Behav Ecol Sociobiol (2001) 50:231–238
DOI 10.1007/s002650100356

ORIGINAL ARTICLE

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Association patterns among male and female spotted hyenas (*Crocuta crocuta*) reflect male mate choice

Received: 26 June 2000 / Revised: 27 February 2001 / Accepted: 18 March 2001 / Published online: 11 May 2001

Abstract Although female animals tend to be choosier than males in selecting mates, sexual selection theory predicts that males should also be choosy when female fecundity varies. Reproductive success among female spotted hyenas varies greatly with social rank. Our goals were therefore to determine whether male hyenas preferentially associate with high-ranking females, and whether male preferences are affected by female reproductive state. Interactions between adult males and females were observed intensively, and association indices calculated for all male-female pairs, over a 7-year period in one population of free-living hyenas. Males initiated most affiliative interactions with females, and males associated most closely with females that were likeliest to be fertile. High- and middle-ranking males associated most closely with high-ranking females, but low-ranking males associated equally closely with females in all rank categories. We used molecular markers to determine the paternity of cubs born during the study period, and found that sires associated more closely with the mothers of those cubs than did non-sires, particularly during the last months before conception. These association data indicate that male spotted hyenas do indeed exhibit selective mate choice, and that they prefer females likeliest to maximize male reproductive success.

Keywords Spotted hyena · *Crocuta* · Association patterns · Male mate choice

Communicated by P. Kappeler

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Introduction

Because female animals produce larger gametes and often invest more time and energy in parental care than do males, access to females usually limits male reproductive success (Parker et al. 1972; Trivers 1972; Andersson 1994). Females can therefore generally be highly selective in their choice of mates. However, Darwin (1871) recognized that males might also sometimes have opportunities to choose the most attractive females from an array of mates. Indeed, male preferences have been documented in various animal species for older females with more experience (Burley and Moran 1979), younger females likely to be virgins (Forsberg 1987), larger and more fecund females (Gwynne 1981; Verrell 1985, 1989, 1995; Sargent et al. 1986; Berglund and Rosenqvist 1993), females with higher reproductive potential (Berger 1989; Schwagmeyer and Parker 1990; Schwagmeyer 1995), and females exhibiting superior parental care (Verrell 1990; Solomon 1993). In general, male mate choice is expected when males invest heavily in reproduction or when there is high variation in the quality of potential mates (Parker 1983; Gwynne 1991; Owens and Thompson 1994). In this study we investigated whether male mate choice occurs in a long-lived social mammal, the spotted hyena (*Crocuta crocuta*). Although males do not invest heavily in reproduction in this species, females vary greatly in their ability to produce surviving offspring.

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 adult immigrant males. *Crocuta* clans are fission-fusion societies in which individuals travel, rest, and forage in subgroups that can change in composition from day to day, or even hour to hour. Although associations among clan members shift frequently, clans are nevertheless rigidly structured by hierarchical rank relationships (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986; Holekamp and Smale 1990, 1993;

Mills 1990), and an individual's social rank determines its priority of access to food (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986). Female hyenas are philopatric, but all males disperse to new clans some time after reaching reproductive maturity at 2 years of age (Smale et al. 1997). Adult females are socially dominant to all adult males not born in the clan (Kruuk 1972; Smale et al. 1993).

Female reproductive success varies enormously with social rank in this species (Frank et al. 1995; Holekamp et al. 1996). In fact, reproductive skew among female *Crocuta* is greater than that observed among females of any other plural-breeding mammalian species for which comparative data are available (Holekamp and Smale 2000). High-ranking female hyenas begin breeding at younger ages, can more frequently support pregnancy and lactation concurrently, experience shorter intervals between litters, and have offspring that are more likely to survive to adulthood than those of lower-ranking females (Holekamp et al. 1996). Considering the significant variation observed in female reproductive success in this species, if males can assess the reproductive value of clan females, then sexual selection theory predicts that male hyenas should be highly selective in their choice of mates, preferring high- over low-ranking females. Male behavior patterns that serve to increase the chances that a particular female will mate with a certain individual male are indicative of mate choice (Halliday 1983; Bercovitch 1991). Here we looked for evidence of male mate choice in *Crocuta* by evaluating variation in interactions observed between males and their potential mating partners, and then inquiring whether variation in these interaction patterns is correlated with male reproductive success. One mechanism by which a male might be able to increase his chances of mating with a particular female is by developing an affiliative relationship with her (Smuts 1983, 1985; Bercovitch 1995). In this paper, we present data addressing the questions of whether male hyenas prefer to associate with high-ranking females, and whether male preferences vary with female reproductive state.

Methods

Study animals and observational techniques

We conducted this study in the Talek area of the Masai Mara National Reserve, 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. We monitored Talek hyenas continuously from June 1988 to June 1995. Throughout this period, we conducted behavioral observations of Talek hyenas on 23–31 days per month, except during April 1991, when observers were only present on 14 days. Between 1988 and 1995, the Talek study clan varied in size from 50 to 80 individuals, consisting on average of 12 adult immigrant males (range: 6–20) and 20 adult females (range: 16–28) and their juvenile offspring. We identified all hyenas in the Talek 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).

We established mother-offspring relations on the basis of regular nursing associations. 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 pelage, size, and other aspects of cub appearance and behavior. We determined social ranks of individual hyenas using the outcomes of several thousand dyadic agonistic interactions during which one individual exhibited submissive behavior to the other, regardless of whether or not the submissive behavior was elicited by aggression from the social partner (Holekamp and Smale 1990; Smale et al. 1993). Adult females and adult immigrant males were ranked in separate intrasexual dominance hierarchies. By convention, we assigned the highest-ranking (alpha) individual in each hierarchy a rank position of 1. Only immigrant males present in the clan for longer than 6 months were included in the male hierarchy. For some analyses, we divided each intrasexual dominance hierarchy into equal thirds: high, middle, and low ranks representing ranks 1–7, 8–14, and ≥15, respectively.

We conducted daily behavioral observations from vehicles between 0530 and 0900 hours and between 1700 and 2000 hours. During the study period, we observed hyenas for a total of 4,407.8 h during 15,353 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 ended either when all hyenas moved out of sight, for example into bushes, or when we drove on to a new location. We identified all individual hyenas present in each session, and we excluded from analyses any sessions in which one or more unidentified hyenas were present. We located hyenas while driving daily circuits around the study clan's home range, visiting the high points of the area, and scanning with binoculars to sample all parts of the home range every day for the presence of subgroups of hyenas. We then visited each subgroup to determine its composition. We also conducted multiple 30-min focal animal surveys (Altmann 1974) on each of 15 adult male and 23 adult female hyenas to compare rates at which males and females initiated and maintained associations with opposite-sex conspecifics. In each survey, we calculated the rate at which the focal animal approached opposite-sex conspecifics, and we also calculated the percent total time in each survey spent by the focal animal in following opposite-sex conspecifics. An approach was scored when a focal hyena moved to within 1 m of another individual. The focal animal was considered to be following another hyena in any observation minute during which it walked behind another individual moving in the same direction. An hourly approach rate was calculated for each focal animal as: (number of approaches/number of minutes observed with opposite-sex conspecific)×60. Percent time spent following was calculated as: (number of minutes spent following/number of minutes observed with opposite-sex conspecific)×100. We calculated mean values for each individual observed during multiple surveys.

Evaluation of male-female associations

We calculated an association index (AI) for each male-female pair using the twice-weight index of association (Cairns and Schwager 1987):

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

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. AIs were calculated only for females observed throughout complete reproductive cycles within the study period. A complete reproductive cycle began at the time of conception of one litter in which at least one cub survived to weaning, and ended at the conception of the subsequent litter. For cases in which paternity of cubs was known, we examined association patterns relative to the date of a female's conception. In other analyses, we divided each complete reproductive cycle into five reproductive states as follows.

- Pregnancy (P). The duration of pregnancy in *Crocuta* is 110 days (Schneider 1926; Kruuk 1972), so we calculated conception dates by subtracting 110 days from estimated birth dates to obtain conception dates that are accurate to ±7 days. However, since the extent of variation in gestation length in this species is not currently known, for analyses in which we focused on male-female interactions around the time of conception, we considered a female's "fertile period" as her date of conception±2 weeks.
- Lactation (L1, L2, L3). The lactation period began with the birth of a litter and ended with its weaning. Weaning conflicts and cessation of nursing indicated when cubs were weaned (Holekamp et al. 1996). 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 ('all-occurrence' sampling; 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, the weaning date was identified as being midway between the last nursing bout and the next sighting of mother and cub together without nursing (Holekamp et al. 1996). All weaning dates used in these analyses were accurate to within ±10 days. Lactation periods varied in length among Talek females from 7 to 21 months (Holekamp et al. 1996; Holekamp and Smale 2000). Therefore, to better compare association patterns among females with different lactation periods, we divided the total period of lactation for each female into three intervals of equal length, represented as L1, L2, and L3.
- Other (O). Females assigned to this condition had weaned one litter but had not yet conceived their next litter. Little is known about the estrous cycle of the spotted hyena. Matthews (1939) and Lindeque (1981) suggest that estrous cycles in this species recur every 14 days. However, there are no apparent morphological indicators of estrus in female spotted hyenas as there are, for example, in many cercopithecine primates (reviewed in Melnick and Pearl 1987), and copulations are rarely observed in *Crocuta*. Although most females weaned one litter weeks or months before conceiving another, females of all social ranks were occasionally observed to conceive while still nursing a previous litter (Holekamp et al. 1996). Here, females known to be pregnant while still nursing a previous litter were assigned a reproductive condition of "P" (see above).

The ability of male hyenas to access or monopolize fertile females should vary with the degree to which estrous cycles are synchronized among clan females. Therefore, we estimated the extent to which female fertile periods overlapped during the study period, by assuming that such overlap was possible if a particular conception occurred within 2 weeks of conception in another female. We considered as asynchronous those conceptions occurring more than 2 weeks before or after any other conception known to occur during the study period.

Most rank positions in the female dominance hierarchy were occupied by multiple individuals during the course of this study. We therefore calculated overall mean association indices for all rank positions in the female hierarchy by summing AIs across all female reproductive states for all females holding each rank, and dividing by the total number of AIs. We then compared mean AIs of male-female dyads among social rank categories and among female reproductive states. Using only associations observed between 1990 and 1995 for a subset of females bearing litters during this period, we also compared female associations with known sires to those with males known not to have sired their litters.

In addition to calculating AIs, we also calculated the mean number of males present with each female and compared these values among female reproductive states and categories of female social rank. Finally, we were interested in comparing male-female associations in *Crocuta* with the male-female "consortships" observed in other mammals. Therefore, we determined the percentage of all sessions in which each male was observed during which he was found alone with a particular female. To do this, we counted the number of sessions during which a pair was seen alone together, without any other hyenas present, divided that value by the total number of observation sessions for the male, and multiplied the result by 100. We did this for each month-long interval surrounding conception of the female's litter.

Paternity determination and statistical analysis

We used microsatellite markers identified from *Crocuta* DNA to determine male parentage in the Talek clan. Between 1990 and 1995, we collected blood from 185 Talek hyenas. Sampling was conducted after individuals were anesthetized with Telazol (2.5 mg/kg) delivered from a CO_2-powered rifle in a lightweight plastic syringe. We then immediately extracted DNA from blood using Puregene kits (Gentra Systems), 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 13 microsatellite markers described elsewhere (Libants et al. 2000; S.M. Funk and A.L. Engh, unpublished data). Paternity was determined using three approaches. First, males were excluded as potential fathers if their genotypes were inconsistent with those of offspring; that is, if each putative father-cub pair did not share an allele at every locus surveyed. Paternity was also evaluated by testing significance of pairwise relatedness (r_{xy}; Queller and Goodnight 1989), and by a maximum-likelihood analysis (program Cervus) which compared likelihoods of paternity for all non-excluded males (e.g., most likely fathers, second most likely fathers, and so on; Marshall et al. 1998). A male was only assigned as the sire of a particular cub if the exclusion probability (Chakraborty et al. 1988) exceeded 0.99, if the calculated r_{xy} value did not differ significantly from 0.5, and if the maximum-likelihood method assigned paternity at a confidence of 95%. If at least two of these conditions were not satisfied, we considered paternity unresolved. A more comprehensive analysis of paternity in the Talek clan is being prepared (A.L. Engh, S.M. Funk, R.C. Van Horn, K.T. Scribner, M.W. Bruford, S. Libants, M. Szykman, L. Smale, K.E. Holekamp, unpublished data).

We analyzed AI data using one-way, two-way and repeated-measures analysis of variance (ANOVA). For analyses in which we compared AIs within a male-female dyad across months, we treated AIs generated monthly by each pair as repeated measures. We evaluated relationships among smaller subsets of the data that were not normally distributed, using Mann-Whitney *U*-tests. We calculated correlation coefficients (Spearman's *R*) to ascertain whether mean male-female AIs varied with female social rank. Where we performed ANOVAs, we present mean values as $\bar{x}$±SE. For non-parametric tests, we present median values±interquartile ranges (IQR). We considered differences between groups to be statistically significant when $P<0.05$.

Results

Effects of social rank and female reproductive state

We calculated overall AIs for 40 immigrant males observed together with 19 adult females. AIs ranged from 0 to 1, with a mean of 0.062±0.002. Social ranks ranged from 1 to 20 for females and from 1 to 19 for males. Overall mean AIs between males and females varied significantly with female social rank, with males associating more closely with high- than with low-ranking females (Spearman rank correlation: $R_s=-0.76$, $n=19$ ranks, $P<0.001$; Fig. 1).

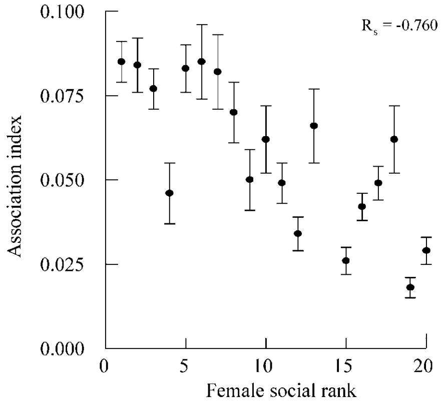

Fig. 1 Mean (±SE) intersexual association indices (AIs) plotted as a function of female social rank. By convention, the highest rank possible is 1. Each point represents the mean AI for all females who held a particular rank with all males observed with each female while she held that rank. *n*=2,665 associating pairs involving 19 females and 40 males associating during all female reproductive states

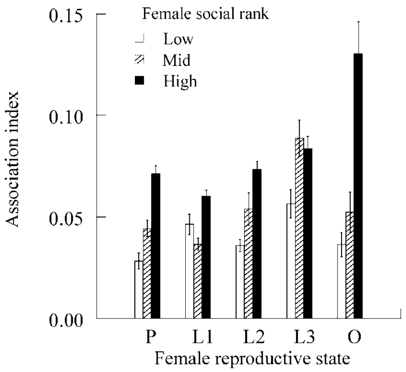

Fig. 2 Mean association indices for male-female pairs measured across all female reproductive states and grouped by female social rank. Female reproductive states are as follows: *P* pregnancy; *L1*, *L2*, *L3* first, second, and third trimester, respectively, of the lactation period; *O* other states when adult females were neither pregnant nor lactating. Rank categories: *High* ranks 1–7, *Mid* ranks 8–14, *Low* ranks 15 and higher. Sample sizes are as in Fig. 1

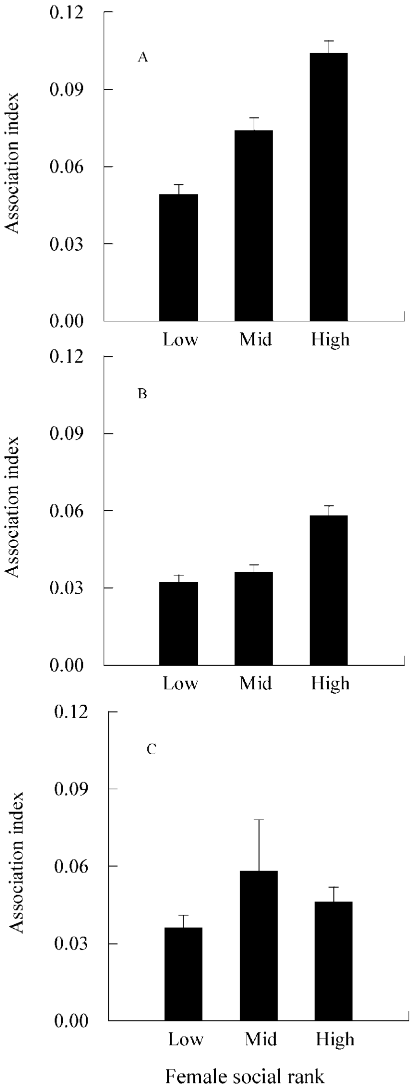

Fig. 3 Mean (±SE) association indices between females in each rank category and high-ranking (**A**), mid-ranking (**B**), and low-ranking (**C**) males. Rank categories are as in Fig. 2 and are the same for both sexes. Sample sizes are as in Fig. 1

We then examined the effects of female reproductive state and rank category on patterns of association. Females were observed over 40 complete reproductive cycles ($\bar{x}$=2.1±0.07 cycles per female). Maximum AIs reached 1.00 in all states except P and L1, which had the lowest maximum AI values of 0.368 and 0.500, respectively. Males not only associated most closely with the highest-ranking females when females were grouped into three rank categories (ANOVA: rank, $F_{2,2650}$=58.325, P<0.001; Fig. 2), but also with females that were most likely to be fertile, i.e., during states L3 and O (reproductive state, $F_{4,2650}$=12.959, P<0.001; Fig. 2). Moreover, there was a significant interaction between female rank and reproductive state, indicating that males associated most closely with high-ranking females at times when these females were most likely to be fertile (two-way ANOVA: $F_{8,2650}$=7.565, P<0.001; Fig. 2).

Male social rank also influenced intersexual association patterns in these hyenas. High-ranking males associated more closely with high-ranking females than did lower-ranking males (two-way ANOVA: $F_{4,2656}$=5.150, P<0.001; Fig. 3). In fact, both high-ranking males and high-ranking females associated more closely overall with members of the opposite sex than did lower-ranking individuals (males, $F_{2,2656}$=45.458, P<0.001; females, $F_{2,2656}$=18.447, P<0.001). Post hoc tests revealed that both high- and middle-ranking males associated most closely with high-ranking females (Fig. 3A, B), while low-ranking males tended to associate more or less equally with females in all three rank categories (high-ranking males, $F_{2,1341}$= 34.917, P<0.001; middle-ranking males, $F_{2,1059}$= 15.767, P<0.001; low-ranking males: $F_{2,256}$=1.291, P=0.28; Fig. 3C).

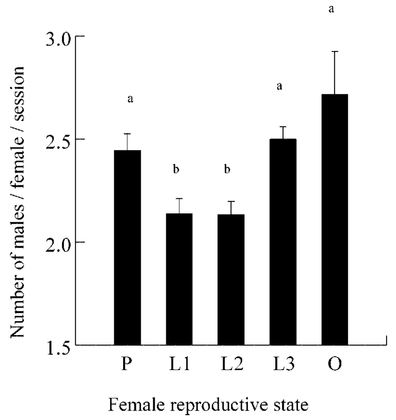

Fig. 4 Mean number of males observed per session with each female across all female reproductive states. n=4,798 sessions for which 19 females were observed with 40 males. *Bars sharing the same letters* represent means not significantly different from one another as determined by Tukey's post hoc comparisons

As a female hyena moves around the Talek area, she may travel alone, with kin, with a single adult male, or with a sizeable entourage of males. The average number of males present with an individual female varied with female reproductive state (ANOVA: $F_{4,4793}=10.347$, $P<0.001$; Fig. 4) but not with female social rank ($F_{2,4795}=1.229$, $P=0.29$). The greatest number of males associated with females during the reproductive states L3 and O, when females were most likely to be fertile, but also during pregnancy (Tukey's post hoc comparisons).

To evaluate the roles played by adults of each sex in initiating associations, we calculated rates of behavior performed during 346 focal animal surveys on 15 adult males, and during 127 focal animal surveys on 23 adult females, for which at least one adult member of the opposite sex was present (males, $\bar{x}=5.5\pm0.7$ focal animal surveys/individual). Males approached females at significantly higher rates than vice versa; in fact, females rarely approached males (median for males=1.92 approaches/h, IQR=1.08–3.18 approaches/hour; median for females=0 approaches/h, IQR=0–0.12 approaches/h; Mann-Whitney U-test: $U_1=16.000$, $n_1=15$, $n_2=23$, $P<0.001$). Similarly, females rarely followed males, and males spent a significantly greater percentage of their focal time following females than females spent following males (males, 7.9%, IQR=4.7–10.1% of their time spent following females; females, 0%, IQR=0–0.3% of their time spent following males; Mann-Whitney U-test: $U_1=10.000$, $n_1=15$, $n_2=23$, $P<0.001$). Thus, associations between male and female spotted hyenas appeared to be initiated and maintained almost exclusively by males.

Reproductive synchrony among Talek females

Dates of 105 fertile periods were known during the study period for 35 female hyenas, so we evaluated reproductive synchrony by measuring overlap among these fertile periods ($\bar{x}=2.7\pm0.2$ fertile periods per female). We found that 56.3% of fertile periods occurred when no other Talek female was concurrently fertile (Fig. 5). Although up to five females were observed to be fertile concurrently during the study period, this occurred only once and, on average, only 1.6±0.1 females were fertile concurrently. Thus, reproductive synchrony among Talek females was generally low throughout the study period.

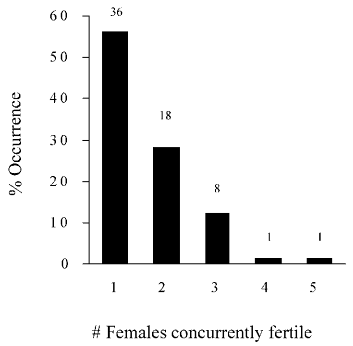

Fig. 5 Synchrony among 105 fertile periods of 35 females observed between 1988 and 1995. Sample sizes represent the number of 2-week intervals during which females were concurrently fertile

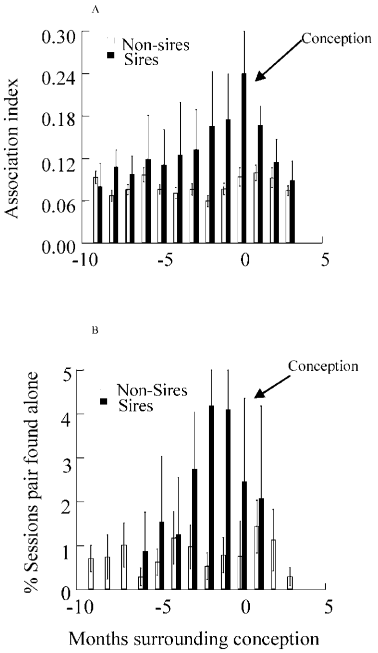

Fig. 6 **A** AIs for eight females with the eight males who sired (*solid bars*) their litters conceived during interval *0* compared with AIs for these same females with 15 males present concurrently who did not sire (*open bars*) their litters. Interval *0* represents the date of conception±2 weeks. Remaining intervals represent month-long periods surrounding the date of conception. **B** Percentage of observation sessions during which sires and non-sires were found alone with females, calculated as: (the number of sessions in which the pair was found alone/the total number of sessions in which that male was observed)×100

Comparing sires with non-sires

We next contrasted intersexual associations involving males who sired cubs with those of males who failed to sire offspring. We examined AIs during month-long intervals surrounding the conception of a litter for which the father was known via paternity analysis for a subset of eight females, each of which had a complete reproductive cycle preceding that conception. Males known to have sired the offspring of these females during these particular reproductive cycles associated significantly more closely with their mates than did other males (two-way repeated-measures ANOVA: $F_{1,86}$=14.064, P<0.001; Fig. 6A), particularly near the time of conception ($F_{12,86}$=1.961, P=0.038; Fig. 6A). Finally, we evaluated a male's ability to maintain exclusive access to a particular female by examining the percentage of all observation sessions in which he was observed during which he was found alone with that female. Sires spent significantly more time alone with their future mates than did males failing to sire offspring (two-way repeated measures ANOVA: $F_{1,86}$=6.501, P=0.012; Fig. 6B), particularly during the months immediately preceding conception ($F_{12,86}$=1.857, P=0.05; Fig. 6B).

Discussion

Our association data clearly indicate that male hyenas can assess the relative reproductive value of individual females, and that they appear to allocate their own reproductive effort among clan females based on this assessment. Male hyenas associate most closely, and in the greatest numbers, with females that are most likely to be fertile. Males of other mammalian species similarly prefer to associate with females when they are most likely to conceive (e.g., bison: Komers et al. 1994; baboons: Seyfarth 1978a, 1978b; Smuts 1985). Since neither visual nor acoustic signals emitted by female hyenas appear to vary with their reproductive condition, males presumably evaluate female reproductive state using olfactory cues. Although large numbers of males associated with females during pregnancy as well as during periods of maximal fertility (Fig. 4), exclusive associations between females and sires were not observed after the first month of gestation (Fig. 6B). Since females and sires do not remain together until cubs are born, exclusive male-female associations in *Crocuta* apparently do not function to reduce infanticide, as occurs in some primates (e.g., Sterck et al. 1997). Instead, male hyenas may be unable to detect the early stages of pregnancy in females, or they may associate with pregnant females to increase the probability of mating with them in the future. Studies of various primates show that a male can increase his chances of mating with a particular female by associating with her, even when she is not fertile (e.g., Smuts 1983, 1985; Hill 1987; Bercovitch 1995), and this may also hold true in *Crocuta*. Male hyenas might also continue to associate with their mates for a short time after conception to guard them from rival males, as occurs in lions (*Panthera leo*: Packer and Pusey 1982).

Like spotted hyenas, lions are polygynous carnivores in which individual males consort with fertile females. Reproduction is highly synchronous within lion prides, and several females may be simultaneously in estrus (Schaller 1972; Bertram 1975). Although rival males are more likely to be found near a consorting pair when availability of other estrous females is low, consorting lion pairs are found alone in approximately 50% of sightings (Schaller 1972; Packer and Pusey 1982). By contrast, consorting hyena pairs are found alone in less than 5% of sightings (Fig. 6B), so male hyenas may be far less successful than male lions in monopolizing access to fertile females. Male lions often "herd" females away from other pride members (Packer and Pusey 1982), but female *Crocuta* are dominant to males, so male behavior does not constrain female movement in this species.

In our study population, reproductive synchrony among females is low (Fig. 5), and this should theoretically permit male hyenas to associate closely with fertile low-ranking females without foregoing mating opportunities with higher-ranking females. Although we found that males associated with dominant females to the greatest extent at times when those females were most likely to be fertile, most males preferred high-ranking females during all stages of the female reproductive cycle. This supports the hypothesis that males actively choose among females, and indicates that males attempt to maximize their chances of mating with females with the greatest potential to produce surviving offspring, and thus also to maximize male reproductive success. Similarly, in many primate species, males show mating preferences for high-ranking females (reviewed in Robinson 1982; Silk and Boyd 1983).

In groups of canids and social mongooses, the highest-ranking individuals of each sex prefer the highest-ranking opposite-sex individual as their resting and grooming partners, closest associates, and mates (Rasa 1977; Derix and van Hooff 1995). In the current study, the social rank of male as well as female hyenas influenced intersexual patterns of association. Both high- and middle-ranking males associated most closely with the highest-ranking females, but low-ranking males failed to exhibit a preference for higher-ranking females. Low-ranking males may thus either be less adept than high-ranking males at assessing the reproductive value of clan females, or low- and high-ranking males may utilize different reproductive strategies.

Our comparison of association patterns of sires and non-sires suggests that by investing time with one prospective mate, a male hyena may obtain a payoff in terms of increasing his chances of mating with that female. However, our data also suggest that time spent with one particular female represents a substantial investment that might compromise the male's ability to explore alternative reproductive possibilities. Sires spend more of their time in exclusive isolation with their future mates than do non-sires, particularly during the last months before conception. One obvious benefit of associating with a female in isolation is exclusive access to that female when she is ready to mate. If a male associating with a particular female can keep her away from rivals, he has a greater chance of siring that female's offspring. Immigrant male *Crocuta* rarely fight among themselves (Kruuk 1972; Frank 1986), but the fission-fusion nature of hyena society may permit males to use physical separation with prospective mates as an effective alternative to combat, as also occurs in lions (Packer and Pusey 1982). Interestingly, although female hyenas in the current study were highly attractive to large numbers of males when females were likeliest to conceive (Fig. 4), known sires were able to maintain exclusive access to females relatively often during these periods of maximal fertility (Fig. 6B).

Close and exclusive intersexual associations were associated with paternity in the current study, but the cause-and-effect relationship involved here remains unknown. That is, a male might make himself more attractive to a particular female by spending more time with her, and thus enhancing his own chances of siring her cubs. Alternatively, a male might spend more time with a female because she has already chosen him to sire her cubs. Thus our data do not rule out the possibility that close intersexual associations in *Crocuta* reflect mate choice by females as well as by males. Indeed, female hyenas make exceptionally heavy and prolonged investment in each of their cubs (Hofer and East 1993, 1995; Holekamp et al. 1996), and receive no help from males in rearing young, suggesting that females should be highly selective in their choice of mates. Nevertheless, the reproductive performance of high-ranking females is far superior to that of low-ranking females (Holekamp et al. 1996), generating extreme variance in female reproductive success, and thus mate quality, as a function of social rank. Therefore, male *Crocuta* ought to be choosy, and our data are consistent with this hypothesis. In fact, we found that male-female associations in this species are almost exclusively initiated and maintained by males. In contrast, intersexual consortships in other social carnivores and in primates frequently involve a cooperative effort by both members of the pair to maintain proximity (Stern and Smith 1984; Small 1990). In these other mammals, consorting pairs are observed to copulate, and consorting males father most offspring (e.g., Packer and Pusey 1982; Bercovitch 1987; Small 1990). We rarely observe hyenas mating so we do not yet know to what extent copulation frequency in *Crocuta* can be predicted by male-female association patterns. However, unusually close intersexual associations are correlated with paternity in *Crocuta*, as they are in other gregarious mammals.

Finally, our data allow us to contrast male-female association patterns in *Crocuta* with patterns previously documented for female-female and mother-offspring associations in this same species. Using the same AI calculations as utilized here, Holekamp et al. (1997) showed that association patterns among adult female *Crocuta* are strongly influenced by both kinship and rank. Adult females associate more closely with their adult female kin than with unrelated adult females, and high-ranking mother-offspring pairs associate more tightly than do low-ranking dyads. When we compare absolute values of association found in that earlier study and in this one, on average, adult males associate with adult females at about the same levels as adult females associate with other unrelated adult females. Furthermore, males siring litters associate with their mates almost as closely as do mothers with their own offspring, with AIs over twice as high as those of males failing to sire those cubs. Although male-male association patterns have not yet been examined in this species, our results suggest that adult males may form their closest associations with the females with whom they eventually mate.

Acknowledgments We thank the Office of the President of Kenya for permission to conduct this research. All work reported here was conducted in accordance with Kenyan law. We thank the Kenya Wildlife Service, the Narok County Council, and the Senior Warden of the Masai Mara National Reserve for their cooperation. We thank N.E. Berry, E.E. Boydston, S.M. Cooper, M. Durham, J. Friedman, P. Garrett, I. Graham, T.H. Harty, C.I. Katona, K. Nutt, G. Ording, K. Weibel, and B. White for their assistance in the field, P. Arctander, M.W. Bruford, T. Burland, T. Coote, S. Dloniak, T. Friedman, S. Jenks, P. Kat, S. Libants, J. Scullon, D. Wasao, and R.K. Wayne for their efforts in the laboratory, and L. Smale, P.M. Kappeler, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. This work was supported by NSF grants BNS8706939, BNS9021461, IBN9309805, IBN9630667, and IBN99-06445.

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