Reproductive skew among males in a female-dominated mammalian society

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The purpose of this study was to document patterns of reproductive skew among male spotted hyenas (Crocuta crocuta), a species in which many normal mammalian sex roles are reversed. We used paternity determined from 12 microsatellite markers together with demographic and behavioral data collected over 10 years from a free-living population to document relationships among reproductive success (RS), social rank, and dispersal status of male hyenas. Our data suggest that dispersal status and length of residence are the strongest determinants of RS. Natal males comprise over 20% of the adult male population, yet they sire only 3% of cubs, whereas immigrants sire 97%. This reproductive advantage to immigrants accrues despite the fact that immigrants are socially subordinate to all adult natal males, and it provides a compelling ultimate explanation for primary dispersal in this species. High-ranking immigrants do not monopolize reproduction, and tenure accounts for more of the variance in male reproductive success than does social rank. Immigrant male hyenas rarely fight among themselves, so combat between rivals may be a relatively ineffectual mode of sexual selection in this species. Instead, female choice of mates appears to play an important role in determining patterns of paternity in Crocuta. Our data support a “limited control” model of reproductive skew in this species, in which female choice may play a more important role in limiting control by dominant males than do power struggles among males. Key words: Crocuta, dispersal, hyena, mate choice, rank, reproductive skew, reproductive success, tenure. [Behav Ecol 13:193–200 (2002)]

Mammalian societies vary in the extent to which reproduction is skewed toward one or a few socially dominant individuals. In societies organized by hierarchical rank relationships, reproductive success (RS) among males is often positively correlated with social rank, which in turn is largely determined by fighting ability. Rank-related reproductive skew among males has now been documented with behavioral and molecular data in many group-living mammals (ungulates; Clutton-Brock, 1988; Pemberton et al., 1992; rodents; Sherman et al., 1991; primates; Altmann et al., 1996; Bercovitch and Nurnberg, 1997; De Ruiter et al., 1994; Smith et al., 1993; carnivores; Creel et al., 1997; Girma et al., 1997; Griffin, 1999; Keane et al., 1994). In all of these species, and in most other mammals as well, sexual selection has favored males that are larger, stronger, and more pugnacious than females (Darwin, 1871). Like societies of many other gregarious mammals, social groups of spotted hyenas (Crocuta crocuta) are structured by linear dominance hierarchies (Frank, 1986; Holekamp and Smale, 1990, 1993; Kruuk, 1972; Mills, 1990). However, in contrast to most other mammals, spotted hyenas exhibit some striking sex-role reversals. That is, among adult hyenas, females are larger and more aggressive than males, and females dominate males in all dyadic contexts (Frank, 1986; Kruuk, 1972). Furthermore, fighting among adult male hyenas is less frequent and less intense than is that observed among adult females (Frank, 1986; Kruuk, 1972; Mills, 1990), suggesting that male-male contest competition over mates may not function as importantly in sexual selection in hyenas as it does in many other mammals.

Reproductive success among female Crocuta is strongly correlated with social rank (Frank et al., 1995; Holekamp et al., 1996), but little is known about RS in males. Limited observations of wild spotted hyenas have suggested that only the highest-ranking immigrant male fathers offspring in this species (Frank, 1986; Mills, 1990). However, copulations are rarely observed, so the extent of reproductive skew among male hyenas remains unknown. Here we combine field observations with the use of genetic markers as indicators of paternity to examine patterns of reproductive skew among male hyenas, as well as to test predictions of competing models suggesting alternative relationships between male rank and RS in this species. The first, null, hypothesis suggests that males of all social ranks should be equally likely to father cubs. Second, a dominance-based priority of access model predicts that the number of offspring sired by a given male should depend on both his social rank and the number of females simultaneously in estrus. In a less restrictive test of the priority of access model, we inquire whether the highest-ranking male observed with a fertile female is the male most likely to sire her cubs.

Spotted hyenas are gregarious carnivores that live in social groups, called clans, composed of multiple matrilines of adult females and their offspring, as well as one or more adult immigrant males. An individual’s social rank determines its priority of access to food (Frank, 1986; Kruuk, 1972; Tilson and Hamilton, 1984). Both male and female cubs “inherit” their mothers’ ranks; that is, they attain ranks in the dominance hierarchy immediately below those of their mothers (Engh et al., 2000; Holekamp and Smale, 1993; Smale et al., 1995). Females are usually philopatric, whereas males invariably emigrate from their natal clans at 25 to 62 months of age (Frank, 1986; Henschel and Skinner, 1987; Holekamp and Smale, 1993).
1998; Smale et al. 1997). Adult natal males dominate adult females ranked lower than their own mothers in the clan’s dominance hierarchy for as long as they remain in their natal clans. However, when males disperse, they behave submissively to all new hyenas encountered outside the natal area (Holekamp and Smale, 1998; Smale et al., 1993, 1997). Thus, by joining a new clan, each immigrant assumes the lowest rank in that clan’s dominance hierarchy, and his status only improves through attrition by death or secondary dispersal of the immigrant males that arrived before him (Smale et al., 1997).

Because males typically remain in their natal clans for several months or years after puberty, there are two classes of reproductively mature males in every Crocuta clan: adult natal males born in the clan and adult immigrant males born elsewhere. Since all natal animals outrank all immigrants, a male’s rank-determined priority of access to food is inevitably worse after he emigrates from his natal clan than before dispersal (Holekamp and Smale, 1998; Smale et al., 1993, 1997). Nevertheless, all males eventually disperse. If dispersal is adaptive, then the fitness benefits of dispersing must exceed the costs associated with reduced access to food. The ultimate cause of male dispersal in this species remains unknown. The most plausible hypothesis to account for a behavior pattern with such dire nutritional consequences is that males may only be able to mate outside of their natal clans. Therefore, in addition to using our genetic data to examine patterns of reproductive skew among males, we also use them to test this hypothesis.

METHODS

Study population

We conducted this study in the Talek area (1°40’ S, 35°50’ E) of the Masai Mara National Reserve. This is an area of open grasslands grazed year round by large concentrations of several ungulate species. The subject population was one large Crocuta clan inhabiting a home range of approximately 65 km². We monitored Talek hyenas from June 1988 to January 1999.

We identified all hyenas in the Talek clan by their unique spot patterns, and we determined their sex from the dimorphic glans morphology of the erect phallus (Frank et al., 1990). All hyenas initially appearing in the Talek home range as adults were photographed when first sighted, and the day an individual was first seen in Talek was considered its date of arrival. Immigrant males remaining in Talek for at least 6 months were called “resident immigrant males,” whereas males remaining for shorter periods were called “transients.” The duration of residence of any given immigrant male in the Talek clan was called its “tenure” in the clan. Between 1988 and 1999, the Talek study clan varied in size from 50 to 78 individuals, and usually contained 20 to 22 adult females (range: 16–28) and their juvenile offspring. On average during the study period, 13.8 ± 2.1 resident immigrant males and 4.4 ± 0.6 adult natal males were present in the clan. In addition, two or three transient immigrant males appeared in the clan’s territory each month and remained for shorter periods, usually only a few days (Smale et al., 1997).

Mother-offspring relationships were established on the basis of regular nursing associations, which last up to 21 months in this species (Hofer and East, 1995; Holekamp et al., 1996). We assigned birth dates to litters by estimating cub ages when the individual was first seen in Talek was considered its date of birth. We identified all individual hyenas present in these sessions, and we excluded from analyses any sessions in which one or more unidentified hyenas were present. Throughout the study period, all mounting behavior and complete copulatory sequences (those involving intromission and ejaculation) were recorded during critical incident sampling (the “all occurrence sampling” of Altman, 1974).

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, as described previously (Holekamp and Smale, 1990; Smale et al., 1993). All resident immigrants present in the clan concurrently were organized into a matrix based on direction, not number, of interactions (Martin and Bateson, 1988). The resident immigrant matrix was composed of 997 dyadic agonistic interactions in which 38 interactions (3.8%) were inconsistent with assigned ranks. By convention, the highest-ranking immigrant, who was able to win against all other immigrants in agonistic interactions, was called the “alpha male,” and was assigned a rank of 1. The period during which any male held alpha status was referred to as his “reign.” Due to male attrition and the arrival of new immigrants, not all resident males present in Talek during a given reign were necessarily there concurrently. For tenure-based analyses, only resident immigrant males whose tenure began after the start of the study period were used.

Sample collection and paternity analysis

Most DNA samples originated from venous blood collected while hyenas were anaesthetized with Telazol (2.5 mg/kg) delivered from a CO₂-powered darting rifle (Telinject, Saugus, California, USA). Most cubs were darted between 8 and 12 months of age, and immigrant males were darted as early in their tenure as possible. We collected body and tooth measurements from all immobilized hyenas. We used a Puregene (Gentra Systems, Minneapolis, Minnesota, USA) kit to extract DNA from blood shortly after collection, and then stored the DNA in liquid nitrogen. We also collected tissue samples from dead hyenas whenever we found them. DNA was isolated from tissues using either standard phenol-chloroform extraction techniques or Qiagen kits (Qiagen, Bothel, Washington, USA). We genotyped sampled individuals using eleven autosomal microsatellite loci and one X-linked microsatellite locus (CCATAndr3) as described elsewhere (Funk SM and Engh AL, unpublished data; Libants et al., 2000). Across the 12 loci, on average, there were 5.1 alleles/locus (range: 2–8), and the expected heterozygosity was 0.62. We estimated typing error (1.0%) from the frequency of mother-cub mismatches. Overall exclusion probability was .998.

All resident immigrant, transient, and unrelated adult natal males present in the clan at conception of a particular litter were considered as potential fathers. Males were considered unrelated to particular females when their maternal coefficients of relatedness, calculated from genealogies, were less than 0.125. We employed a maximum likelihood-based approach (Meagher, 1986; Thompson, 1975) to assign paternity to cubs with known, genotyped mothers using the program...
Table 1

Patterns of paternity during eight alpha male “reigns”

<table>
<thead>
<tr>
<th>Alpha male</th>
<th>Dates of reign as alpha</th>
<th>% resident immigrants sampled (N)</th>
<th>% adult natal males sampled (N)</th>
<th># of known conceptions</th>
<th># of known fathers</th>
<th># sired by alpha male</th>
<th># sired by adult natal males</th>
<th># sired by non-alpha resident immigrant males</th>
</tr>
</thead>
<tbody>
<tr>
<td>1019</td>
<td>12/7/90–11/9/91</td>
<td>100% (15)</td>
<td>92% (12)</td>
<td>15</td>
<td>13</td>
<td>9</td>
<td>1 (11%)</td>
<td>0</td>
</tr>
<tr>
<td>MRB</td>
<td>11/10/91–6/1/92</td>
<td>100% (13)</td>
<td>86% (7)</td>
<td>8</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>EN</td>
<td>6/2/92–2/20/93</td>
<td>100% (10)</td>
<td>86% (7)</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>2 (50%)</td>
<td>0</td>
</tr>
<tr>
<td>HOL</td>
<td>2/21/93–3/29/93</td>
<td>100% (7)</td>
<td>100% (5)</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>3 (100%)</td>
</tr>
<tr>
<td>QUA</td>
<td>3/30/93–6/21/93</td>
<td>100% (6)</td>
<td>100% (5)</td>
<td>6</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>2 (100%)</td>
</tr>
<tr>
<td>ZIP</td>
<td>6/22/94–4/21/94</td>
<td>100% (9)</td>
<td>86% (7)</td>
<td>29</td>
<td>12</td>
<td>7</td>
<td>0</td>
<td>2 (29%)</td>
</tr>
<tr>
<td>SY</td>
<td>4/22/94–2/13/97</td>
<td>95% (21)</td>
<td>100% (10)</td>
<td>69</td>
<td>37</td>
<td>23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>FN</td>
<td>2/14/97–1/1/99</td>
<td>95% (22)</td>
<td>100% (8)</td>
<td>61</td>
<td>36</td>
<td>25</td>
<td>1 (4%)</td>
<td>0</td>
</tr>
<tr>
<td>ALL</td>
<td>12/7/90–1/1/99</td>
<td>95% (37)</td>
<td>92% (38)</td>
<td>189</td>
<td>110</td>
<td>75</td>
<td>4 (5%)</td>
<td>2 (3%)</td>
</tr>
</tbody>
</table>

CERVUS (Marshall et al., 1998). We used the following parameters in CERVUS: 85 candidate males (total number of resident immigrant males + adult natal males + sampled transient males), 92% of candidate males sampled, 91% of loci typed, and a 1% error rate. A male was considered the father of a cub when CERVUS assigned him at 95% confidence. Confidence levels were derived based on population allele frequencies at each locus and represent levels of tolerance of false paternity that would be assigned to males whose genotypes are consistent with those of cubs by chance alone (see Marshall et al., 1998 for details).

Modeling the relationship between male rank and male RS

We used results of our paternity analysis to examine predictions of two mutually exclusive models, each suggesting a different relationship between male rank and RS in Crocuta. The first hypothesis suggests that males of all social ranks should be equally likely to father cubs. A second, dominance-based priority of access model predicts that the number of offspring fathered by a given male should depend on both his dominance status and the number of females simultaneously in estrus (Altmann et al., 1996). Since a male can monopolize only one fertile female at a time, the priority of access model predicts that the alpha immigrant male will father all offspring conceived when only one female in the group is in estrus, the alpha and beta males will equally share paternity of cubs sired when two females are simultaneously in estrus, and so on (Altmann et al., 1996). Conception dates of hyena litters were calculated by subtracting the gestation period of 110 days (Schneider, 1926) from birthdates. The 2-week interval surrounding each conception date was considered the fertile period during each breeding cycle of each female hyena. In addition, we determined whether the highest-ranking male present with a particular female during her fertile period was the male most likely to father her cubs. To do so, we recorded the identities and social ranks of all males found with that female during her fertile period. Finally, to evaluate whether access to females was affected by male rank, we calculated the percent of all adult male western male hyenas that were encountered by each immigrant male per observation session during 26 2-week intervals in 1994 as ((number of females encountered/number of females present in the clan)/number of sessions each male observed)*100.

Statistical analysis

Correlations between behavioral variables or measures of male RS and male social rank were evaluated with Spearman correlation coefficients using SYSTAT software. The results were assessed using Pearson’s R. Probabilities of fathering cubs were compared for adult natal and adult immigrant males using chi-square tests, as were observed and predicted values obtained in testing the priority of access model. We compared reproductive rates of age-matched immigrant and adult natal males with a Mann-Whitney U test, and used analysis of variance to evaluate differences in measures of RS among males based on total tenure and highest rank achieved. For analyses in which the dependent variable was a proportion (percent of assigned cubs sired), we used an arcsine-square root transformation to normalize the distribution of the data. Differences between groups were considered significant when p < .05.

Please note that the data presented in Figures 1 and 6 represents the same male at more than one rank or in more than 1 year. Almost all resident immigrant males were present for several years (range = 0.67–8.08) and occupied several ranks (range = 1–12) during their tenure in the clan, and we believe that using data from these same individuals over multiple years and ranks presents a more complete view of long term male reproductive success than simply presenting a “snapshot” of RS at only one point in a male’s life. However, to avoid pseudoreplication, we include additional analyses in which individual males are represented only once or repeated measures where each male is represented over the same time/rank span.

RESULTS

Paternity assignment and multiple paternity

DNA samples from 199 hyenas were collected between December 1990 and August 2000, including 85 natal females, 74 natal males, 5 transient males, and 35 resident immigrant males. Between December 1990 and January 1999, each of eight different resident immigrant males held alpha status in Talek for 1 to 34 months. DNA was sampled from at least 92% of all resident immigrant and adult natal males during this period, and paternity was verified in 75 (68.2%) out of 110 cubs sampled (Table 1). Twelve of the 75 cubs assigned fathers had mismatches with their putative fathers at one locus. The rate of cub-father mismatches is 0.97%, which is similar to the 1.0% mismatch rate for known mother-cub pairs. No male assigned paternity by CERVUS at 95% confidence had more than a single mismatch with his putative offspring.

Seventeen cubs for which paternity could be assigned were from singleton litters, and 58 were from 31 twin litters. Of 14 twin litters in which sires could be assigned for both litter-
mates, three (21.4%) were fathered by two different males, and 11 (78.6%) were fathered by single males. In five (38.5%) of an additional 13 twin litters in which only one cub could be assigned a father, the assigned father could be excluded from siring the other cub at two or more loci. Because litter size varied from one to two cubs and the proportion of cubs in a litter sired by a single male differed in this population, all analyses below use individual cubs rather than litters as the units of analysis unless otherwise indicated.

Male dispersal status

Of the 75 cubs for which paternity could be assigned, 73 (97.3%) were fathered by immigrant males, and two (2.7%) by adult natal males (Table 1). No cubs were found to be sired by transient immigrant males; however, only five transients were sampled. Of 31 sampled cubs conceived during the 24 months when all five natal and 22 resident immigrant males were sampled (August 1995–September 1997), 22 (71.0%) were fathered by immigrants and none were sired by natal males. Twenty-nine of these 31 cubs (93.5%) could be assigned to Talek males using CERVUS at 80% or greater confidence, and the remaining two cubs (6.5%) could not be assigned with confidence to any Talek males. Uncertain paternity of these two cubs could be due to their having been sired either by unsampled transient males in the Talek area or by males encountered during female excursions into surrounding territories. We observed several transient males in the Talek home range each month (Smale et al., 1997), and females occasionally made forays into surrounding territories. On average, 94.4 ± 1.9% of all locations at which adult Talek females are found fall within the clan’s territorial boundaries (Boveston et al., 2001).

Mean annual RS among immigrant males was 0.66 ± 0.12 cubs/year (range, 0–2.33; N = 35), and was thus over 10 times higher than mean annual RS among adult natal males (mean = 0.06 ± 0.06 cub/year; range, 0–2.15; N = 35). Natal males were less likely to father any cubs at all than were immigrants (1 of 35 sampled adult natal males versus 22 of 35 immigrants; X² = 28.6, p < .001). When we restricted our analysis of RS to immigrant males estimated to be less than 3 years old, the mean annual RS of immigrant males (mean = 0.35 ± 0.19 cubs/year; N = 12) was still higher than that of adult natal males (Mann-Whitney U = 255.0; p = .02). It is therefore unlikely that adult natal males are simply too young to reproduce. These data indicate that adult natal males generally experience very low RS compared to that of males managing to join a new clan after emigration from their natal groups.

Male rank and the priority of access model

Most immigrant males that eventually attained alpha status sired at least one cub (range, 0–13 cubs; N = 8 males), but these males sired an average of 87.5 ± 11.0% of their sampled offspring before they attained alpha status. Clearly, alpha males were not monopolizing reproductive opportunities (Table 1 and Figure 1).

Social rank of resident immigrant males was positively correlated with their annual reproductive rate (Figure 1; R² = −0.31; p = .041; N = 35 males). In a conservative analysis in which each male’s rate of yearly cub production was calculated for a single, randomly assigned rank, we still found a positive correlation between male rank and RS (R² = −0.30; p < .042; N = 35). These data allowed us to rule out the null hypothesis, which suggested that males of all ranks were equally likely to sire cubs. However, although the correlation we found between male rank and RS was significant, rank failed to account for even half of the variance in male RS, and the pattern of RS observed among Talek males failed to match that predicted by the priority of access model (Figure 2; χ² = 170.2, p < .001).

One potential problem with the application of the priority of access model to the fission-fusion society of the spotted hyena is that it assumes that males obtain perfect information about the whereabouts and reproductive status of breeding females. In fact, however, higher-ranking immigrants typically encountered a larger proportion of clan females per time interval than did lower-ranking immigrants (Figure 3; R² = −0.66; p < .005; N = 20 males). Thus high-ranking immigrant males may be more efficient than their lower-ranking peers with respect to moving around the Talek territory or meeting up with multiple females. On average, males are only observed with 22.7% of females during each two-week period,
suggesting that even high-ranking males may not have accurate information about the reproductive status of most clan females.

We next assessed the possibility that the sire of a female’s litter is likely to be the highest-ranking male meeting up with her during her fertile period. We recorded the behavior of 29 females during 53 fertile periods in which we assigned paternity to the litter conceived. On average, each fertile female was observed for 260 ± 32 min in 11.4 ± 1.4 sessions. In 10 (18.9%) of the 53 fertile periods, the highest-ranking male observed with the female failed to sire any of her cubs. In fact, the highest-ranking male observed with a fertile female was no more likely to sire her cubs than any other immigrant male observed with her (χ² = 1.37, p < .25, N = 64 cubs). On average during these fertile periods, females were found with 2.51 ± 0.33 immigrants that were higher-ranking, and with 1.17 ± 0.19 unrelated adult natal males that were higher-ranking, than the sires of the cubs conceived.

Copulatory behavior

We watched Talek hyenas for over 30,000 person hours during the study period, but we observed only 39 mounting bouts and 20 bouts of complete copulation (Figure 4). Each bout typically included several mounts or complete copulations over a period of hours. Five of 39 mounting bouts (12.8%) were performed by five different adult natal males, and the remainder (87.2%) by 16 different immigrant males. Adult natal males were never observed to achieve intromission, so all complete copulations involved immigrants. Neither the number of mounting bouts performed (R = −0.38; ns) nor the number of copulations achieved (R = −0.14; ns) was significantly correlated with immigrant male social rank (N = 24 males), and long term male RS was positively correlated with total time in the clan (Figure 5; R = 0.82; p < .001; N = 24 males). One possible explanation for this pattern is that males failing to reproduce soon after immigrating to Talek engaged in secondary dispersal whereas successful males remained there longer. However, this interpretation seems unlikely since immigrant males that remained in Talek for several years were no more likely to have fathered cubs during their first two years in Talek than were immigrants that disappeared during their third year (2 of 6 versus 3 of 8 males, χ² with Yates’s correction for small samples = 0.18; ns).

To disentangle the effects of rank and tenure in Talek on immigrant male RS, we simultaneously regressed the transformed dependent variable of percent of assigned cubs sired against total male tenure in the clan and highest social rank achieved during that tenure. Whereas both of these independent variables were significantly related to percent cubs sired by immigrant males, total tenure (p = .02) explained 60% of the total variance in this model whereas highest rank achieved (p = .45) explained only 18% of the variance (N = 24 males). The rate at which males produce cubs is low early in their fourth through sixth in the immigrant male hierarchy.
tenure, then it increases after they have resided in the clan for several years (Figure 6; $F_{1,198} = 2.457; p = .021$). Repeated measures analysis of the three males who were present in the clan for a minimum of 5 years and eight social ranks detected a similar relationship between tenure and reproductive rate despite the small sample size and low power ($F_{1,8} = 4.25; p = .04$), but found no relationship between rank and reproductive rate ($F_{7,14} = 0.58; ns$).

Tenure was not significantly correlated with any measure of male body size, including body length ($R_p = 0.277; ns; N = 35$), skull length ($R_p = 0.289; ns; N = 35$) and shoulder height ($R_p = 0.201; ns; N = 35$). Thus immigrant males who had been present in the Talek clan for an extended period were not any larger than those males that had arrived more recently, and the observed relationship between male tenure and RS did not appear to be due to an effect of increasing body size.

**DISCUSSION**

The spotted hyenas in our Kenyan study clan exhibit a promiscuous mating system. Approximately one fifth of all twin litters are sired by multiple males. Genetic paternity tests have revealed that multiple paternity similarly occurs in many other carnivore species (Eurasian badgers; Da Silva et al., 1994; Ethiopian wolves; Gottelli et al., 1994; dwarf mongooses; Keane et al., 1994; lions; Packer et al., 1991). The most important determinants of RS in male hyenas appear to be an individual’s dispersal status and the duration of his residence in his new clan after dispersal. Adult natal male hyenas win all fights against immigrants and show sexual interest in clan females (Holekamp and Smale, 1998), yet they seldom father any cubs. It seems unlikely that natal males are too young to father cubs. This suggests a compelling ultimate explanation for lower than reproductive rates of age-matched immigrant cubs, since reproductive rates of natal males were significantly lower than those of their natal areas for superior access to mates elsewhere. Male-biased dispersal is common in mammals (Chepko-Sade and Halpin, 1987; Dobson, 1982; Greenwood, 1980; Pusey and Packer, 1987; Stenseth and Lidicker, 1992), and this behavior may have evolved in many species as a mechanism to promote outbreeding, either directly via selection on males or indirectly via female preferences for immigrant males as mates.

Among resident immigrant males, social rank is correlated with male RS, but tenure is a far better predictor of RS than is rank. Our data do not conform to predictions of a dominance-based priority of access model (Altmann et al., 1996), and the data documenting associations between males and fertile females are inconsistent with the hypothesis that the highest-ranking male present with a female during her fertile period is most likely to sire some or all of her offspring. Our results thus stand in striking contrast to those obtained from other mammalian carnivores in which male RS increases with social dominance and ability to win fights with other males (e.g., sea lions; Campagna and LeBoeuf, 1988; Cape hunting dogs; Creel et al., 1997; raccoons; Gehrt and Fritzell, 1999; meerkats; Griffin, 1999; kinkajous; Kays et al., 2000; wolves; Packard et al., 1985; polar bears; Ramsay and Stirling, 1986). The social lives of spotted hyenas are similar in many respects to those of most cercopithecine primates (Frank, 1986; Holekamp et al., 1999). However, most studies of paternity in wild cercopithecine primates generally find that, as in most other mammals (Ellis, 1995), male social rank is highly correlated with reproductive success (Altmann et al., 1996; de Ruiter et al., 1994; Melnick, 1987).

Several different hypotheses might explain why high-ranking male hyenas are not monopolizing reproduction. Social rank of male hyenas is not correlated with body size, so unlike high-ranking males in other polygynous mammals, high-ranking male hyenas cannot necessarily physically exclude lower-ranking males from mating. In fact, fighting among male hyenas is rare, and when it does occur, it is usually restricted to low-level threats (Frank, 1986; Kruuk, 1972). The only stage in the life history of this species in which males confront intense aggression from other males is during the process of immigrating into a new clan, and male-male fighting is rare even under these circumstances. Whereas all males disperse, few successfully immigrate. From 1988 to 1997, although 49% of 291 prospective immigrants remained in Talek for more
than 1 month, only 15% remained there for longer than 2 years (Smale et al., 1997). Aggression directed toward potential immigrants might permit only the best fighters to gain entry into the clan, and successful immigrants might then be too well matched to risk escalated fights. This scenario, however, seems unlikely, since most new immigrants behave extremely submissively to both male and female residents when trying to enter a new clan (Smale et al., 1997), and because substantial variation in body size, and thus presumably in fighting ability, exists within the immigrant male hierarchy.

High-ranking male hyenas may not be able to monopolize reproduction because they cannot adequately keep track of female location and reproductive state. Hyenas live in fission-fusion societies in which subgroup composition changes from day to day, or even hour to hour (East et al., 1993; Holekamp et al., 1997), so tracking multiple reproductive females might be difficult. Our analysis of male rank in relation to the proportion of clan females encountered shows that high-ranking males have a slight advantage over low-ranking males with respect to encountering females, so high-ranking males may fare better in scramble competition over mates. However, unlike lions, hyenas do not appear to respect “ownership” of estrous females by the first male to mate (Packer and Pusey, 1983). Indeed, we have observed two males alternately mounting a single estrous female (Szykman, 2001). Furthermore, our behavioral data show that even when high-ranking males are observed with fertile females, they are unlikely to father cubs. This is unlikely to be the result of sperm depletion (Preston et al., 2001), since estrus is asynchronous in female hyenas, and 60% of fertile periods do not overlap at all with those of any other females (Szykman et al., 2001). Thus, neither difficulty in finding receptive females nor inability to fertilize them can satisfactorily explain the patterns of reproductive skew observed among male hyenas.

Prohibitive energetic costs might keep high-ranking males from monopolizing reproduction. We frequently observed males following particular females for days or even weeks (Szykman, 2001). These “consorting” males may undergo serious energetic stress unless they periodically leave the females to feed. Female hyenas always have higher priority of access to food than immigrant males, so it may be difficult for a male to guard a female continuously for extended periods of time without starving. Male hyenas with the highest priority of access to food at ungulate kills may be best able to fortify themselves for extended attendance of females, and thereby obtain an advantage during male-male scramble competition (see also Bercovitch, 1997; Bercovitch and Nurnberg, 1996, 1997).

If this were true, however, we would expect to see a stronger relationship between male rank and RS than between tenure and RS.

Finally, high-ranking males may not be able to monopolize reproduction if females choose not to mate with them. Female hyenas are dominant to immigrant males, and their unusual genital morphology makes forced copulation impossible. Several lines of evidence suggest that female choice has important effects on patterns of paternity in Crocuta. First, despite the fact that adult natal males can always win in fights with immigrants, and although they express sexual interest in Talek females, natal males rarely father any cubs. These patterns suggest that females strongly prefer immigrants over natal males, perhaps to avoid the deleterious consequences of inbreeding. Second, patterns of association between Talek female and immigrant males show that the highest-ranking male present with a female during her fertile period fathers her cubs in only 19% of cases, and mid-ranking males do better than expected based on their ability to win in either agonistic interactions or scramble competition with other males. Third, RS varies substantially within most male rank positions, and also within any given year of immigrant tenure in the Talek clan, suggesting that some males present during each alpha reign are more attractive to females than others. These data suggest that female choice of mates may limit control of reproduction by high-ranking male hyenas.

Optimal skew models (e.g., Reeve et al., 1998; Vehrencamp, 1983) suggest that dominant individuals have full control of subordinate reproduction and allow subordinates to breed only when necessary to entice them to remain in the group and cooperate. Although optimal skew models may be applicable to some animal societies, they fail to account for observed partitioning of reproduction within many vertebrate social groups, including those of other mammalian carnivores (e.g., Clutton-Brock et al., 2001). Instead, these recent empirical data are more consistent with predictions of limited control models of reproductive skew which predict that subordinates will breed when dominants’ capacity for control of reproduction is reduced. Similarly, the data presented here for male spotted hyenas are more compatible with limited control than optimal skew models, but control in this species is clearly limited by variables other than those associated with male-male fighting. Indeed, as suggested recently by Koenig and Haydock (2001), interactions between males and females, including incest avoidance and mate choice, may limit dominance control of reproduction.

In contrast to what occurs in most polygynous mammals, male-male contest competition appears to have little influence over male reproductive success in the spotted hyena. The highest-ranking (natal) males have very low reproductive success, and high-ranking immigrant males cannot prevent lower-ranking males from copulating with females. Rather than favoring big, fierce males, sexual selection in hyenas has apparently favored males who compete by successfully immigrating, persisting in their new clans for several years, and overcoming the energetic handicaps imposed by low social rank.

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