

# Rank and reproduction in the female spotted hyaena

K. E. Holekamp<sup>1</sup>, L. Smale<sup>2</sup> and M. Szykman<sup>1</sup>

Departments of <sup>1</sup>Zoology and <sup>2</sup>Psychology Michigan State University, East Lansing, MI 48824, USA

Female reproductive success varies with social rank in many gregarious mammals, including primates, ungulates and carnivores. Social groups of spotted hyaenas (*Crocuta crocuta*) are structured by hierarchical dominance relationships that determine individuals' priority of access to food and other resources. The influence of female social rank on several measures of reproductive success was examined in a population of free-living *Crocuta* in Kenya. The study population was continuously observed for seven years, making it possible to document litter sizes, interbirth intervals, ages of cubs at weaning, intervals between weaning one litter and conceiving the next, annual rates of production of cubs, and survival of offspring to reproductive maturity. The relationship between availability of food, social rank, and female fertility was examined by monitoring abundance of prey throughout the study period. Most measures of reproductive performance were strongly influenced by social rank. High-ranking females began breeding at younger ages, were more frequently able to support pregnancy and lactation concurrently, experienced shorter intervals between litters, and produced more surviving offspring than did lower-ranking females. Low-ranking females exhibited better reproductive performance when prey animals were abundant than when prey were relatively scarce. By contrast, reproductive performance among high-ranking females was always superior to that exhibited by low-ranking females, and did not vary with prey abundance. Fertility among high-ranking females thus appeared to be less vulnerable to fluctuations in the food supply than was that among low-ranking females.

## Introduction

Reproductively successful organisms leave more surviving offspring than do other members of their species. Increased production of viable offspring by female mammals may be accomplished in several different ways. The reproductive lifespan of a female may be lengthened by earlier onset, extended duration, or both. Other mechanisms by which females can improve their reproductive performance include increasing litter size, reducing intervals between successive litters, or enhancing survival of offspring. Improvement in one or more of these parameters should result in superior reproductive success (Clutton-Brock *et al.*, 1982; Clutton-Brock, 1988). Intrasexual variation in reproductive success is associated with social rank in many gregarious mammals (primates: Dunbar, 1980; Silk 1987; Altmann *et al.*, 1988; Wasser and Starling, 1988; ungulates: Clutton-Brock *et al.*, 1988; canids: Malcolm and Marten, 1982; Packard *et al.*, 1985; viverrids: Rasa, 1979; Creel *et al.*, 1992). High-ranking individuals in these societies generally enjoy greater reproductive success than do animals of lower social status.

Spotted hyaenas (*Crocuta crocuta*) 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 immigrant adult males. Clans are rigidly structured by hierarchical rank relationships (Kruuk, 1972;

Tilson and Hamilton, 1984; Frank, 1986; Mills, 1990; Holekamp and Smale 1990, 1993), and the social rank of an individual determines its priority of access to food and other critical resources (Kruuk, 1972; Tilson and Hamilton, 1984; Frank, 1986). Adult females are socially dominant to all adult males not born in the clan (Kruuk, 1972; Smale *et al.*, 1993). Before cubs reach reproductive maturity they attain ranks in the dominance hierarchy of the clan immediately below those of their mothers (Holekamp and Smale, 1993; Smale *et al.*, 1993). Subadult individuals of both sexes can maintain their maternal ranks as long as they remain in the natal clan (Smale *et al.*, 1993). Female *Crocuta* generally spend their entire lives in their natal clans (Frank, 1986), but all males disperse to new clans between the ages of 2 and 5 years. When males leave their natal clans, they behave submissively to all new hyaenas encountered, and this is the point during ontogenetic development at which females come to dominate males (Smale *et al.*, 1993).

In many polygynous species competition among males over access to mates is extremely intense; success in this competition often varies with male social rank, and the outcome of this competition profoundly influences male reproductive success (Clutton-Brock, 1988). Competition among females, which is more often related to food access, is usually less dramatic than male–male competition, and has received considerably less attention (Floody, 1983). Nevertheless, competition among females can promote rank-related differences in reproductive performance (for example, Dunbar, 1980; Holekamp and Smale, 1995), which in turn appear to be mediated by differences in

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behaviour and physiology (for example, Keverne, 1979; Adam *et al.*, 1985). In *Crocuta*, competition among females over access to food is unusually intense, and dominant females enjoy better success in feeding competitions than do subordinates (Frank, 1986).

In contrast to the situation characteristic of many other gregarious carnivores, including canids and social mongooses in which only the alpha pair usually breeds, all adult female members of a *Crocuta* clan usually breed. However, Frank *et al.* (1995) found that high-ranking female *Crocuta* enjoy greater reproductive success than do lower-ranking females, and that reproductive success in the alpha matriline appeared to be qualitatively different from that of all other matriline in the clan. Here this dichotomy is explored further, and attempts are made to elucidate its causes. Specifically the various components of female reproductive performance among free-living hyaenas are dissected apart to determine which of these vary with female social rank. In addition, the possibility that differential food access mediates rank-related variation in female reproductive success is explored.

## Methods

The study site was the Talek area of the Masai Mara National Reserve, in southwest Kenya. This is an area of open, rolling grasslands grazed year round by large concentrations of several different ungulate species, the most numerous of which are Thompson's gazelles (*Gazella thomsonii*), topi (*Damiscilus korrigum*) and impala (*Aepyceros melampus*). Each year the resident ungulate populations are joined for three or four months by large migratory herds of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*). The migratory herds typically arrive in the Talek area in July or August, and depart in October or November.

The subject population was one large *Crocuta* clan inhabiting a home range of approximately 60 km<sup>2</sup>. All hyaenas in the study clan were known individually by their unique spots, and sex was determined from the dimorphic glans morphology of the erect phallus (Frank *et al.*, 1990). From June 1988 to June 1995, observers were present in the study area 23 to 31 days per month, except during April 1990. Mother-offspring relationships were established on the basis of regular nursing associations, and other genealogical relationships were as described by Frank (1983) and Holekamp *et al.* (1993). Juvenile hyaenas were those less than three years old, and adults those three years or older.

Female social ranks were established on the basis of outcomes of several thousand dyadic agonistic interactions among adult female members of the study clan, as described by Holekamp and Smale (1990) and Smale *et al.* (1993). By convention, the highest-ranking (alpha) individual was assigned a rank position of one. During the study period members of 14 different matriline were present in the clan. In addition to individual social ranks, matriline rank was also used in some analyses; in these analyses, all members of a matriline were assigned the same rank.

The gestation period in the spotted hyaena is 110 days (Schneider, 1926; Kruuk, 1972). Female *Crocuta* bear their litters in isolated natal dens, and then transfer cubs to the communal den of the clan when cubs are 2–5 weeks old. When cubs were

first observed above ground in the present study, at natal or communal dens, their ages were estimated to  $\pm 7$  days based on their pelage, size, and other aspects of their appearance and behaviour (for example, folded ears, callous pads on carpals; motor coordination). Birthdates were thus assigned to litters on this basis.

Throughout the study period, the following eight indicators of female reproductive performance were continuously monitored in the Talek study clan.

### *Age at first parturition*

Body mass of female *Crocuta* fluctuates dramatically with food intake, which may exceed 15 kg of meat in as little as 15 min while feeding at an ungulate carcass. Therefore unambiguous determination of pregnancy based on the physical appearance of the female is extremely difficult. Furthermore matings are rarely observed. However, if observers continuously monitor a clan, age at first parturition can readily be established in female *Crocuta* based on the fact that the female's pseudopenis tears when her first litter is born (Frank and Glickman, 1994), and heals leaving a large patch of pink scar tissue on the posterior surface of the phallus. Here the condition of this surface was carefully monitored in all nulliparous females older than 2 years, during the phallic erections so commonly exhibited when hyaenas greet each other (Kruuk, 1972; East *et al.*, 1993). Thus, even when a female's first litter was lost before her cubs first appeared above ground, it was possible to determine reliably when (to within 10 days) she had delivered her first litter.

### *Litter size and composition*

Free-living *Crocuta* generally bear litters of either one or two cubs, although triplet litters are frequently borne by captive hyaenas (Frank *et al.*, 1991). In the current study, litter size was determined based on the number of cubs observed when a litter first appeared above ground. No assumptions were made here regarding litter reduction due to siblicidal aggression (Frank *et al.*, 1991, 1995) or other mortality sources before cubs first appeared above ground. The sex of all cubs surviving to 3 months of age was determined when cubs exhibited phallic erections at dens.

### *Duration of the interbirth interval*

This measure was calculated as the number of months between consecutive parturitions when at least one member of the first litter survived to weaning. Interbirth intervals following twin litters were calculated only for cases in which both littermates survived to weaning. If one member of a twin litter died before 6 months of age but the remaining cub survived to weaning, the litter was counted as a singleton for purposes of calculating interbirth intervals.

### *Duration of the lactation period*

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. Weaning conflicts between cubs and their mothers are easily observed in this species due to the characteristic begging behaviour and loud whining exhibited by cubs at this time. All weaning conflicts were recorded in field notes as critical incidents (Altmann, 1974). In determining weaning dates, all field notes were searched for observations of nursing behaviour when mother and cubs 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. However, only intervals of 20 days or less were used in this analysis, so all weaning dates used here were accurate to within  $\pm 10$  days. Cub ages at weaning in twin litters were calculated only when both cubs survived to weaning.

#### *Duration of the recovery period*

The recovery period of the mother was defined as the interval (in months) between weaning of one litter and conception of her subsequent litter. Since the duration of gestation in this species is 110 days, conception dates were calculated by subtracting 110 days from birth dates. Since some females were found to be pregnant with a subsequent litter while still nursing their previous one, duration of the recovery period could assume either a negative or a positive value, indicating that the second litter was conceived, respectively, before or after weaning of the first.

#### *Duration of the interval between loss of one litter and conception of the next*

On every day on which observers were present in the study area, all active hyaena dens there were visited. Thus mortality of cubs residing at dens could be identified within 3–4 days based on the sudden disappearance of cubs, and on the searching behaviour of their mother. Dates of losses of pre-weaning cubs who no longer resided at dens were identified as the dates on which cubs were last sighted. Dates of cub losses could thus be estimated to within 10 days.

#### *Annual rate of cub production*

All females in the current study were represented only by partial reproductive lifespans. Therefore an annual rate of cub production was calculated for each female by dividing the total number of cubs she bore during the study period by the number of years she was present in the clan after reaching 36 months of age, or after conceiving her first litter for females who bore their first litters before they were 36 months old.

#### *Survival of offspring to reproductive maturity*

Although all male *Crocuta* eventually disperse from their natal clans, dispersal behaviour before 24 months of age has never been observed in this study, or described in any other published reports. Therefore males in the current study who vanished before 24 months were considered to have died, as were females who vanished before 36 months. Spermato-

genesis occurs in the testes of male *Crocuta* by 24 months of age (Matthews, 1939). Therefore, males who survived to 24 months, and females who survived to 36 months were considered to have reached reproductive maturity.

All adult females in the clan were anaesthetized one to four times during the study with Telazol ( $2.5 \text{ mg kg}^{-1}$ ; Butler Co, Brighton, MI) administered in a lightweight plastic dart fired from a  $\text{CO}_2$ -powered rifle. To determine whether female body size varied with social rank, body mass (kg), body length (cm) and leg length (cm) were measured while hyaenas were immobilized. When an adult female was darted more than once, mean values were used for each body size measurement.

The relationship between food availability and reproductive performance of female *Crocuta* was determined by regularly estimating abundance of local prey by counting all prey animals found within 100 m of 4 km transect lines in two different areas of the home range of the study clan. Both transects were run at bi-weekly intervals, between 08.00 and 10.00 h. All biweekly ungulate census estimates were averaged for each month of the study. Monthly variation in prey counts have been described by Holekamp *et al.* (1993). Numbers of prey animals counted per census ranged from 24 to 4306, with a mean of  $427 \pm 50$ . If the mean monthly prey count during a month in which a litter was weaned exceeded 400 antelope, that month was called a 'high game month', but if fewer than 400 antelope were counted, it was called a 'low-game month'.

Correlation coefficients (Spearman's *R*) were obtained to indicate whether reproductive performance varied with female rank, and the statistical significance of correlations was evaluated using analysis of variance (ANOVA). Possible interaction effects between food availability and social rank on female reproductive success were examined by assigning each female to one of two rank categories, depending on whether she was a member of the alpha matriline or a lower-ranking matriline. Members of the alpha matriline included only the alpha female, her mother and her breeding daughters and granddaughters. For females who weaned singleton litters during months of both high and low game abundance, effects of food availability during the month of weaning (high versus low game), and rank category of mother (alpha versus other matriline), on litter weaning ages were then evaluated using two-way ANOVA. Mean values were presented  $\pm \text{SEM}$ , and differences between groups were considered statistically significant when  $P < 0.05$ .

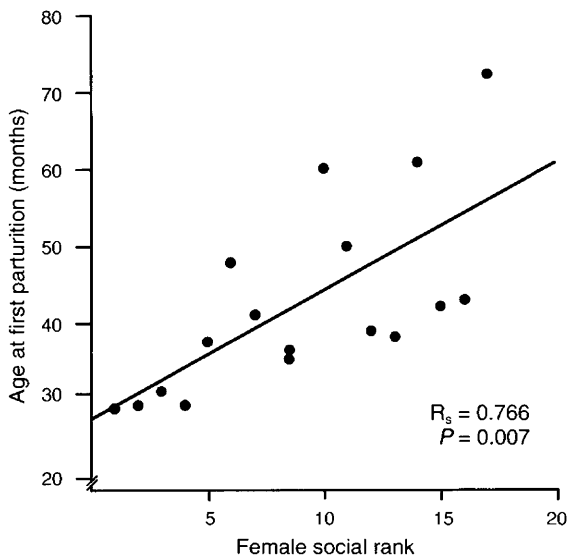
## Results

### *Rank-related variation in female reproductive performance*

*Age at first parturition.* Most measures of female reproductive performance were characterized by a great deal of variance (Table 1), and much of this variance was related to intrasexual social rank. Daughters of high-ranking females started bearing offspring at significantly younger ages than did their lower-ranking counterparts (Fig. 1:  $F = 9.97$ ;  $\text{d.f.} = 1,15$ ;  $P = 0.007$ ), and little variance in age of first parturition was observed among daughters of females in the first four rank positions. Variance in this measure of reproductive success increased as social rank decreased. The mean age at first parturition of

**Table 1.** Measures of central tendency in parameters of reproductive performance among female *Crocuta*

Reproductive parameter	<i>n</i>	Mean ± SEM	Range
Age of first parturition (months)	17	42.4 ± 2.9	29.1–73.0
Interbirth interval (months) after			
Singleton male	19	16.0 ± 1.2	6.6–28.7
Singleton female	13	14.1 ± 1.0	9.2–21.7
Twins	19	17.5 ± 0.6	12.9–22.9
Weaning ages (months)			
Singleton male	20	12.4 ± 0.7	7.1–18.8
Singleton female	10	11.5 ± 1.4	6.7–17.9
Twins	23	13.3 ± 0.5	8.5–18.6
Weaning to next conception (months) after			
Singleton male	19	0.5 ± 0.4	– 2.0–3.4
Singleton female	10	0.3 ± 0.4	– 3.0–1.0
Twins	12	0.8 ± 0.4	– 2.0–2.4
Annual rate of cub production	37	1.2 ± 0.1	0.4–2.5
Annual rate of production of cubs surviving to reproductive maturity	21	0.4 ± 0.1	0–0.9

**Fig. 1.** Ages at first parturition as a function of social rank for 17 female *Crocuta* who started breeding during the study period. Females holding rank positions 1 to 4 were all members of the alpha matriline.

females in the alpha matriline was  $29.83 \pm 0.45$  months, compared with  $46.31 \pm 3.15$  months for lower-ranking females ( $t = -2.931$ ; *d.f.* = 15;  $P = 0.01$ ). Assuming an overall adult reproductive lifespan in this species of approximately 13 years (Frank *et al.*, 1995), the average difference in age at first parturition between daughters of alpha females and those of lower-ranking females represents a 10% increase in reproductive lifespan for members of the alpha matriline.

**Litter size.** One hundred and six litters were first observed above ground before they were 5 weeks old. Of these, 60 were singletons, 45 were twin litters, and one contained three cubs. Sex ratios in these litters have been described by Holekamp and Smale (1995). Litter size did not vary with maternal rank

( $F = 0.03$ ; *d.f.* = 1,104;  $P = 0.863$ ). Furthermore, mean numbers of cubs per litter produced by females in the alpha matriline did not differ significantly from those produced by females from lower-ranking matrilines, regardless of maternal parity (Table 2). Within the alpha matriline, maternal parity had no significant effect on litter size. However, within lower-ranking matrilines, multiparous females produced significantly larger litters than did primiparous females ( $t = -2.154$ ;  $P = 0.036$ ).

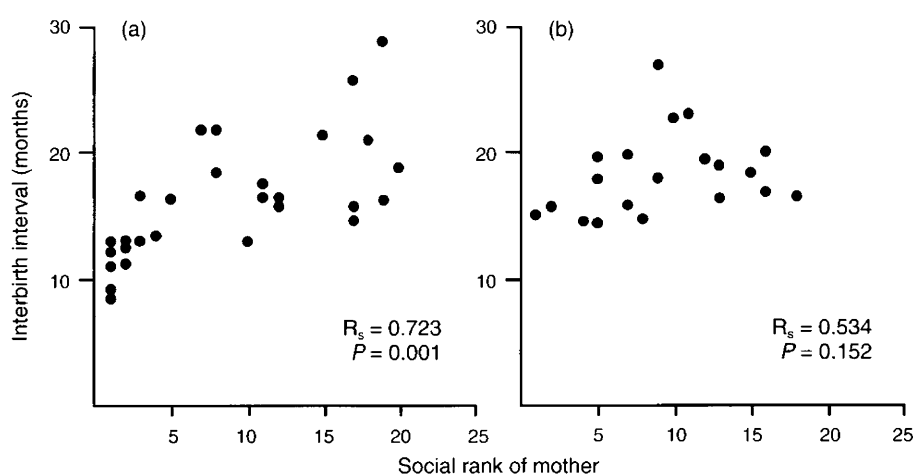
**Duration of the interbirth interval.** The overall correlation between maternal rank and duration of interbirth interval was significant ( $R_s = 0.599$ ;  $F = 12.633$ ; *d.f.* = 1,58;  $P = 0.001$ ), indicating that high-ranking females experienced shorter interbirth intervals than did lower-ranking females. This relationship was significant for interbirth intervals following singleton litters (Fig. 2a:  $R_s = 0.723$ ;  $F = 23.828$ ; *d.f.* = 1,30;  $P < 0.001$ ), but not for those following twin litters (Fig. 2b:  $R_s = 0.534$ ;  $F = 4.183$ ; *d.f.* = 1,17;  $P = 0.152$ ). No significant difference in duration of the interbirth interval was found following male versus female singletons ( $t = 1.16$ ; *d.f.* = 30;  $P = 0.254$ ), but interbirth intervals following twin litters were significantly longer than were those following singletons ( $t = -2.01$ ; *d.f.* = 58;  $P = 0.049$ ). Interbirth intervals did not differ significantly between primiparous females in the two different rank categories, but they were significantly shorter for multiparous females from the alpha matriline than for those from lower-ranking matrilines (Table 2). Maternal parity had no significant effects within matrilines on duration of interbirth intervals (alpha matriline:  $t = -1.11$ ,  $P = 0.318$ ; other matrilines:  $t = 0.633$ ,  $P = 0.527$ ).

These intervals were divided into their three component parts of gestation, lactation and maternal recovery to determine how interbirth intervals were shortened in high-ranking females. Few copulations were observed, so the gestational component of the interbirth interval was assumed to be constant at 110 days. However, substantial variation was observed in duration of both the lactation interval and the maternal recovery period.

**Table 2.** Effects of parity of mother on parameters of reproductive performance in *Crocuta*

Parameters	Alpha matriline	Other matrilines	t value
Littersize			
Primiparous	1.4 ± 0.3 (n = 5)	1.2 ± 0.1 (n = 22)	-0.775
Multiparous	1.5 ± 0.1 (n = 28)	1.5 ± 0.1 (n = 45)*	0.384
Weaning age (months)			
Primiparous	11.3 ± 1.9 (n = 3)	13.9 ± 0.5 (n = 6)	1.810
Multiparous	10.6 ± 0.8 (n = 15)	13.2 ± 0.5 (n = 25)	3.06**
Interbirth interval (months)			
Primiparous	14.6 ± 1.8 (n = 3)	18.0 ± 2.0 (n = 7)	1.267
Multiparous	12.5 ± 0.7 (n = 21)	16.7 ± 1.1 (n = 25)	3.231**

\* $P < 0.05$ ; \*\* $P < 0.005$ .

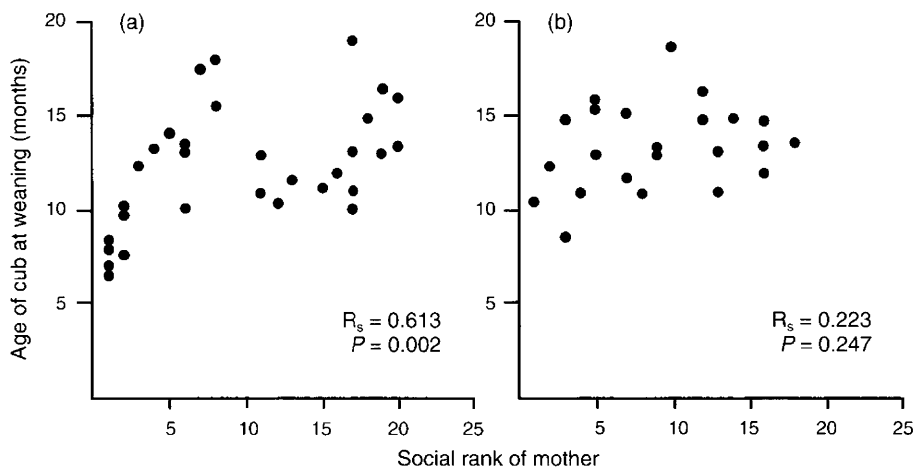


**Fig. 2.** Interbirth intervals following (a) singleton and (b) twin litters of *Crocuta* expressed as a function of the social ranks of the mother.

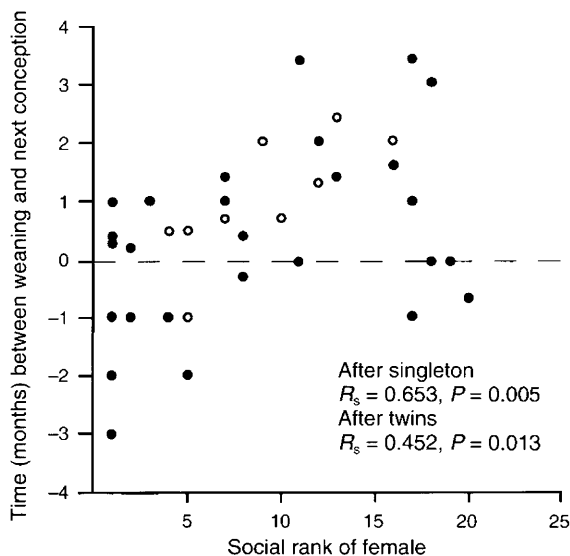
*Duration of the lactation period.* At least one member of 66 litters survived to weaning age during the study period. Cub ages at weaning were known to within 10 days for 53 of these litters. Overall, the ages at which litters were weaned increased significantly as social rank decreased ( $R_s = 0.894$ ;  $F = 12.49$ ;  $d.f. = 1,51$ ;  $P = 0.001$ ). However, this was due to the fact that high-ranking females weaned their singleton litters at significantly younger ages than did lower-ranking mothers (Fig. 3a:  $R_s = 0.613$ ;  $F = 11.22$ ;  $d.f. = 1,28$ ;  $P = 0.002$ ). Ages of cubs at weaning did not vary significantly with maternal rank for twin litters (Fig. 3b:  $R_s = 0.223$ ;  $F = 1.418$ ;  $d.f. = 1,21$ ;  $P = 0.247$ ). No significant difference was found between the weaning ages of male and female singletons ( $t = 0.694$ ;  $d.f. = 29$ ;  $P = 0.493$ ), nor between those of singleton and twin litters ( $t = -1.456$ ;  $d.f. = 50$ ;  $P = 0.150$ ). Cub ages at weaning did not differ significantly between primiparous females in the two rank categories, but sample sizes for primiparous females from the alpha matriline were small (Table 2). Cub ages at weaning were significantly lower for multiparous females from the alpha matriline than for those from lower-ranking matrilines (Table 2). Within matrilines, parity had no significant effect on weaning age of offspring (alpha matriline:  $t = -0.359$ ,  $P = 0.724$ ; other matrilines:  $t = 0.731$ ,  $P = 0.473$ ).

*Duration of the maternal recovery period.* Nine females conceived 17 litters before they weaned their previous litters. These nine females spanned the female rank spectrum, so inability to conceive before weaning did not reduce the reproductive success of low-ranking females. Nevertheless, high-ranking females were able to concurrently support pregnancy and lactation more frequently than were lower-ranking females. The duration of the recovery period of the mother was positively correlated with maternal rank (Fig. 4:  $F = 9.945$ ;  $d.f. = 1,39$ ;  $P = 0.003$ ). Thus, of the two component parts of the interbirth interval examined, durations of both lactation and recovery periods were correlated with the social rank of the mother for singleton litters, but only duration of recovery period varied with maternal rank following twins. When recovery periods following singleton litters were compared with those following twin litters among eight females who bore both types of litters during the study period, maternal recovery periods following twin litters were found to be significantly longer than were those following singletons ( $t = -2.610$ ;  $d.f. = 7$ ;  $P = 0.035$ ).

*Duration of the interval between loss of one litter and conception of the next.* Eighteen females who lost entire litters before



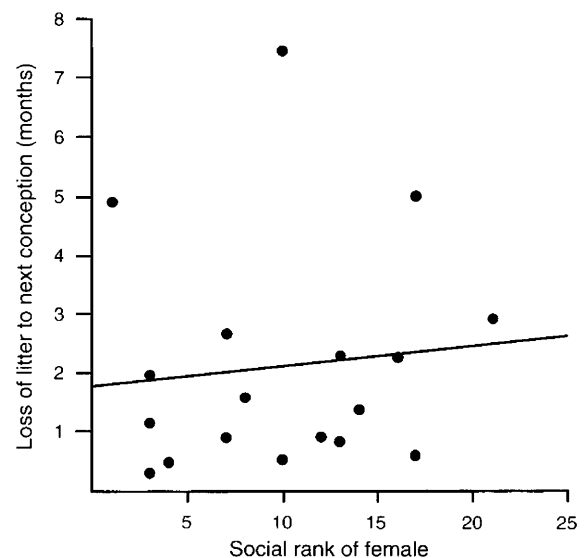
**Fig. 3.** Cub ages at weaning for members of (a) singleton and (b) twin litters of *Crocuta* expressed as a function of the social rank of the mother.



**Fig. 4.** Duration of maternal recovery period (between weaning of one litter and conceiving a subsequent litter) following weaning of singleton (●) and twin (○) litters of *Crocuta* expressed as a function of the social rank of the mother.

weaning had at least one year in which to conceive a subsequent litter during the study period. Females who lost entire litters generally conceived another litter within 2.5 months ( $\bar{x} = 2.11 \pm 0.45$  months). Duration of the interval between loss of one litter and conception of the next was not correlated with cub age at death ( $R_p = -0.163$ ; d.f. = 1,16;  $P = 0.518$ ). Furthermore, following loss of an entire litter, the duration of the interval before conception of the subsequent litter did not vary significantly with maternal rank (Fig. 5:  $R_s = 0.193$ ;  $F = 0.156$ ; d.f. = 18,  $P = 0.698$ ). Thus delayed pregnancy induction following litter loss did not appear to reduce reproductive success among low-ranking females.

**Annual rate of cub production.** Thirty-seven females bore young during the study period, and their annual rates of cub

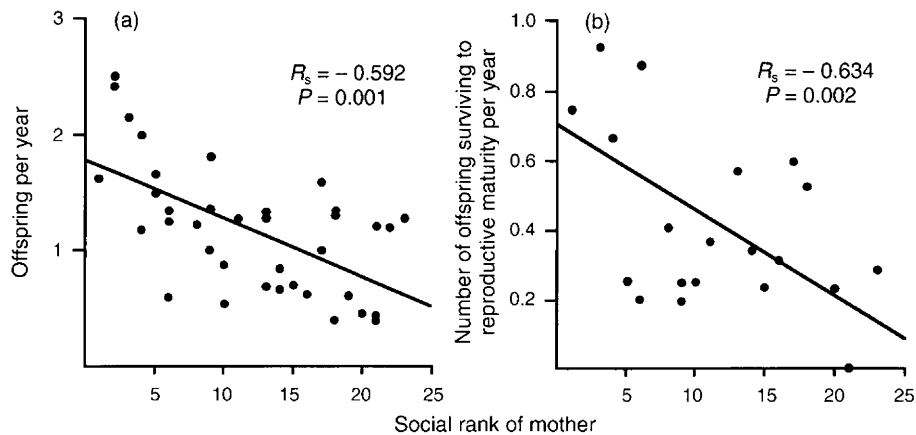


**Fig. 5.** Duration of the interval between early loss of one litter to conception of the subsequent litter of *Crocuta* expressed as a function of the social rank of the mother.

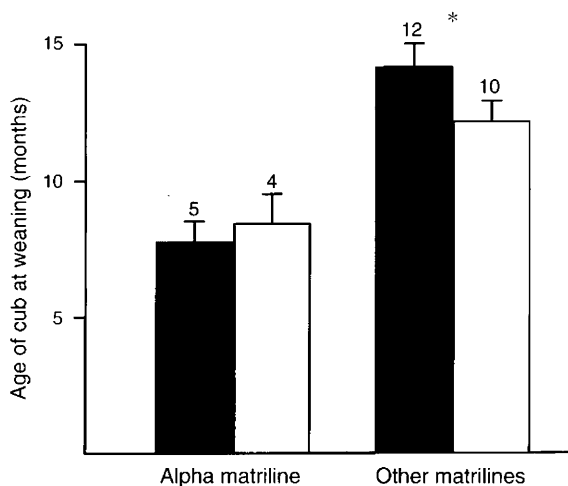
production decreased significantly with decreasing social rank (Fig. 6a:  $R_s = -0.592$ ;  $F = 18.93$ ; d.f. = 1,35;  $P < 0.001$ ).

**Survival of offspring to reproductive maturity.** Twenty-one females produced young that might have reached reproductive maturity during the study period. The annual rate of production of cubs surviving to reproductive maturity varied significantly with maternal rank (Fig. 6b:  $R_s = -0.634$ ;  $F = 12.742$ ; d.f. = 1,19;  $P = 0.002$ ). Thus, high-ranking females bore young at higher rates than did subordinate females, and their offspring tended to exhibit better survival than did offspring of low-ranking females.

**Female body size.** Among adult female *Crocuta* in this study population, body mass did not vary significantly with intra-sexual rank ( $n = 23$ ;  $F = 0.643$ ; d.f. = 1,21;  $P = 0.432$ ). Furthermore, neither body length ( $F = 0.040$ ; d.f. = 1,25;  $P = 0.843$ )



**Fig. 6.** (a) Total number of offspring produced per year the mother was observed as an adult, expressed as a function of the social rank of the mother for 37 female *Crocuta* who produced litters during the study period. (b) Number of offspring surviving to reproductive maturity produced per year the mother was observed as an adult, for 21 females whose offspring might have survived to reproductive maturity during the study period.



**Fig. 7.** Effects of abundance of prey (■: little game; □: much game) on duration of lactation following births of singleton litters by adult female *Crocuta* in the alpha ( $n = 4$  females) and lower-ranking ( $n = 9$  females) matriline. Sample sizes represent numbers of singleton litters born. \* $P < 0.05$ .

nor foreleg length ( $F = 0.001$ ; d.f. = 1,25;  $P = 0.971$ ) varied with female rank ( $n = 27$ ). Thus, high female rank was not associated with greater body size.

#### Interaction of food and rank on reproductive performance

Four females in the alpha matriline and nine lower-ranking females weaned singleton litters under conditions of both high and low game availability, as indicated by biweekly censuses of prey. Females in the alpha matriline always weaned their singleton cubs at younger ages than did lower-ranking mothers (Fig. 7). Ages at which alpha cubs were weaned under high and low game conditions did not differ significantly ( $t = 1.334$ , d.f. = 3;  $P = 0.274$ ), but cubs of lower-ranking mothers were weaned at significantly younger ages when game was abun-

dant than when it was scarce ( $t = -3.043$ ; d.f. = 8;  $P = 0.016$ ). This suggests that the reproductive performance of alpha matriline females may be largely unaffected by fluctuations in the food supply, but that food availability can profoundly alter reproductive performance of lower-ranking females.

## Discussion

Several different measures of female reproductive performance varied significantly with social rank in this *Crocuta* study population. Given that superiority in any single one of these measures would endow high-ranking females with a long-term reproductive advantage, the additive effects of superiority in several parameters concurrently should result in substantially higher reproductive success among high-ranking females. Indeed, assuming carrying capacity of a clan's home range remains stable for extended periods, Frank *et al.* (1995) calculated that enhanced reproductive success among members of the alpha matriline would allow that matriline to make up the entire adult female component of the clan after only 15 generations. Thus high dominance rank confers a profound selective advantage to female *Crocuta*, as it does in many gregarious mammals whose social relationships are organized hierarchically (reviewed by Clutton-Brock, 1988).

Frank *et al.* (1995) reported that high-ranking female hyaenas do not tend to live longer than lower-ranking animals, so the reproductive lifespan is not increased by greater longevity. However, the current data show that high-ranking females start bearing young earlier than do lower-ranking females, such that high-ranking females may accrue a 10% overall increase in the length of their reproductive lifespan. Similarly, daughters of high-ranking savannah baboons (*Papio cynocephalus*) attain reproductive maturity at younger ages than do daughters of low-ranking females, yielding roughly a 7% increase in duration of the reproductive lifespan (Altmann *et al.*, 1988).

Although maternal parity influenced litter size, maternal rank did not. Female *Crocuta* usually have only two teats, so production of litters larger than two should generally result in

the death of at least one cub by starvation. Interestingly, the one triplet litter observed during the current study was borne by a female with a remnant third teat, located on the ventral midline anterior to the usual pair. Although milk could be expressed from the posterior pair of mammae when this female was immobilized, no milk could be expressed from the midline nipple. One of her cubs died within 4 weeks, apparently because its siblings prevented it from obtaining enough milk to survive. The remaining cubs in this litter died within 3.5 months of birth.

The recovery periods observed for females whose litters survived to weaning varied with female rank, but the interval between early death of one litter and conception of a subsequent litter did not. The observations that all females recovered quickly after total early litter loss, but that rapid recovery after weaning a first litter occurred most frequently among high-ranking females, suggest that the energetic demands of lactation on the mother may be substantially higher near the end of the lactation period than at the beginning, as is also true in small mammals (for example, Bronson and Marsteller, 1985). These observations also suggest that substantial energetic benefits might accrue to lactating hyaenas that can shift their offspring to a diet of solid food when cubs are still relatively small. This interpretation supports the hypothesis that the entire suite of masculinized traits found in female *Crocuta*, including larger body size and higher levels of aggressiveness in females than in males (Frank *et al.*, 1989), has been favoured by natural selection because it permits females to facilitate cub access to carcasses even when feeding competition among clan members is extremely intense (Hamilton *et al.*, 1986).

One of the goals of the current research was to begin elucidating the proximal mechanisms by which social rank influences female reproductive success in the spotted hyaena. Two major socioecological variables have been shown to decrease fertility in subordinate female primates: low-ranking females may experience poorer access to food (for example, Dittus, 1979; Whitten, 1983), higher rates of 'social harassment' (Wasser and Barash, 1983; Abbott, 1987, 1988; Harcourt, 1987), or both. To date there has been no evaluation of the role that social harassment via intrasexual aggression might play in reproductive suppression in *Crocuta*. However, results of the current study suggest that food access mediates much of the effect of female social rank on fertility in this species. In contrast to other members of a spotted hyaena clan, the highest-ranking females are little affected by fluctuations in the food supply. Because high-ranking females can usurp food from all other clan members at all times (Tilson and Hamilton, 1984; Frank, 1986), and thereby provide adequate nutrition to their immature offspring, they can wean their cubs and conceive their subsequent litters more quickly than can lower-ranking females. This appears to be true regardless of whether prey animals are available in the home range at normal or super-normal levels of abundance. Thus, in effect, high social rank buffers females from fluctuations in the local food supply.

Food availability is one of the most important environmental factors known to affect the reproductive performance of female mammals. In female laboratory rodents and livestock, chronic food restriction suppresses GnRH release and, hence, LH secretion, steroidogenesis and ovulation (reviewed in Bronson, 1989). The specific physiological mechanisms by which inferior

access to food might influence the reproductive parameters shown here to vary with social rank are currently under investigation in this *Crocuta* study population.

Chronic food restriction retards reproductive development and suppresses oestrous cycling among adults in many mammalian species (Bronson, 1989). The relationship between regulation of energy balance and endocrine control of reproduction in female mammals has received a great deal of recent attention (for example, Morin, 1986; Bronson, 1989; Wade and Schneider, 1992). Temporal aspects of reproduction in various species of small mammals have been shown to be affected by body mass, body fat stores, and availability of oxidizable metabolic fuels such as fatty acids and glucose (French, 1982; Barnes, 1984; Bushberg and Holmes, 1985; Wade and Schneider, 1992). Whereas body mass of female *Crocuta* did not vary with social rank in the current study, rank-related variation in body fat stores or metabolic fuel availability have not yet been examined in this species. Perhaps one or both of these mechanisms mediate the rank-related variation observed in age at first parturition and interbirth intervals among female *Crocuta*.

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