observed in that state * 24 hrs). We assigned any adult female who was observed but not attacked by males while she was in a given reproductive state a daily rate of zero for that state.

We next examined the occurrence of male aggression relative to the date of a female's nearest conception. We calculated time relative to conception by subtracting the female's nearest conception date from the date on which she was observed being attacked by males, and then dividing occurrence of these attacks into month-long intervals. Together, the two 2–week intervals on either side of the conception date represented month ''zero.''

Paternity Determination and Statistical Analysis

We used determination of paternity to compare rates of male aggression toward each female *Crocuta* between males who sired a particular litter of her cubs and males who did not sire those cubs but who were present with that female during the period in which that litter was conceived. We used nuclear genetic markers to determine paternity of cubs born in the Talek clan [Engh et al., 2002]. Between 1990 and 1999, we collected blood from 191 Talek hyenas anaesthetized with Telazol (2.5 mg/kg) delivered from a CO_2-powered rifle in a lightweight plastic syringe. We then immediately extracted DNA from whole blood using Puregene kits (Gentra Systems, Inc.), and stored the extracted DNA in liquid nitrogen.

We considered all adult males present in the clan at the time of conception as potential sires. Paternity assignments were based on 12 microsatellite markers described elsewhere [Engh et al., 2002; Libants et al., 2000]. We employed a maximum-likelihood approach [Meagher, 1986; Thompson, 1975] to assign paternity to cubs with known, genotyped mothers using the program CERVUS [Marshall et al., 1998]. A male was considered the father of a cub when CERVUS assigned him as such with 95% confidence. A more comprehensive analysis of paternity in the Talek clan is presented by Engh et al. [2002].

Our behavioral data were not normally distributed, so we conducted all analyses using non-parametric tests. Mean values were presented as $X \pm SE$, and we considered differences between groups to be statistically significant when $P < 0.05$. All statistical tests were two-tailed.

RESULTS

Sex Differences in Aggression

We first compared rates at which intrasexual and intersexual aggression occurred among spotted hyenas. Adult male hyenas behaved aggressively toward other adults at far lower mean daily rates than did adult females (Fig. 1A; Mann-Whitney U: $U_1 = 409.000$, $P < 0.001$). In particular, the aggressive behavior of males and females toward adult females differed dramatically (Mann-Whitney U: $U_1 = 444.000$, $P < 0.001$). In contrast to females, who were frequently aggressive toward other females, adult males very rarely attacked adult females, and did so at significantly lower rates than they attacked other males (Wilcoxon signed-ranks test: $Z = -3.621$, $N = 20$, $P < 0.001$). In fact, during over 30,000 observer hours watching Talek hyenas between 1988 and 1995, we observed only 256 individual acts of aggression in 195 attacks directed at adult Talek females by adult immigrant males, compared to 1,207 aggressive acts in 826 attacks on adult immigrant males by adult females during the same period. The 256 acts of aggression directed by males toward females involved 30 different adult females, and 40 different adult immigrant males participated in at least one of these events. On average, each of these 40 males participated in 12.4 ± 1.8 (range: 1–51) attacks directed at adult females during his tenure in the Talek clan.

Intensity of aggression varied among intrasexual and intersexual attacks (Fig. 1B). Male attackers exhibited a significantly lower proportion of high-intensity aggression than we observed for female attackers, regardless of the sex of the target animal ($\chi_1^2 = 94.52$, $P < 0.001$). Immigrant males exhibited the lowest proportion of high intensity aggressive behaviors when attacking adult females (($\chi_1^2 = 26.02$, $P < 0.001$). Adult females exhibited the greatest proportion of high intensity aggressive behaviors, with 60% of individual acts of aggression by females being of high-intensity, regardless of the sex of the target animal.

In contrast to male-male aggression and aggression directed against either sex by adult females, most (76%) male attacks upon females occurred in coalitions (Fig. 1C). The proportion of total attacks on adult males that occurred in coalitions was similar for male and female aggressors ($\chi_1^2 = 1.475$, NS), but a significantly larger proportion of attacks on adult females occurred in coalitions formed by male aggressors than by female aggressors ($\chi_1^2 = 232.99$, $P < 0.001$). Both males and females were significantly more likely to form coalitions to attack females than to attack males (male attackers: $\chi_1^2 = 161.2$, $P < 0.001$; female attackers: $\chi_1^2 = 34.18$, $P < 0.001$).

Interestingly, females were significantly more likely to respond aggressively to males approaching them in an aggressive manner than to males who approached females without exhibiting any aggression ($\chi_1^2 = 44.05$, $P < 0.001$). In general, females responded with counter-attack to males who approached aggressively, whereas they tended to ignore or investigate males who approached in a non-aggressive manner. Male hyenas thus increased their own risk of injury by behaving aggressively towards females.
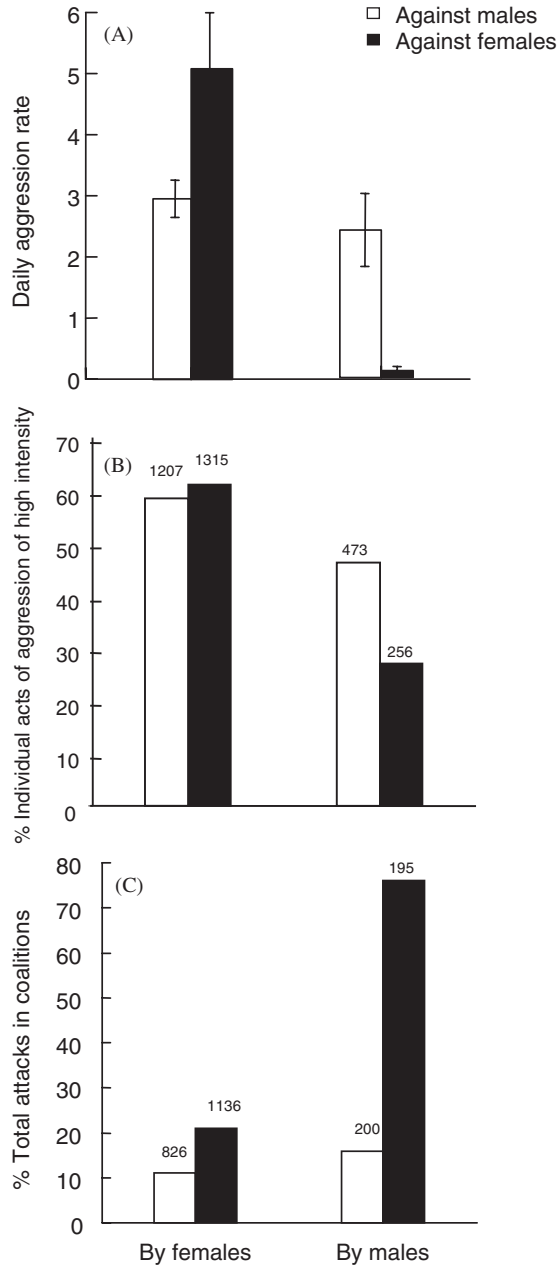
Figure 1. Comparison of intra- and intersexual aggression observed among adult Talek hyenas between 1988 and 1995. (A) Daily rates (mean ± SE) at which adult hyenas (N = 23 females and 20 immigrant males) directed aggression toward other adults of each sex, controlled for the number of hours observed during which each adult was found in the presence of other adults of each sex. (B) Percent of total individual acts of aggression of high intensity directed by male and female hyenas toward members of the same and opposite sex. Sample sizes indicate total number of individual aggressive acts observed. (C) Percent of total attacks on other adults that occurred in coalitions. Sample sizes indicate total number of attacks observed.

Male Aggression Toward Females

Having thus established that male aggression toward females is relatively rare in this species, we next described the conditions under which male attacks on females occurred. The number of males participating concurrently in attacks on adult females varied from one to six (Fig. 2), with a mean of 2.5 ± 0.1 males joining forces per attack. On average, each male who participated in these attacks directed 1.9 ± 0.1 (range: 1–19) individual acts of aggression at the female per attack. The two most intense forms of aggression, chasing and biting, were directed at females in 15.6% of attacks. On average, male attacks on females lasted 3.84 ± 0.49 min (range 0.5 to 49 min), and attack duration did not vary with the number of males participating (Kruskal-Wallis: $KW_5 = 3.204$, NS).

Male aggression toward females was remarkably consistent in appearance, despite variability in the number of participating males. As males approached, they typically bristled their manes and tails, and surrounded and rushed the female, who crouched defensively in their midst with her teeth bared (Fig. 3). Because the form of male attacks upon females was so consistent in appearance, and because it invariably resembled the intersexual aggressive interactions Kruuk [1972] called "baiting behavior," we adopted Kruuk's terminology. Thus "baiting" will henceforth be used here to refer to an unprovoked aggressive attack directed by one to several adult males toward a single adult female, who responds by defending herself, and sometimes also with counter-aggression.

During most intrasexual aggressive interactions, and aggressive interactions in which females attacked immigrant males, approach or attack by one or more dominant animals elicited unambiguous submissive behavior from the targeted lower-ranking individual [Smale et al., 1993]. That is, when aggressors approached targets, the aggressors' heads were held high, their ears were cocked forward, their manes and tails were bristled, and they stood their ground at the end of the interaction. During these ordinary aggressive interactions,
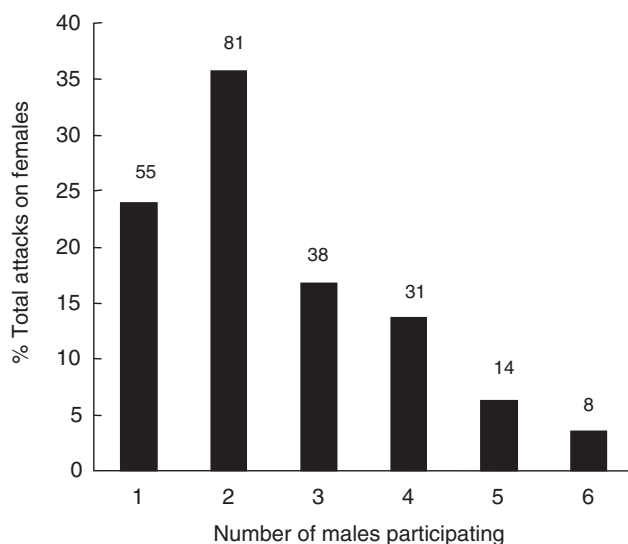

Figure 2. Numbers of individual males participating in 227 attacks on adult females. Sample sizes indicate numbers of interactions observed between 1988 and 1999 in which adult immigrant males attacked adult females.

Figure 3. Example of male coalitionary aggression toward a female. Three males surround and attack a female, who crouches in the center of the photograph with her teeth bared. Note the males' bristled tails, indicating a high level of excitement. Note also, however, that the second male from the left simultaneously bristles his tail and flattens back his ears, indicating motivational conflict. Photo by M. Szykman.

subordinates flattened their ears back against their heads, tucked their tails between their legs, exhibited a facial expression called a "fear grin," bobbed their heads up and down, and backed off or fled to terminate the interaction. By contrast, males engaging in baiting behavior usually held their heads high with their ears cocked forward and manes and tails bristled (e.g., Fig. 3), yet they often simultaneously bobbed their heads up and down, backed away spontaneously from the crouching female, and fled when singled out and chased by the targeted female. Thus, males participating in baiting appeared to experience conflicting desires to attack and flee. Although females targeted during baiting crouched to defend vulnerable body parts and flattened their ears back, they did not otherwise exhibit typical submissive behavior. The baring of teeth by baited females clearly involved the contraction of a different set of facial muscles from those contracted during normal "fear grins" [Kruuk, 1972]. When baited by a lone male, an individual female was readily able to demonstrate her dominant status, and she never backed off from, or submitted to, the attacking male. However, when surrounded by a group of males, the female appeared to experience greater difficulty protecting herself from simultaneous attack by multiple individuals. Thus, males acting in groups launched attacks against socially dominant females, yet these coalitionary attacks did not result in any change in dyadic rank relationships between individual males and females.

Males baited females at a variety of locations where many hyenas were found together. Eleven percent of male attacks upon females occurred at dens, 26% occurred at sites of ungulate kills, and 63% occurred at locations away from dens or food (Table IA). Whereas

TABLE I. (A) Locations and (B) Contexts in Which Individual Acts of Aggressive Behavior Were Observed Between 1988 and 1995.*

		Female-Female		Female-Male		Male-Male		Male-Female	
		Number	%	Number	%	Number	%	Number	%
A	Location								
	Dens	483	58.5	378	33.3	47	23.7	28	10.8
	Kills	307	37.2	391	34.4	102	51.0	67	26.2
	Other	36	4.3	367	32.3	51	25.4	161	63.1
	Total	826		1136		200		256	
B	Context								
	Food	342	54.0	194	43.7	97	60.6	0	0.0
	Intervention	16	2.5	1	0.2	0	0.0	0	0.0
	Pestering	40	6.3	11	2.5	0	0.0	0	0.0
	Displacement	42	6.6	19	4.3	25	15.6	0	0.0
	Unprovoked	151	23.9	215	48.4	35	21.9	256	100.0

Column headings specify each individual's role in the dyadic interaction, i.e. aggressor –victim. (Note: aggressive acts by males toward females observed between 1996 and 1999 are considered in the text but are not included in this table.)

the duration of male attacks on females did not vary with location (Kruskal-Wallis test: $KW_2 = 3.269$, NS), the number of participating males was significantly greater at kills than at dens or other locations (Kruskal-Wallis test: $KW_2 = 13.841$, $P < 0.001$). This may be due to the fact that average numbers of hyenas of both sexes present at kills were greater than average numbers of hyenas found at dens or locations away from dens or food (Kruskal-Wallis test: $KW_2 = 535.225$, $P < 0.001$). Nevertheless, even when males outnumbered females at kills, males were never able to usurp food from feeding females. At 886 fresh ungulate carcasses where both immigrant males and adult females were present during 640 hours of observation, not once was an adult immigrant male ever observed displacing an adult female from food.

Regardless of the location of these aggressive interactions, all male baiting of females appeared to be entirely unprovoked (Table 1B). No male aggression toward females occurred during feeding competition, even when food was present at the location of the interaction. Furthermore, no baitings occurred during defensive interactions on behalf of another hyena, during displacement aggression, or in response to the female pestering males. By contrast, male-male aggression occurred in a variety of different contexts (Table IB), most often during displacement aggression and feeding competition, where high-ranking males were able to supplant lower-ranking males from desired resources. Thus, the context and nature of female-directed male aggression distinctly differed from other, more frequently observed, intrasexual aggression.

Effects of Male Rank and Tenure in the Clan

We next examined the identity of individual males participating in attacks against females. Baiting rates varied significantly as a function of male rank category. High- and middle-ranking males baited females at higher rates than did lower-ranking males (Kruskal-Wallis

test: $KW_2 = 28.683$, $P < 0.001$). This was not merely a function of high-ranking males behaving more aggressively in general. High-ranking males were no more aggressive toward other immigrants than were lower-ranking males, even when taking into account the number of potential targets available to males at each rank (Kruskal-Wallis test: $KW_2 = 0.202$, NS).

Individual males baited females at rates that varied greatly (range: 0.4–6.4 baitings/day observed/tenure year in clan). There was a 15–fold difference between the minimum and maximum rates at which males baited females over their full tenure in the clan. However, due to the high variation among years for individual males, differences in baiting rates among individual males were not statistically significant (Kruskal-Wallis test: $KW_{31} = 40.024$; NS). Nevertheless, individual males varied significantly with respect to the number of individual aggressive acts directed towards females during each baiting (Kruskal-Wallis test: $KW_{31} = 65.610$, $P < 0.001$).

Male tenure is a better predictor of male reproductive success than is social rank in the spotted hyena [Engh et al., 2002], but here tenure could not predict baiting rates better than could male social rank. Daily baiting rates did not vary significantly with year of male tenure (Kruskal-Wallis test: $KW_{10} = 15.384$; NS). However, the proportion of males who were observed baiting females did generally increase with tenure in the clan ($\chi^2_{10} = 20.796$, $P = 0.02$). Only 30% of males in their first year in the clan baited Talek females, whereas 50–70% of males remaining in the clan for 2 to 9 years were observed baiting females in each respective year of tenure. All males remaining in the clan for 10 or 11 years were observed to bait females during their last years of residence in the clan, although only two males persisted in the Talek clan for such a long period of time.

Effects of Female Reproductive State and Female Social Rank

Female reproductive state dramatically influenced the overall daily rate at which females were baited (Fig. 4; Kruskal-Wallis test: $KW_5 = 19.313$, $P = 0.002$). We found females being baited in all six reproductive states. We observed individual females in each reproductive state for a range of 0–844.6 hours. Mean ($\pm SE$) hours of observation for females in each phase of their reproductive cycle were $X_N = 17.9 \pm 8.4$, $X_P = 66.2 \pm 14.8$, $X_{L1} = 120.5 \pm 22.1$, $X_{L2} = 84.8 \pm 18.2$, $X_{L3} = 56.0 \pm 12.4$, $X_O = 24.5 \pm 6.8$ hours per female. Baiting rates were significantly higher when females were in either the last third of the lactation interval, or between weaning and conception, than when females were in any other reproductive state. This is noteworthy because it is while females are in these two particular reproductive states that they are known to conceive. As mentioned earlier, females are probably often cycling during the "other" state, and must also often cycle during their last trimester of lactation, as females are sometimes known to maintain lactation and pregnancy concurrently. Mean baiting rates did not differ significantly between the L3 and O intervals (Mann-Whitney U test: $U_1 = 300.000$; NS).

Most baitings occurred during the last months preceding conception, with the greatest number of baitings observed during the month in which conception occurred (Fig. 5). However, we never observed males mounting females during, or immediately after (on the same day as), a baiting event. The number of observed baitings dropped off sharply during the second month post-partum. Overall, males baited females at significantly higher rates before than after conception (Wilcoxon signed-ranks test: $Z = 2.184$, $N = 97$, $P = 0.029$).

Neither the number of male participants per baiting (Kruskal-Wallis test: $KW_5 = 6.557$, NS), nor baiting duration (Kruskal-Wallis test: $KW_{15} = 8.544$, NS) varied with female
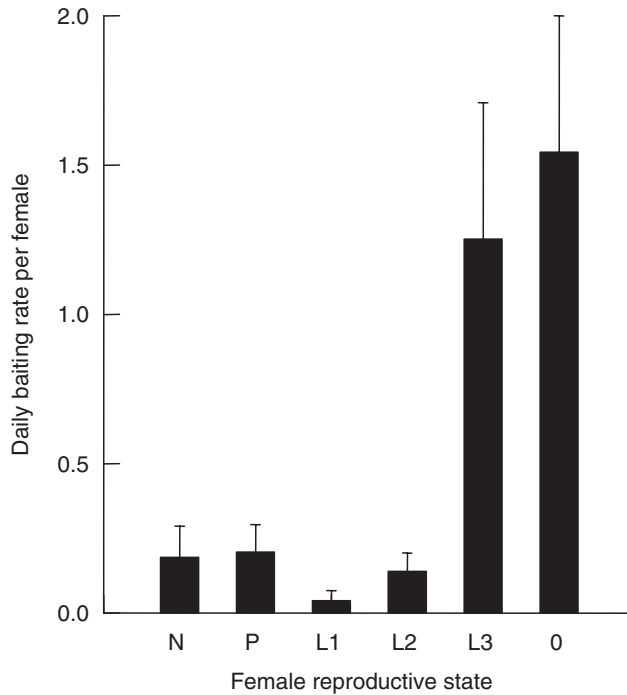
Figure 4. Daily baiting rates (mean±SE) per female for 22 females observed in all six reproductive states between 1988 and 1995. "N" indicates nulliparous, "P" indicates pregnant, "L1" represents the first trimester of the lactation interval, "L2" indicates the second trimester of the lactation interval, "L3" indicates the third trimester of the lactation interval, and "O" indicates the period between weaning one litter and conceiving the next.

reproductive state. Proportions of high and low-intensity acts of aggression directed at the female by participating males did not vary with female reproductive state ($\chi^2_5 = 3.77$, NS). The proportion of baitings in which the target female responded to male aggression with an aggressive counterattack also did not vary with female reproductive state ($\chi^2_5 = 3.90$, NS). Furthermore, in 68% of male attacks upon females that were either in the last trimester of lactation or between weaning one litter and conceiving the next, the female left her defensive crouch to threaten or chase one or more of the participating males, whereas in 32% of these interactions her behavior was entirely defensive. Thus, even when females were most likely to be sexually receptive, they usually responded to male aggression with aggressive counterattack.

We observed females of all social ranks being baited. We found no significant relationship between daily baiting rates and female rank for females in any particular reproductive state, or overall (Spearman rank correlation: $r_s = -0.301$, N = 18, NS). Furthermore we found no significant relationship between a female's social rank and either the number of males participating in her baitings (Kruskal-Wallis test: $KW_{18} = 20.311$, NS) or the duration of her baitings (Kruskal-Wallis test: $KW_{15} = 18.807$, NS).

Baiting Behavior Compared for Sires and Nonsires

We next contrasted baiting behavior of males who sired cubs with that of males present concurrently with sires who failed to sire offspring to determine if baiting behavior was
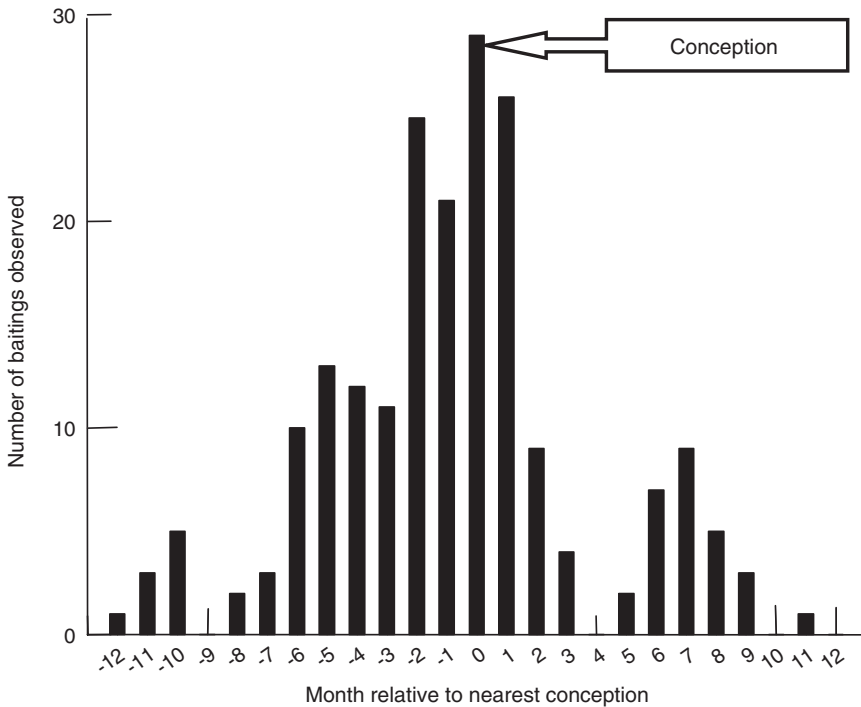
Figure 5. Observations of baitings relative to the date of the nearest female conception. The interval labeled "0" represents the period starting 2 weeks prior to conception and ending 2 weeks after conception. The interval labeled "1" thus represents the period 2–6 weeks after conception, and so forth. For this analysis, we only included baitings that took place within one year of a female's nearest conception. (N = 172 baitings of 27 females)

correlated with male reproductive success. During the period 1991–1999 for which we have paternity data, we observed 201 baitings. Only 49 (24.4 %) of these baitings were observed within six months of conceptions of litters with known paternity. When we compared the proportion of baitings in which sires and non-sires participated during six-month time blocks before and after conception, we found no significant difference between sires and non-sires ($\chi_1^2 = 0.178$, NS). Nor did overall rates of baiting behavior differ between sires and non-sires during this year-long time period (Mann-Whitney U test: $U_1 = 613.000$, NS). However, whereas sires baited females at similar rates both before and after conception (Wilcoxon signed-ranks test: $Z = 0.356$, $N = 11$, NS), non-sires baited females at significantly greater rates before than after conception (Wilcoxon signed-ranks test: $Z = 2.106$, $N = 86$, $P = 0.035$). We found no significant difference between the mean number of individual acts of aggression per male per baiting for males who sired cubs during a female's reproductive cycle and those males who did not sire cubs of that particular female at that time (Mann-Whitney U test: $U_1 = 1096.000$, NS). Finally, females did not appear to respond differently to attacks carried out by males who went on to sire cubs with them and to those by males who did not sire cubs. That is, the proportion of male attacks to which females responded aggressively did not differ significantly between sires and non-sires ($\chi_1^2 = 3.342$, $P = 0.07$, NS).

DISCUSSION

Features of Male Aggression Toward Females

Kruuk [1972] first observed that female spotted hyenas appear to be more aggressive than males, and our results quantitatively confirm that females are indeed more aggressive than males in this species. Adult immigrant male hyenas exhibit intrasexual aggressive behavior at far lower daily rates, and at lower intensities, than do adult females, and rates of intrasexual aggression are higher for both sexes than are rates of intersexual aggression. Rates of male aggression toward females are far lower in *Crocuta* than in most other species for which male aggression directed toward females has been quantified [e.g. chimpanzees, *Pan troglodytes*: Goodall, 1986; rhesus macaques, *Macaca mulatta*: Lindburg, 1983; Bercovitch et al., 1987; Japanese macaques, *Macaca fuscata*: Soltis et al., 1997; savanna baboons: Hausfater, 1975; orangutans: Mitani, 1985; elephant seals, *Mirouanga elaphus*: LeBoeuf and Mesnick, 1990; Mesnick and Le Boeuf, 1991; wild horses, *Equus* sp.: Berger, 1983, Berger, 1986 #338; dolphins, *Tursiops* sp.: Connor et al., 1992a,b]. Darwin [1871] noted that males of most polygynous species are "more pugnacious" than females, but the reverse is clearly true in the spotted hyena. Male attacks on females occur rarely in hyenas and usually involve coalitions of several males. These attacks occur wherever male hyenas encounter adult females, and all male attacks on females are entirely unprovoked.

High- and middle-ranking males baited females at higher rates than did lower-ranking males, and the proportion of males who participated in baitings increased with male tenure. Although reproductive success among male hyenas tends to increase with rank and tenure [Engh et al., 2002], we could detect no differences in rates or intensities of baiting between males who sired cubs and males who did not sire cubs. However, our failure to detect such differences may be due to small sample sizes.

Females of all social ranks were baited with equal frequency and comparable intensity. Females were baited throughout the reproductive cycle, but baiting rates were highest during periods when they were most likely to conceive litters. Kruuk [1972] believed that baiting in spotted hyenas was unrelated to sexual behavior because, whereas high levels of intersexual aggression are observed during baiting, aggression by males toward females is never observed in association with copulation. Our observations confirm that male hyenas never attempt to mount females during baiting as, for example, do male dolphins during coalitionary "herding" of females [Connor et al., 1992b]. However, our analysis of baiting behavior revealed a strong association with female reproductive state. Baiting rates were extremely low during pregnancy and during the first two-thirds of the lactation interval and were highest for females in the two stages of their reproductive cycle during which they were most likely to conceive. Similarly, male aggression toward females in many other mammalian species is most commonly observed near the time of conception [reviewed in Smuts and Smuts, 1993]. Our data lead us to conclude that, despite their unlikely appearance, male attacks on females are somehow related to sex in the spotted hyena.

Possible Functions of Male Aggression Toward Females

Four hypotheses suggest possible adaptive functions of male attacks directed toward females in the spotted hyena. First, male hyenas might attack females to displace them from desired resources. This hypothesis predicts that baiting should occur in temporal association with feeding competition, and that males should at least occasionally be able to usurp food

from females. Although 26% of observed baitings occurred at sites where ungulates were killed and devoured, no male attacks against females involved contests over food or any other resource. Furthermore, since immigrant male hyenas invariably defer to females during feeding competition [Frank, 1986b; Kruuk, 1972; Tilson and Hamilton, 1984], we can promptly reject this hypothesis.

A second hypothesis suggests that aggressive behavior might allow males to test female receptivity [Beach, 1976]. If males are using aggressive acts to test female receptivity, then we would predict that responses by females to male attacks should vary with female reproductive condition, but we found no such variation. In many other mammalian species, males assess female reproductive state via investigation of chemical signals emitted by females [e.g., Johnston, 1983], yet such assessment is generally not associated with attack behavior directed by males at females. Male *Crocuta* also frequently engage in a variety of nonaggressive behaviors that appear to give them information about a female's current reproductive state, such as sniffing her body and recently excreted urine and feces which contain gonadal steroid hormones and their metabolites [Koretz, 1992; Dloniak et al., Glickman et al., unpublished data]. Our observations demonstrate that male approach is less likely to be met with aggression by the female if the male approaches non-aggressively than if he approaches during attack. As a result, risk of injury to both the male and the female is lower for non-aggressive interactions. Therefore, we conclude that baiting behavior does not appear to function to yield information about female receptivity.

Third, male attacks directed toward females might serve in this species as a form of sexual coercion. That is, baiting behavior might function to increase the probability that a female will mate with a particular male at a time when she is likely to be fertile, and to decrease the probability that she will mate with other males at that time. As summarized by Smuts and Smuts [1993], this hypothesis predicts that male aggression toward females should occur frequently when females are most likely to conceive new litters, should occur infrequently when females are in other phases of their reproductive cycles, and should incur some cost to the female. These predictions are confirmed by our observations of male aggression toward females among *Crocuta*.

Clutton-Brock and Parker [1995] suggested that three general forms of sexual coercion occur in animal societies: (1) intimidation, where males punish females who refuse to mate and thus increase the probability of securing future matings, (2) forced copulation, where physical force is used to achieve intromission, and (3) harassment, where male aggression imposes costs on females that increase the probability of immediate mating. Intimidation seems unlikely here considering that adult female *Crocuta* are approximately 10% larger than males [Frank, 1986b; Kruuk, 1972; Matthews, 1939; Wildon, 1968], and sport weapons that are indistinguishable from those of males [Van Horn et al., 2003]. Forced copulation can be ruled out altogether in this species in light of the monomorphic external genitalia of males and females. That is, the female's clitoris is elongated into a fully erectile pseudopenis, through which the urogenital canal extends, and through which the female urinates, copulates, and gives birth [Frank et al., 1990; Matthews, 1939; Neaves et al., 1980]. The bizarre genital morphology of the female makes rape impossible, and intromission by the male requires complete female cooperation.

Male aggression toward females might serve as sexual harassment and function to elevate stress levels in females or alter female reproductive endocrinology. Baiting of lactating females might induce stress that reduces milk production, and thus might hasten the end of lactation. Stress is known to depress milk production in other mammals [e.g. dairy cows,

Bos taurus: Ray et al., 1992; Tancin et al., 1995]. Baiting of female hyenas during the early weeks of pregnancy might stress females when embryos are highly vulnerable, and thus induce abortion [Wasser and Barash, 1983]. Although we currently have no method for detecting abortions in free-living hyenas, we found that 13 of 20 (65%) observed copulations failed to result in the birth of a litter. Baiting during the period between weaning one litter and conceiving the next might alter the reproductive endocrinology of the non-pregnant female to bring her more rapidly into estrus. We can infer that baiting imposes costs on female *Crocuta* because females sometimes sustain wounds during baiting, females often fight back in ways that risk further injury, baiting appears stressful for female targets, and baiting occupies time and uses energy that females might otherwise spend resting, foraging, or caring for their cubs.

Finally, baiting might function to demonstrate some aspect of male fitness to prospective mates. This hypothesis predicts that aggressive behavior directed at females should vary among individual males, and that male reproductive success should vary with some parameter of male aggressive behavior. Although rates of baiting did not vary with statistical significance among individual males, there was a 15–fold difference between the minimum and maximum rates at which any individual male baited females. This, together with our results showing that individual males did vary significantly with respect to numbers of aggressive acts they directed toward females during each baiting, suggests that there are individual differences in baiting behavior among males, which might potentially reflect male fitness. However, males did not appear to gain direct mating opportunities as a result of baiting. Males who sired the cubs of particular females did not bait them at greater rates or higher intensities than did males who failed to sire those cubs. Nevertheless, females might assess males based on some particular aspect of individual male behavior during baiting. Therefore, the hypothesis remains viable that males may demonstrate some aspect of their fitness to females during baiting. Here, cases in which we were able to reliably record all specific behavioral acts by all participating males were too few to yield much statistical power, so this matter remains unresolved.

In spotted hyenas, male aggression directed towards females remains a fascinating and mysterious phenomenon. The tight association between male attacks on females and their time to conception provides strong evidence for some role for male aggression in hyena sexual behavior. None of the functional hypotheses presented here satisfactorily explain all aspects of baiting behavior. Nevertheless, our data are most consistent with hypotheses suggesting that male attacks on females serve as sexual harassment or play a role in informing females about some aspect of male fitness.

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