

Courtship and mating in free-living spotted hyenas

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Summary

Female spotted hyenas (*Crocuta crocuta*) are larger and more aggressive than males, and their genitalia are heavily 'masculinized'. These odd traits in females pose unusual challenges for males during courtship and copulation. Here our goals were to describe and quantify the behavior patterns involved in courtship and copulation in *Crocuta*, and determine whether rates of affiliative behavior directed toward females by males vary with female age, social rank, or time to conception. We also inquired whether consort formation with a particular female was necessary for a male to sire that female's cubs. Behavioral observations and paternity data based on 12 microsatellite loci were collected over 11 years from free-ranging hyenas in Kenya. Several of the courtship displays exhibited by male hyenas differed from those found in other carnivores, and appeared to reflect intense motivational conflict between tendencies to approach and flee from females. Most male advances were either ignored by females or elicited aggression from females toward males. Rates of male affiliative behavior toward females peaked around the time of conception. Although males behaved similarly toward young and old females in the highest social rank category, males directed more affiliative behavior toward older than younger females that were mid- and low-ranking. Multiple short mounts usually preceded a long mount, but intromission and ejaculation appeared to occur only during long mounts. Female receptivity was indicated by inhibited aggression toward the male and assumption of a distinctive receptive stance. The only behavior indicative of female proceptivity was following of the male by the female in mating contexts. Some males who sired cubs formed consortships with females whereas others did not, suggesting that individual male hyenas may adopt alternative reproductive tactics to attract and acquire mates. Our results also suggest that low fertility may be an important cost of female virilization in this species.

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Introduction

In addition to synchronizing physiological and behavioral processes necessary for fusion of gametes (Crews, 1975; Verrell, 1997) and permitting opportunities for mate choice (Clutton-Brock et al., 1982; Bradbury & Gibson, 1983; Karino, 1995; Hoikkala et al., 1998), courtship behavior may also help break down barriers that prevent mates from coming together to copulate, particularly in solitary or aggressive species (Caro, 1994). Courtship and mating in mammalian carnivores can be particularly challenging, since these behaviors bring together mates that are well armed, and sex partners may, therefore, risk injury while mating. Courtship and mating behaviors have been extensively studied in members of the dog, cat and weasel families (e.g., Ewer, 1973; Carroll et al., 1985; Beaver, 1992; Sisk et al., 1992; Hayssen et al., 1993; Asa & Valdespino, 1998), but little is known about them in any member of the hyena family (Hyaenidae). Here we describe courtship and sexual behavior observed among free-living spotted hyenas (*Crocuta crocuta*).

Spotted hyenas are particularly interesting subjects for the study of sexual behavior for two reasons. First, males and females possess identical weaponry in this species (Van Horn et al., 2003); females are larger and more aggressive than males and female hyenas are socially dominant to adult breeding males (Kruuk, 1972; Mills, 1990; Smale et al., 1993). These traits may render approach and courtship of females by male hyenas unusually risky, even in comparison to other mammalian carnivores. Second, female *Crocuta* possess heavily masculinized genitalia (Matthews, 1939). There is no external vagina, as the labia are fused to form a pseudoscrotum, and the clitoris is elongated and fully erectile such that it strongly resembles the male's penis in size and structure (Matthews, 1939; Neaves et al., 1980; Hamilton et al., 1986; Drea et al., 2002a). This pseudopenis is traversed to its tip by a central urogenital canal, through which the female urinates, copulates and gives birth (Drea et al., 2002a). This unique female morphology makes intromission by the male considerably more difficult than it is in other mammals (Drea et al., 2002a) and also makes copulation by force physically impossible (East et al., 1993). Although a sexually receptive female hyena

retracts her clitoris into the abdomen to permit penetration by the male's penis, her clitoral opening is far anterior to the position occupied by the external vagina in other female carnivores, so the male hyena typically experiences unusual difficulty locating this opening and achieving intromission (Drea et al., 2002a). Thus males must overcome the mechanical challenges posed by having to reach an anterior position on the female's abdomen during mating, and then achieving intromission at the site of the retracted clitoris (Drea et al., 2002a). Furthermore, due to the peculiar behavioral and physical characteristics exhibited by female *Crocuta*, males must overcome unique motivational challenges associated with approaching and courting large, aggressive, well-armed females.

As do many felids (e.g., Caro & Collins, 1987), spotted hyenas mate promiscuously, and no enduring pair bond develops between the sexes (Szykman et al., 2001; Engh et al., 2002; East et al., 2003). Females have been observed mating with up to three males during a single estrous period, and members of both sexes have been known to copulate with several different mates over the course of several years (Engh et al., 2002). All adult female *Crocuta* mate and bear young, but reproductive success varies with female social rank (Holekamp et al., 1996). Both observations of mating and paternity tests based on microsatellite data confirm that high-ranking males do not monopolize reproduction in this species, as they do in many other polygynous mammals (e.g., Clutton-Brock, 1988; Altmann et al., 1996). Modal litter size in *Crocuta* is two (Holekamp et al., 1996), and 20-40% of twin litters are sired by multiple males (Engh et al., 2002; East et al., 2003).

Spotted hyenas are gregarious carnivores that live in social groups called clans. Each clan contains one to several matriline of adult females and their offspring, as well as one to several adult immigrant males. Clans are rigidly structured by hierarchical rank relationships, and an individual's social rank determines its priority of access to food and other resources (Kruuk, 1972; Tilson & Hamilton, 1984; Frank, 1986; Mills, 1990). Adult females are socially dominant to all adult males not born in the clan (Kruuk, 1972; Smale et al., 1993). Female hyenas are philopatric, and typically bear their first litters in their third or fourth year (Holekamp et al., 1996). By contrast, males reach reproductive maturity at around 2 years of age, and then disperse from their natal clans (Smale et al., 1997; East & Hofer, 2001; Van Horn et al., 2003). Males may remain in their natal clans up to 5 years after puberty (Smale et al., 1997) and, therefore, two types of reproductively competent

adult males occur in every clan: adult natal males and adult immigrant males. Natal males are significantly more aggressive toward other adult males than are immigrants, are socially dominant to all immigrants and are the winners of all fights with immigrants (Holekamp & Smale, 1998b). Despite the fact that they outrank immigrant males, natal males court females at significantly lower rates than do immigrants, and natal males have significantly lower plasma testosterone levels, even when controlling for male age and body size (Holekamp & Smale, 1998b).

Although Drea et al. (1999) describe mating postures assumed by captive *Crocuta*, little is currently known about courtship and mating among free-living hyenas, mainly because matings are seldom observed in the wild. During separate 4-year studies of *Crocuta* in Tanzania and Kenya, respectively, Kruuk (1972) and Frank (1986) each observed complete mating sequences on only 5 occasions. Both these earlier workers noted that males appeared fearful of females during courtship and that males exhibited simultaneous tendencies to approach and avoid prospective mates. In this paper, we present data collected over 11 years from free-living spotted hyenas in Kenya to describe and quantify their courtship and sexual behavior, including pre-copulatory affiliative interactions between the sexes, as well as postures and actions involved in mating itself. We examine rates of male affiliative behaviors toward females during the months surrounding conception, report detailed sequences of events from field observations of courtship and mounting, document aspects of *Crocuta*'s sexual behavior not previously described in the literature, and compare adult natal and immigrant males with respect to their interactions with females.

Methods

Study population

We conducted this study in the Talek area of the Masai Mara National Reserve, Kenya, an area of open, rolling grassland. Our subject population was one large *Crocuta* clan inhabiting a home range of approximately 65 km². We monitored Talek hyenas continuously from June 1988 to August 1999. During this period, the Talek study clan varied in size from 45 to 79 individuals, not including transient individuals present in the clan for less than 6 months. The clan consisted on average of 14 adult immigrant males (range

5-16), 19 adult females (range 12-26) and their juvenile offspring. We identified each individual hyena in the Talek clan by its unique spot patterns and determined its sex from the dimorphic glans morphology of the erect phallus (Frank et al., 1990).

We determined mother-offspring relations on the basis of regular nursing associations and confirmed these via genotyping (Van Horn et al., 2004). We assigned birth dates to litters by estimating cub ages when they were first observed above ground at natal or communal dens. Cub ages could be estimated to ± 7 days based on their pelage, size and other aspects of cub appearance and behavior. We could then calculate conception dates by subtracting the gestation period of 110 days (Schneider, 1926; Kruuk, 1972) from estimated birth dates. Ages of hyenas born before 1988 were calculated based on data available for Talek hyenas in Frank (1983). We determined social ranks of individuals based on outcomes of several thousand dyadic agonistic interactions during which one individual exhibited appeasement behavior to the other, regardless of whether or not the appeasement was elicited by aggression from the social partner (Holekamp & Smale, 1990; Smale et al., 1993). Adult females and adult immigrant males were ranked in separate intrasexual dominance hierarchies, but adult natal males were assigned the same social ranks as those of their mothers since they retain their natal ranks until they disperse. Natal males were born in the Talek clan whereas immigrants originated elsewhere. Only immigrant males present in the clan longer than 6 months were included in the immigrant male hierarchy. By convention, we assigned the highest-ranking (alpha) individual in each hierarchy a rank position of 1.

Routine behavioral sampling 1988-1999

Throughout the entire 11-year study, we conducted behavioral observations from vehicles between 0530 and 0930 h and between 1630 and 2000 h. During the study period, we observed hyenas for 16 332 person-hours during a total of 39 600 observation sessions. Clans are fission-fusion societies in which sub-group composition changes many times each day (Holekamp et al., 1997). Adult female and adult male hyenas were present together for 3477 hours during 7260 observation sessions. We initiated an observation session when we first drove up to one or more hyenas separated from others by at least 200 m. An observation session ended either when all hyenas

moved out of sight, or when we drove on to a new location. Session length varied from 5 min to several hours. We located hyenas while driving daily circuits around the study clan's home range and by scanning from hilltops with binoculars to sample all parts of the home range every day for presence of subgroups of hyenas. We then visited each subgroup to determine its composition and identified all individual hyenas present. We excluded from our analyses any sessions in which one or more unidentified hyenas were present.

We defined a 'mating session' as an observation session during which we observed any mounting behavior by adult hyenas. Sessions without mounting were assigned to 'other' contexts, and these included observations of hyenas present at dens, at carcass sites and at other locations. We calculated daily mating rates by dividing the number of mating sessions observed during morning (0530-0930 h) and evening (1630-2000 h) sessions by the total number of hours hyenas were watched during these periods and then multiplying by 24. We recorded mount duration as the number of seconds during which a male remained mounted atop the female, and inter-mount interval as the time elapsed between long mounts. Matings were considered fertile (i.e., resulting in conception) when a litter was observed within 1 month of the predicted birth date. This represents an extremely liberal criterion for assessing the fertility of any particular mating. We calculated expected birth dates by adding 110 days (average gestation period) to each date on which we observed copulation or mounting.

We used both all-occurrence and focal animal sampling (Altmann, 1974) to collect behavioral data. To quantify intersexual affiliative behavior we recorded all occurrences of all behaviors listed in Table 1 for all individuals. In addition, we monitored following behavior during 30-min focal animal observations (Altmann, 1974) of adult males and females. Here we recorded the total number of minutes in each focal animal sample during which each focal hyena followed a member of the opposite sex. Adult males and females were selected as focal animals here based on a regular schedule of rotation among adults currently present in the clan.

Detailed behavioral data on courtship interactions 1997-1999

Some of our analyses utilize data from only 2 of the 11 total years, because certain types of behavioral data were collected from 1997 to 1999 that were not collected earlier. During all inter-sexual affiliative interactions observed

between 1997 and 1999, we calculated daily rates of approach, investigation and courtship behavior by dividing the number of times each behavior occurred within a male-female pair by the total number of hours each pair was observed together during each of seven month-long intervals surrounding a female's known conception date, and then multiplying this number by 24. Together, the two 2-week intervals on either side of the conception date represented month 'zero'. To be included in this analysis, we required that the male and female be observed together for at least 1 hour during each month-long interval. Investigatory behavior included sniff, lick and greet, whereas courtship behavior included approach-avoid display, present, bowing display and paw ground (Table 1). We evaluated how rates at which males emitted these behaviors varied with female age and social rank. Female social rank was divided into high, middle and low rank categories representing ranks 1-7, 8-14 and >15, respectively. Female age was similarly divided into young, middle and old age classes representing ages 2-6, 7-11 and 12-16 years, respectively. To assess male-female associations, we also calculated the total number of hours each female was observed in the presence of at least one immigrant male, and the number of males with which she was observed during each monthly interval surrounding conception.

We calculated rejection coefficients (RC) as in Beach & LeBoeuf (1967) to determine whether females responded differently to sexual advances from adult natal and immigrant males. The RC for each male-female pair was calculated as follows: $((\text{No. of affiliative behaviors to which the female responded with aggression} / \text{Total No. affiliative behaviors exhibited by the male towards the female}) \times 100)$. Female aggressive responses included threat postures, chases, intention movements to bite and actual biting.

Paternity determination and analysis of male-female associations

DNA from each Talek hyena was extracted from blood or tissue, and we genotyped individuals using 11 autosomal microsatellite loci and one X-linked microsatellite locus as described elsewhere (Libants et al., 2000; Engh et al., 2002). All adult males present in the clan at the time of conception of a particular litter were considered as potential fathers. We employed a maximum-likelihood approach (Thompson, 1975; Meagher, 1986) to assign paternity to cubs with known, genotyped mothers using the program CERVUS (Marshall et al., 1998), but only if data were available for at least

6 autosomal loci in sire, cub and mother genotypes (see Engh et al., 2002 for details). A male was considered the father of a cub when CERVUS assigned him paternity at 95% confidence and he met one of the following two additional criteria: he was the only potential sire by simple exclusion or, in the case of a single mismatch between the multi-locus genotypes of the putative sire and cub, the software program KINSHIP (Queller & Goodnight, 1989) indicated that the two animals' pairwise genetic similarity (i.e., R in Queller & Goodnight, 1989) reflected sire-cub kinship at 95% confidence. Confidence in paternity and kinship was determined from the simulated distribution of the ratio of two likelihoods: the likelihood that the male was the sire of the cub (e.g., paternally related at $R = 0.5$) and the likelihood that the male was not the sire of the cub (e.g., paternally related by $R = 0$).

Using only litters for which sires could be identified by paternity analysis, we compared sires and non-sires with respect to their association patterns with females around the time each litter was conceived. Here, we recorded whether each male was present with the female during each consecutive session in which the female was observed, starting 3 months before conception and ending 1 month after conception. Numbers of consecutive sessions varied considerably among females for this 4-month-long period, but this analysis was useful nonetheless to inquire whether sires appeared to be engaging in any sort of consortship or mate-guarding behavior.

We calculated an association index (AI) for each known male-female mating pair using the twice-weight index of association (Cairns & Schwager, 1987), calculated as:

$$(A + B)_{\text{together}} / ((A_{\text{without } B}) + (B_{\text{without } A}) + (A + B)_{\text{together}}),$$

where $(A_{\text{without } B})$ represents the number of observation sessions in which female A was observed but male B was not present, $(B_{\text{without } A})$ represents the number of observation sessions in which male B was present but female A was absent and $((A + B)_{\text{together}})$ represents the number of sessions in which both female A and male B were present (as in Szykman et al., 2001). To inquire whether primate-like consortships with females were typical of the males known to sire litters, we also calculated an association index for each mother-sire pair observed during the month prior to conception of the relevant litter and evaluated the distribution of these AIs.

To determine whether males or females initiated intersexual associations, for each mating pair we calculated the rate at which each animal approached

its partner, as well as the percent total time during each mating session each animal spent following its partner. An hourly approach rate was calculated for each individual as ((No. of approaches/No. of minutes observed during mating session) \times 60). Percent time spent following was calculated as ((No. of min spent following/No. of min observed during mating session) \times 100). To avoid pseudo-replication, we calculated mean values for individuals if they were observed during multiple mating sessions. Finally, we compared the rates of approach and following behavior by males and females between mating and 'other' sessions during which no mounting was observed.

Male choice: logistic regression

Between June 1997 and June 1999, we recorded two additional aspects of male behavior to evaluate male mate choice. First, when a male sniffed an individual female during an observation session, we subsequently recorded whether or not that male stayed near the female he had sniffed (sniff-and-stay) until they disappeared out of sight together or until observers left that session. Second, a male was considered to be exhibiting a clear preference (choice) for a particular female when he repeatedly courted and/or followed her throughout a session in which multiple females were present. Both of these male decisions were considered to be mutually exclusive: sniff-and-stay vs. sniff-and-go and choice vs. no choice.

We then used logistic regression (Legendre & Legendre, 1998; Hosmer & Lemeshow, 2000) to inquire which female characteristics influenced these dichotomous male decisions. Here predictor variables included female social rank, time to conception and female age. Because we were specifically interested in a male's preference as it was expressed among multiple females, and because up to 12 females were present concurrently in a given session, we assigned each female in each session a value for rank, time to conception and age relative to the other females in that session. All three explanatory variables were simultaneously used in the model and were analyzed using the Logit Estimate model in the Systat 8 statistical software package (Systat, 1998).

We present mean values as $\bar{X} \pm \text{SE}$. We analyzed data that were not normally distributed using non-parametric tests. Two-way ANOVAs were conducted on rank-transformed data to test for interactions. Where we asked multiple questions of a single data set, we corrected p values using Bonferroni adjustments for multiple comparisons. We considered differences between groups to be statistically significant when $p < 0.05$.

Results

We first examined patterns of associations between 21 males and 20 females during the months surrounding conception between 1997 and 1999. Time to conception was significantly associated with the number of hours males and females were observed together (Figure 1A; repeated measures ANOVA: $N = 20$ females, $F_{6,114} = 5.707$, $p < 0.001$). Males spent significantly more time with females during the month surrounding conception than during the preceding months. Furthermore, more individual males were observed associating with females during the months surrounding conception than at other times (Figure 1B; repeated ANOVA: $N = 20$ females, $F_{6,114} = 5.832$, $p < 0.001$).

Next we examined rates at which the 21 immigrant males approached, investigated and courted 20 different females near their time of conception between 1997 and 1999. This analysis included interactions observed within 202 male-female pairs. Time relative to conception had a significant influence on male approach and investigation, but only a marginal influence on courtship behaviors (Figure 2; Kruskal-Wallis: approach: $K_6 = 21.918$, $p = 0.001$; investigate: $K_6 = 27.844$, $p < 0.001$; court: $K_6 = 11.083$, $p = 0.086$). Interestingly, the highest rates of approach and investigatory behaviors were observed in the month immediately preceding the female's fertile period. Rates at which males displayed courtship behaviors were highest during the month of conception and the month preceding conception.

Rates of male affiliative behavior also varied as a function of female rank category and female age class (Figure 3). Female social rank alone did not significantly influence male affiliative behavior. However, we observed an interaction between female rank category and female age class for male approach, investigation and courtship (2-way ANOVA: approach: $F_{4,117} = 4.250$, $p = 0.003$; investigate: $F_{4,117} = 2.407$, $p = 0.05$; court: $F_{4,117} = 3.346$, $p = 0.012$). Males directed more affiliative behaviors towards older than younger females in the middle- and low-ranking categories, but males behaved similarly toward high-ranking females of all ages.

The youngest age at which natal males were first observed courting or mounting adult females was 19.7 months. Compared to immigrants, adult natal males performed relatively few affiliative behaviors toward adult females. Ten different adult natal males approached, investigated, or courted 16 different females, representing only 4% of all affiliative interactions ob-

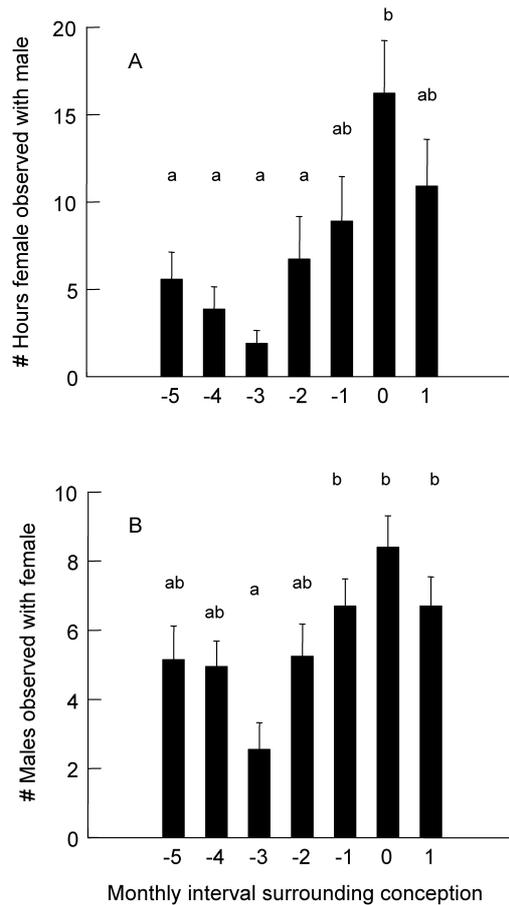


Figure 1. (A) Total time from 1997 through 1999 during which 21 immigrant males were observed with 20 females. (B) Number of immigrant males that were observed associating with same females, during the months surrounding each female's conception. Interval '0' represents the date of conception ± 2 weeks. Remaining intervals represent month-long periods surrounding the date of conception. Letters over bars represent means significantly different from one another at $p < 0.05$.

served between adult males and females from 1997 to 1999. Rejection coefficients (RC) for immigrant males (mean = 16.1 ± 2.1) were significantly higher than were those for natal males (mean = 4.0 ± 4.0 ; Mann-Whitney U : $U_1 = 3042.000$, $p = 0.001$), indicating that females responded more aggressively to sexual interest expressed by immigrant males than to that exhibited by natal males.

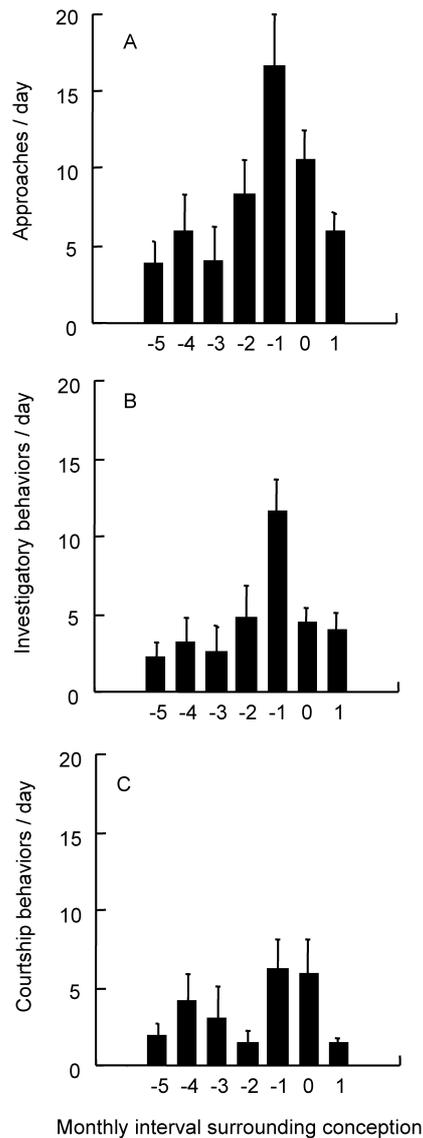


Figure 2. Mean daily rates (\pm SE) from 1997 through 1999 at which males engaged in (A) approach to females, (B) investigation of females and (C) courtship behaviors, plotted as a function of time relative to conception in targeted females. Interval '0' represents the date of conception \pm 2 weeks. Remaining intervals represent month-long periods surrounding the date of conception. $N = 202$ male-female pairs involving 20 females and 21 immigrant males observed together during each of 7-month-long intervals. Note that all y-axes are on the same scale.

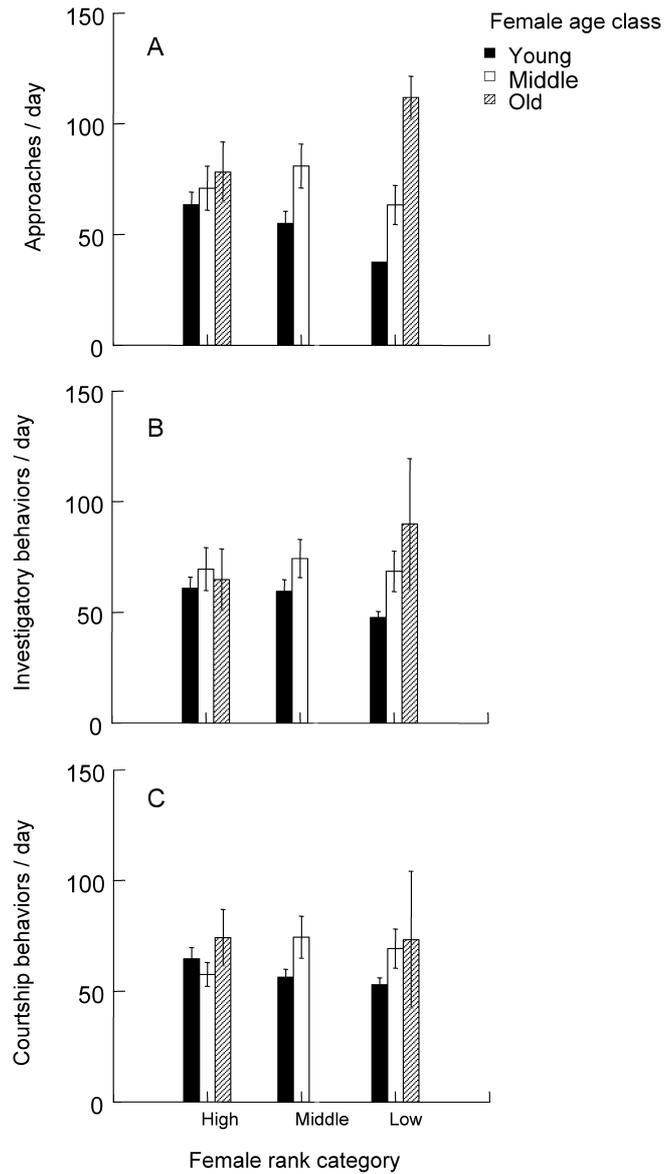


Figure 3. Daily rates from 1997 through 1999 at which males engaged in (A) approach, (B) investigation and (C) courtship, plotted as a function of female social rank and age categories. Daily rates were rank transformed to perform 2-way ANOVA on data that were not normally distributed (see Methods for details). Transformed rates are plotted here (mean \pm SE). No 'old' females were available in the 'middle' rank category. Sample sizes as in Figure 2.

Mating behavior

Between 1988 and 1999, male hyenas were observed mounting females in only 39 of 39 600 observation sessions. Observed mating sessions lasted for 57.8 ± 6.6 min (range 4-149 min). We saw 20 'complete' copulations, which included intromission and ejaculation by immigrant males, and an additional 19 mounting events, with or without intromission, but without post-ejaculatory rest. Seventeen immigrant males mounted or copulated with 18 adult females, and five adult natal males mounted four different adult females. Mating behavior occurred throughout the year, as did known conceptions (e.g., Holekamp et al., 1999), and most (35/39) mating sessions occurred during our morning observation hours, between 0530 and 0930.

Copulations generally involved a predictable sequence of events. The male first made a series of pre-mounts (Table 1), often rushing at the female as if to mount, then veering off at the last second. Assumption of the receptive stance by the female appeared to signal the male that it was safe to mount her. After several pre-mounts, the male mounted the female, and repeatedly attempted to achieve intromission. This task was apparently made extremely difficult by the female's peculiar genital morphology. The male had to squat down and under the female, so low that his rump was sometimes on the ground, to maneuver his erect penis into the female's flaccid phallus (Figure 4A). This typically took multiple attempts over a period of several minutes. Once intromission was achieved, the male then assumed a more typical male position mounted behind the female, stretching the female's flexible phallus posteriorly (Figure 4B). Some thrusting usually occurred at this time. Finally, the male ceased thrusting while remaining mounted, sometimes licking or biting the female's back, and ultimately engaging in post-ejaculatory rest for several minutes (Figure 4C).

Figure 5 shows temporal patterning of events during some typical mating sequences among wild hyenas. It can be seen here that one to several short mounts preceded each long mount. Entire sequences of mounting, thrusting and resting were sometimes repeated several times over the course of several hours. However, although we sometimes saw the female mating with a different male the following day, we never observed any one mating pair copulating repeatedly on successive days. Figure 5A depicts a single male mounting a single female when no other hyenas were present. On 10 of 15 occasions when no other hyenas were present with the mating pair, we observed only

Table 1. Definitions of behaviors monitored in free-living hyenas.

Investigatory behaviors exhibited by the male	
Sniff	A hyena approaches within 1m of another individual, or its fresh urine, puts its nose down, and inhales its scent. After sniffing an adult female or her urine, a male may display flehmen, a behavior exhibited by many mammals and characterized by an open mouth and retraction of the upper lip, often with head extended or elevated (Estes, 1972).
Lick	The tongue of one hyena makes contact with the body of another individual.
Greet	Two hyenas stand head-to-tail and sniff each other's genitals, as described by Kruuk (1972) and East et al. (1993).
Appetitive behaviors exhibited by both sexes	
Approach	A hyena walks to within 1-2 m of another individual.
Follow	One hyena walks closely behind another.
Male courtship behavior	
We included here those behaviors that were only exhibited by adult male spotted hyenas toward adult females, and that appeared to indicate a male's sexual interest in a particular female.	
Approach-avoid display	A male walks within 10 m of a female, who is usually lying down, and repeatedly alternates taking a few steps toward her, then retreating a few steps back. It is not necessary for the female to make any motion to prompt the male's retreat.
Present	A male stands in front of a female, at right angles to her, with his legs stiff and outstretched anteriorly and posteriorly, letting the female sniff his side, ventrum and genitalia. The male often is very skittish as the female sniffs him.
Foot cross	A three-legged stance in which the male lifts one foreleg and crosses it over the other while he faces the female.
Foreleg auto-grooming	While standing facing the female, the male repetitively licks his foreleg and/or rubs his snout on his forelegs.
Bowing display	A display exhibited as the male approaches a female in which he repeatedly stops, lowers his head, and engages in foot-crossing behavior and foreleg auto-grooming.
Paw ground	A male approaches a female and repeatedly scratches the ground in front of her with his forepaw.
Pre-mount	The male attempts to mount the female but either aborts midway or retreats after grazing one or both paws on the female's back.

one long mount during the course of the mating sessions, as shown in Figure 5A. Figure 5B and 5C depicts events occurring during a mating session in which two different males mated alternately with one female during the same observation session.

Table 1. (Continued).

Appetitive behavior exhibited by the female	
Receptive stance	Assumption of a body posture (presumed) to facilitate mating in which the female is standing, her head held low toward the ground, and her legs braced and apart. The female maintains this posture when the male approaches and attempts to mount.
Male contact with the female	
Mount	An adult male, positioned behind a standing female, lifts his forepaws up on top of the female's back or hindquarters.
Intromission	A male successfully inserts his penis into the female's urogenital canal. Observers can usually determine when intromission has occurred (e.g., see Figure 4). Only when intromission is known to occur during a mount, do we refer to it as copulation.
Thrusts	Rhythmic intra-vaginal pelvic thrusting. Ejaculation is presumed to occur when thrusting ceases.
Post-ejaculatory rest	A period of time, presumably post-ejaculation, when the male remains mounted on the female after cessation of pelvic thrusting, but with his penis still inserted. During this phase the male typically rests his chin on the back of the female. The rest period ends when the male dismounts and withdraws his penis.
Mating behavior	As used here, this involves any of the behaviors listed above in which the male contacts the female.

We observed two different males copulate with a single female on three separate occasions. In 24 of the 39 (62%) mating sessions, hyenas other than the focal pair were present ($\bar{X} = 2.6 \pm 0.4$ other hyenas present, range = 1-8). During three of these 24 sessions (12.5%), a second adult male attempted to interrupt the mating pair. Twice, the individual who interrupted was an immigrant male higher-ranking than the mating male, and the interrupting male succeeded in gaining access to the female on these occasions. Aggression among males over females was generally very mild in these sessions, usually only involving displacement. Furthermore, although subordinate males could be displaced by dominants, they were not deterred for long, and often resumed mounting the female within moments of being displaced. Only five adult natal males were observed to mount females, and these mounting sequences involved only short mounts. Natal males never remained mounted for longer than 1 s, and none of them ever achieved intromission.

We recorded a total of 462 mounts during the 39 mating sessions observed. We were able to record duration ± 2 s for 275 mounts in which mount duration ranged from 1 to 1080 s (Figure 6; $\bar{X} = 40.0 \pm 6.9$ s).

A



B



C



Figure 4. Mating postures. (A) The male squats behind the female as he attempts to achieve intromission. (B) The male stands and thrusts after achieving intromission. (C) The male engages in post-copulatory rest with his chin on the female's back. Photos by S.A. Wahaj, J. Bro-Jørgensen and M. Szykman, respectively.

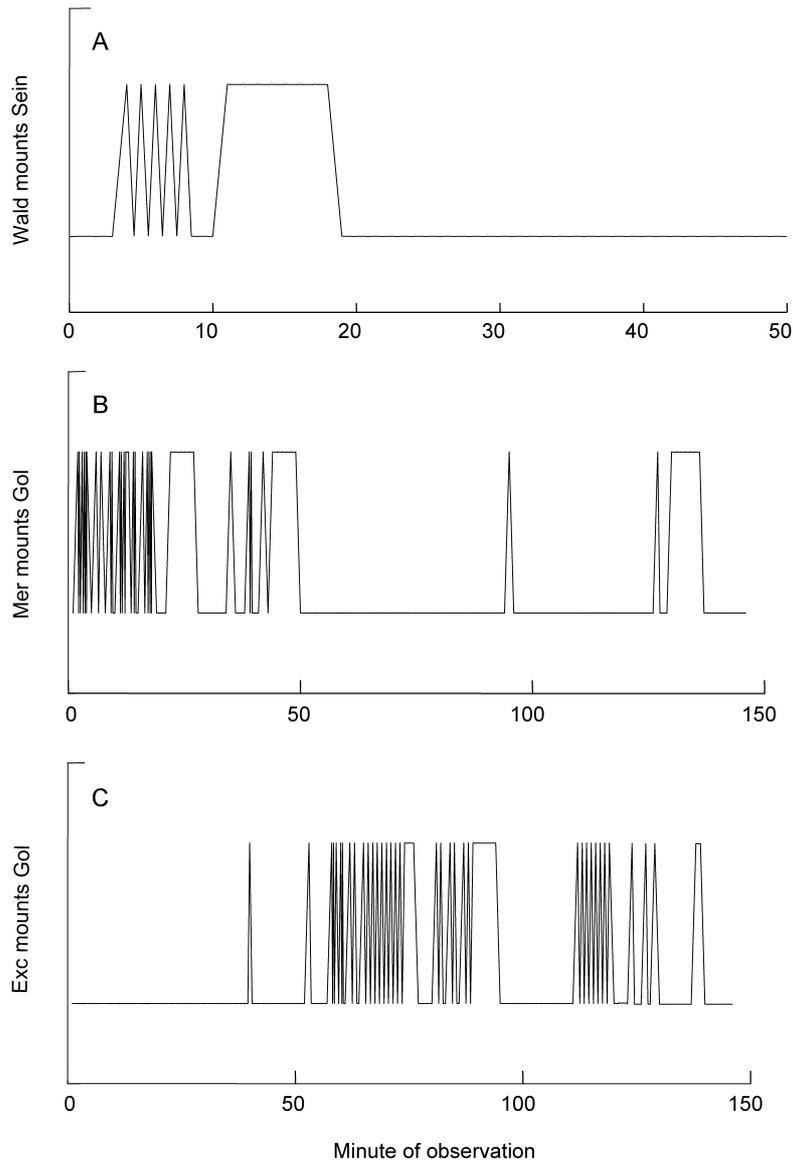


Figure 5. Temporal patterning of mounting behavior. (A) A single male (WALD) mounting a single female (SEIN) when no other hyenas were present. Observers remained with this pair through minute 50. (B and C) Two males (B, MER; C, EXC) alternately mounting a single female (GOL) during a single observation session. Observers remained with these animals through minute 150. MER was higher-ranking than EXC, and each male sired one of the cubs in the twin litter produced by GOL 110 days after these copulations were observed.

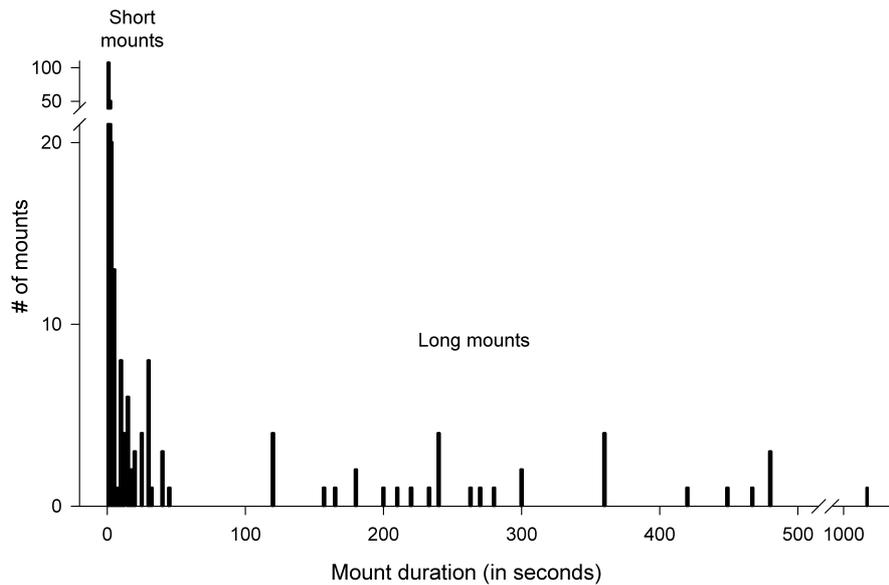


Figure 6. Duration of 275 mounts observed during 39 mating sessions between 1988 and 1999, suggesting a possible functional distinction between short (<60 s) and long (>100 s) mounts.

Mounts were clearly divisible into short mounts, ranging in duration from 1 to 45 s ($\bar{X} = 5.3 \pm 0.5$ s), and long mounts, which lasted longer than 100 s ($\bar{X} = 302.9 \pm 32.2$ s, range = 120-1080 s). Intromission was observed in only 4 of 248 (1.6%) short mounts. Long mounts were observed in 20 mating sessions. Males performed an average of 1.8 ± 0.3 (range 1-5) long mounts during these 20 sessions. Males performed an average of 1.9 ± 0.9 (range 0-11) short mounts during the inter-mount interval. It took males an average of 24.0 ± 6.7 min (range 1-86 min) to achieve a second long mount, but two of the longest inter-mount intervals were influenced by the interference of another male who achieved a long mount of his own during that time. When these two samples were excluded, we found that it took males only 16.8 ± 4.9 min to achieve a second long mount. Although successful intromission was not consistently observable, it is likely that males achieved intromission during all long mounts. Males performed more than one long mount in 8 of 18 of the mating sessions in which we observed any long mounts at all. This suggests that multiple long mounts over the course of several hours or days may be typical for free-living hyenas.

Initiation and duration of intersexual interactions

When we used our focal animal data to compare approach and following behavior by males and females in ‘mating’ contexts to those same behaviors observed in ‘other’ contexts (traveling, resting, at dens and at kills), we found both main effects and interaction effects between context and gender for both behaviors (Figure 7; 2-way ANOVA: approach: $F_{1,61} = 17.744$, $p < 0.001$; follow: $F_{1,61} = 13.967$, $p < 0.001$). We, therefore, conducted post-hoc t -tests on each pair of samples, with Bonferroni corrections. Males approached females at higher rates than females approached males during mating sessions ($t_{25} = -3.949$, $p = 0.001$) and also in other contexts ($t_{36} = -6.220$, $p < 0.001$). Both males and females approached individuals of the opposite sex at higher rates during mating sessions than in other contexts (male: $t_{30} = 5.312$, $p < 0.001$; female: $t_{31} = 5.267$, $p < 0.001$). However, although males spent a greater proportion of focal animal time following females in non-mating contexts than vice versa ($t_{36} = -5.879$, $p < 0.001$), females tended to spend a greater proportion of their focal animal time following males than vice versa during mating sessions ($t_{25} = 1.780$, $p = 0.087$). Females were more likely to follow males during mating sessions than in other contexts ($t_{34} = 4.863$, $p < 0.001$), but male following behavior did not vary significantly between contexts ($t_{27} = 0.140$, $p = 0.890$).

We next analyzed consecutive observation sessions to inquire how consistently individual males were found together with particular females around the time of conception, and whether these patterns differed for sires and non-sires. Individual males varied in the extent to which they associated with females around the time of conception (Figure 8). One male in particular (the 5th ranked male in Figure 8A and 8B) was consistently observed with females during the weeks preceding conception, and clearly succeeded in fathering cubs using this strategy. Other males, of both high and low rank (ranks 2 and 16, respectively) succeeded in siring offspring without exhibiting a clear pattern of tight association with their mates before conception (Figure 8C and 8D). Thus, male hyenas may sometimes ‘shadow’ or ‘guard’ their mates (East & Hofer, 2001), but intensive mate-guarding is clearly not necessary in this species to ensure that a male will sire the cubs of a particular female.

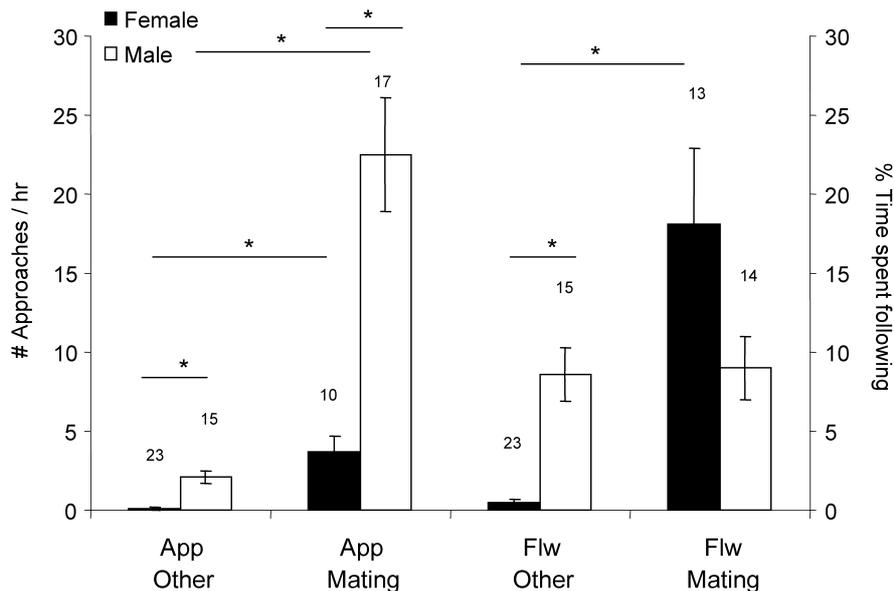


Figure 7. Mean (\pm SE) hourly rates between 1988 and 1999 at which individuals approached, and mean (\pm SE) percent of focal animal time during which individuals followed, members of the opposite sex in two different contexts. Open bars represent adult males and solid bars represent adult females. The 'mating' context consists of sessions during which we observed mounting behavior. The 'other' context includes all other sessions, involving observations of hyenas present at dens, at kill sites and at locations other than dens and kills. Numbers over bars represent number of individuals included in each sample. * $p < 0.001$

Factors influencing male choice behavior

We used logistic regression to evaluate male choices for 210 male-female pairs involving 20 male and 27 female hyenas during the 2-year period from 1997 to 1999. Male hyenas clearly preferred some females over others, and decisions made by male hyenas to stay with or pursue a particular female were strongly influenced by certain female characteristics. Males who sniffed a particular female during an observation session were significantly more likely to stay with that female when she was closer to the time of conception, than to leave the scene or to stay with another female (Table 2). Female social rank and age did not significantly influence males' choices to stay with females or leave them after sniffing them (Table 2). Given a choice among several females, male hyenas exhibited the strongest preferences for, and actively pursued, high-ranking females, but males also preferred females when they were closer to the time of conception (Table 2).

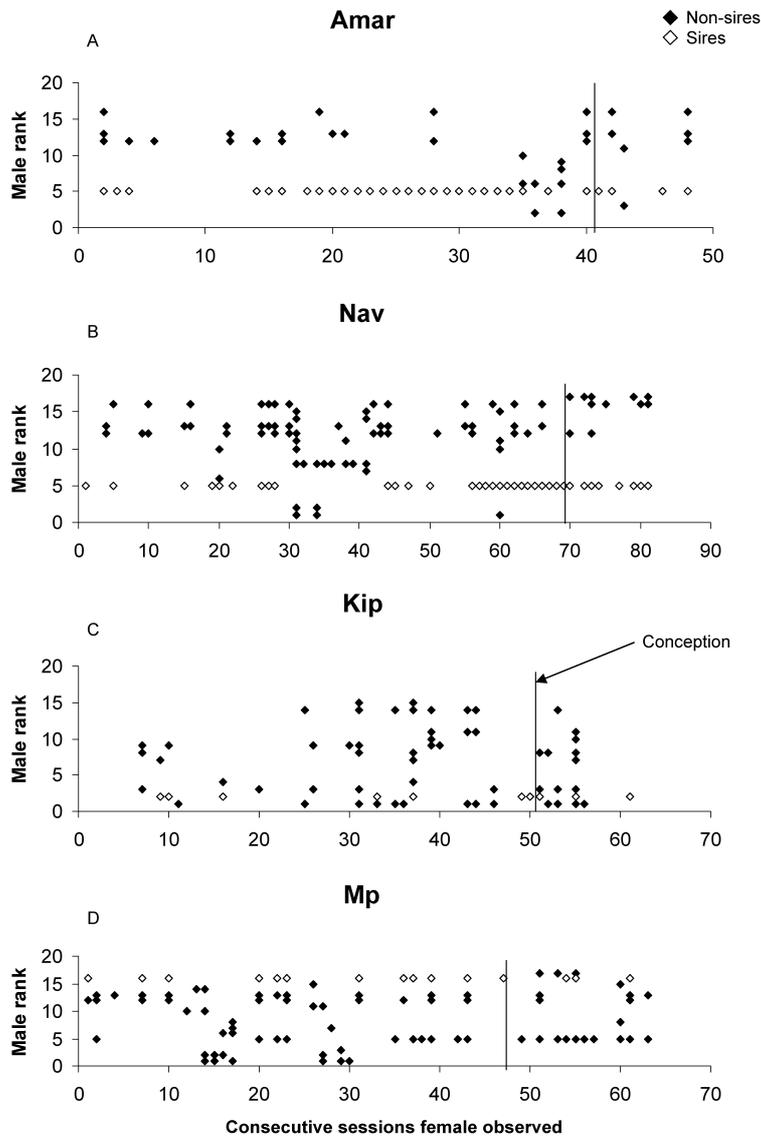


Figure 8. Association patterns between four females and the males who sired (open diamonds) their litters ($N = 3$ males; open diamonds in (A) and (B) represent the same male), as well as the 17 males present concurrently who did not sire (solid diamonds) their litters. Estimated day of conception is indicated by the solid vertical line. Although the number of consecutive sessions varied during which each female was observed, the time scales in (A) through (D) are all standardized to include the three months preceding and the first month following conception.

Table 2. Results of logistic regression evaluating the influence of female characteristics on male choice behavior.

Female characteristic	Estimate	S.E.	<i>t</i> -ratio	<i>p</i> -value
Sniff-and-stay				
Rank	-0.064	0.077	-0.823	0.410
Time to conception	-0.395	0.085	-4.630	<0.001
Age	0.037	0.074	0.507	0.612
Log likelihood = -292.896				
<i>N</i> = 492				
Correct predictions = 62.0%				
Choice				
Rank	-0.222	0.087	-2.547	0.011
Time to conception	-0.162	0.080	-2.011	0.044
Age	0.007	0.078	0.093	0.926
Log likelihood = -303.077				
<i>N</i> = 459				
Correct predictions = 55.5%				

Female cycle length and fertility

Although exact duration of the estrous period is unknown in *Crocuta*, we observed one female mating with three different males in a single 60-h period. Therefore, we surmise that estrus lasts at least 60 h in this species. The shortest interval between two consecutive estrous periods, as indicated by one female copulating again when her first mating was apparently infertile (i.e., no litter produced), was 23 days, and the next shortest was 64 days.

The youngest age at which female hyenas were observed copulating during the present study was 24.2 months, and the youngest female known to conceive was 25.4 months of age. The oldest female to conceive was our alpha female who was approximately 16 years old when she conceived her last litter.

Whether or not a litter was observed 80-140 days after mating could not be predicted based on the mean duration of mounts per mating session (Mann-Whitney *U*: $U_1 = 62.000$, $p = 0.247$), the number of short mounts per session (Mann-Whitney *U*: $U_1 = 114.000$, $p = 0.81$), the number of long mounts per session (Mann-Whitney *U*: $U_1 = 84.000$, $p = 0.17$), whether or not at least one long mount was observed during the session ($\chi^2 = 0.869$, $p = 0.35$), or whether or not ejaculation was assumed to have

occurred ($\chi^2 = 0.028$, $p = 0.87$). Of the 39 matings we observed, only 15 (38.5%) were associated with later production of known litters, suggesting that females might often need to mate two to three times, over repeated estrous cycles, to achieve a fertile conception or successful pregnancy.

Discussion

Courtship by male spotted hyenas is unusual among mammals because it appears to reflect such extreme conflicting desires to approach the female and flee from her. Even in other carnivore species in which females sport weapons as formidable as those of the female hyena, males do not repeatedly direct unsolicited appeasement behavior toward females during courtship as they do in *Crocuta*. In addition, some of the locomotor patterns observed during hyena copulation are unique and take an unusually long time to perform, presumably due to the female's masculinized genitalia. Overall, mating in *Crocuta* is a slow, difficult process that may put members of mating pairs at risk of predation from lions (*Panthera leo*) or humans.

Some of the general affiliative and investigatory behaviors described here for wild spotted hyenas also occur among other mammalian carnivores (e.g., felids: Schaller, 1972; Beaver, 1992). For example, despite the fact that female *Crocuta* dominate males, male hyenas still initiate most courtship interactions as usually occurs in carnivore species in which males dominate females. However, female dominance and masculinized genitalia may have generated some patterns of sexual behavior that appear to be unique to *Crocuta*. Approach-avoid and bowing displays both reflect strong motivational conflict and hesitancy on the part of the male, supporting the notion that interactions with females may be unusually risky for male *Crocuta*, and that males fear females (Kruuk, 1972; Holekamp & Smale, 2000). Bowing displays in *Crocuta* do not resemble the 'play-bows' exhibited by many canids when soliciting play. Approach-avoid and bowing displays may have evolved from displacement activities associated with conflicting desires to approach the female and flee from her.

The female seems to take little notice of the male hyena's sexual advances. *Crocuta* show neither any of the vigorous chasing, play and mutual scent-marking that occur during courtship in banded mongooses (*Mungos mungo*; Neal, 1970), nor the courtship feeding that occurs in some canids (e.g., golden jackals *Canis aureus*; Golani & Mendelsohn, 1971). When the female

hyena does respond to a male's advances, it is often with aggression, and she does little to encourage the male to pursue or approach her further. Yet, despite the female's apparent disinterest or irritation, immigrant male hyenas approached, investigated and courted females throughout their reproductive cycles. Rates at which all these behaviors occurred peaked roughly one month before conception (Figures 1 and 2). From these data, we can infer that female attractivity (*sensu* Beach, 1976) increases during the months leading to conception and declines thereafter. Rates of male affiliative behavior also varied as a function of female rank category and female age class, with males preferring high-ranking females overall, and preferring older to younger females in the lower rank categories (Figure 3). Female age did not show any interaction with female rank among high-ranking females, perhaps because the reproductive value of dominant females is high throughout the lifespan (Holekamp et al., 1996).

Natal male hyenas court females at significantly lower rates than do immigrant males (Holekamp & Smale, 1998b), and natal males also sire far fewer cubs than do immigrants (Engh et al., 2002). This is clearly not the result of females responding to sexual advances from natal males with higher levels of aggression than they do to advances from immigrants. Rejection coefficients calculated in response to male affiliative behaviors indicate that females respond more aggressively to the advances of immigrant males than to those of natal males, yet immigrants father 97% of cubs (Engh et al., 2002). This represents an interesting paradox: female hyenas behave most aggressively towards males with whom they will ultimately mate, and they generally ignore advances by adult natal males. Among domestic dogs (*Canis familiaris*), male affiliative behaviors and female responses are highly variable (Beach & LeBoeuf, 1967) as they are in *Crocuta*. Individual male dogs vary in their attractiveness to females, and individual females vary in their selectivity among males. Beach & LeBoeuf (1967) ultimately found that rejection by the female did not affect the frequency of male-female interactions or the probability of a copulatory lock in dogs. Similarly, in hyenas, aggressive responses by the female did not appear to discourage immigrant males.

Mating behavior and female receptivity

Copulations are rarely observed in field studies of *Crocuta*. This may be because *Crocuta* often mate at night (Kruuk, 1972; Frank, 1986), or because

mating pairs actively try to isolate and conceal themselves to avoid either predators or interference by other clan members. Either factor would tend to make it difficult for us to find and observe mating pairs. In fact, on several occasions during mating sessions in the current study, the courting pair vanished into thick bushes after the male had mounted the female once or twice, but had not yet achieved intromission. Thus, we were unable to continue observing the pair. However, the fact that other hyenas were often present with the mating pair suggests that whatever efforts the pair may make to isolate themselves from conspecifics are only of limited success. Thus, perhaps mating pairs often mate in thickets to minimize their vulnerability to lions, humans or other mortality sources.

Tentative approaches by the male, and attempted mounts that are aborted at the last second, may serve to test the female's receptivity, as she may respond by either turning to chase the male, or by assuming the receptive stance, which is incompatible with female aggression toward the male. By placing her mouth near the ground, the female appears to be signaling inhibition of aggression and receptivity to the male's advances.

We observed male hyenas ejaculate multiple times during a single mating session, as inferred from repeated long mounts followed by post-ejaculatory rest periods (e.g., Figure 4). This suggests that females might require multiple matings, both during a single estrous cycle and over successive estrous cycles, to ensure conception. Male hyenas appear to have greater difficulty achieving intromission than other male carnivores due to the strange genital morphology of the female hyena, with her long, flexible phallus and urogenital opening facing anteriorly (Drea et al., 2002a). Repeated mounting without intromission is not commonly reported in other carnivore species. The extended time the male hyena spends in post-ejaculatory rest might function to facilitate sperm transfer, as does the copulatory lock in canids (Asa & Valdespino, 1998).

Male *Crocota* may require a great deal of practice during early development to successfully impregnate females during adulthood. Practice mounting can effectively only be obtained during play with peers at dens long before males reach puberty. Rates of play-mounting are very high among male *Crocota* between two and four months of age (Holekamp & Smale, 1998a), and rates of play-mounting vary with maternal rank such that sons of high-ranking females mount at far higher rates during early play than do

their lower-ranking peers (Dloniak et al., 2006). If the practice obtained during early play-mounting affects adult sexual performance, then one potential benefit accruing to sons of high-ranking females may be greater competence at achieving the difficult motor patterns required for mating with masculinized females.

Maintenance of associations and female proceptivity

Association patterns between adult male and female hyenas clearly have some relevance to sexual behavior in this species, as male hyenas who sire cubs often associate more closely with their future mates than do males who fail to sire cubs (Szykman et al., 2001). These associations in *Crocuta* are not usually cooperatively maintained by both partners as commonly occurs in primate consortships (Stern & Smith, 1984; Small, 1990), nor are they as exclusive. However, we found here that female hyenas approached and followed males at significantly higher rates during mating sessions than during observations conducted in other contexts (Figure 6). This suggests that female approach and following behavior directed at immigrant males should appropriately be considered to be proceptive behavior (Beach, 1976), indicating the female's active interest in mating. Although we looked carefully for other signs of female proceptivity (e.g., the female's 'posterior present' behavior described in captive hyenas; Coscia et al., data not shown), we were unable to identify any others in the wild. The subtlety of proceptive behavior in female hyenas stands in marked contrast with that observed in other female carnivores, which commonly exhibit very obvious and striking proceptive behavior. For example, a lioness in estrus repeatedly approaches and rubs her chosen male, rolls and swishes her tail in front of him and presents her genital area for him to sniff, frequently initiating mating (Schaller, 1972; Rudnai, 1973). Domestic cats (*Felis catus*) sometimes show dramatically exaggerated forms of these same behaviors, adding to them loud vocalizations to call for males (Leyhausen, 1979; Beaver, 1992). Proceptive behavior by female domestic dogs is also very clear; an estrous female seeks out a male and presents her anogenital region near the male's muzzle for his inspection (Beach et al., 1982). Perhaps, in addition to making parturition more difficult than it is in other female mammals (Frank & Glickman, 1994; Drea et al., 2002a), masculinization of female *Crocuta* also attenuates proceptive behavior in this species.

Male reproductive tactics

Male hyenas frequently sniff female conspecifics, presumably to evaluate each female's reproductive state via pheromonal cues (Drea et al., 2002b). It is, therefore, interesting that time to conception emerged here as the only significant female characteristic influencing a male hyena's decision to stay with a female after he has sniffed her (Table 2). A male's choice of mates is also indicated by his persistent following of, or extensive courtship behavior directed toward, a particular female, even in the presence of multiple other females. A male's decision regarding whether or not to invest more time in a particular female appears to be influenced by the female's time to conception and by her social rank (Table 2). We interpret these data to indicate that male hyenas can discriminate among female hyenas, and that they may make strategic choices based on female social rank and time to conception.

Like East et al. (2003) we found no evidence that mate-guarding or consortship (what they called 'shadowing') strongly influenced female mate preference. That we sometimes saw a female mating with different males on consecutive days, but never observed any one mating pair copulating repeatedly on successive days, suggests that mate-guarding is not necessarily a successful male strategy. East et al. (2001, 2002) argued that shadowing appears to be "a tactic to foster extended relationships with particular females", and they suggested these relationships might enhance male reproductive success. Although some of our data support this idea, they also show clearly that either an extended relationship with a female is not required for a male to sire her cubs or that such relationships can be fostered without consortship. If mating precedence affects probability of paternity when a female mates with multiple males, then mate-guarding might offer a selective advantage. Competition to mate first with a lioness often prompts male lions to mate-guard starting some days before a female comes into heat (Packer & Pusey, 1982, 1983).

Female fertility

Many matings among *Crocuta* appear to be infertile. In total we observed 39 copulations during 11 years of continuous daily observation. This represents a surprisingly small number of mating observations considering that, during the same time period, we recorded 158 conceptions associated with

births of litters eventually observed above ground ($\bar{X} = 14.4$ known conceptions/year). Our mating data would further suggest that the 158 litters produced might have required over 400 copulations, of which we observed at most only 10%. Moreover, fewer than half of the matings we observed ultimately resulted in the production of a litter. Thus, in addition to the negative effects of the female spotted hyena's odd genital morphology on her ability to expel young at parturition (e.g., Frank & Glickman, 1994), another cost of female virilization in this species may express itself as difficulty conceiving litters, perhaps resulting from masculinized genital morphology or ovarian physiology (Frank et al., 1995; Frank, 1997; Drea et al., 2002a).

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