



Research article

Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective

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Abstract. We assessed the importance of three behavioral processes on the fitness of individual females as mediated via maternal care in matrilineally organized social groups of spotted hyenas *Crocuta crocuta*. These were maternal choice of foraging tactic, the maintenance of individual dominance rank (social status) within the adult female hierarchy, and the behavioral support provided by mothers to their daughters when daughters acquired their position in the adult female hierarchy. The effects of all behavioral processes were closely linked. Maternal care was dependent on maternal social status because high ranking females had priority of access to food, and individual maternal choice of foraging tactic was frequency – and social status-dependent when medium prey abundance provided an opportunity for such a choice. At medium prey abundance, low ranking females went on costly long distance commuting trips to forage on migratory herds outside the group territory, whereas high ranking females fed on kills within the group territory. As a consequence, offspring of high ranking females grew faster, had a higher chance of survival to adulthood, and thus high ranking females had a higher lifetime reproductive success. Daughters of high ranking females usually acquired a social status immediately below that of their mother provided they enjoyed the effective support from their mothers as coalition partners, and they gave birth to their first litter at an earlier age than daughters of low ranking mothers. Spotted hyenas are therefore an example of the ‘silver-spoon effect’. This study shows that the frequency-dependent outcome of behavioral processes can be a key determinant of maternal reproductive success in social carnivores and have a profound influence on the reproductive career prospects of offspring.

Key words: costs of co-existence, *Crocuta crocuta*, density dependence, frequency dependence, group living, growth rate, life history, maternal care, Serengeti, social status, spotted hyena, survival

Introduction

The fitness benefits that drive the evolution of cooperative behavior and sociality have been subject to numerous investigations and reviews (e.g. Bourke, 1997; Dugatkin, 1997; Emlen, 1997; Solomon and French, 1997). Many studies

have been undertaken to demonstrate that living in groups is beneficial, elucidate the precise factor that facilitated sociality, classify cooperative behaviors in game-theoretical terms and analyze their evolutionary consequences, in particular their evolutionary stability (Maynard Smith, 1982; Dugatkin, 1997).

The fitness costs of group living, the costs of co-existence as we refer to them below, have received less attention. In many social vertebrates, specific classes of group members such as adult offspring experience fitness costs in the sense that they delay their breeding and are reproductively suppressed until suitable opportunities for reproduction arise elsewhere. These costs, and the circumstances that favor the evolution of such societies, are most suitably described by an economic model of family formation (Emlen, 1997). Briefly, in these systems ecological constraints limit dispersal opportunities and lead to the reproductive suppression of adult offspring, as in many canids (Moehlman and Hofer, 1997). In many social primates, some social carnivores such as spotted hyenas *Crocuta crocuta* (Kruuk, 1972) and some cetaceans, female philopatry and male dispersal lead to societies organized as matrilineal societies of female relatives that live in dominance hierarchies. In such societies, the suite of social behaviors (social tactics) that determine success and failure in the social environment may become the prime determinant of Darwinian fitness of group members, if social status and reproductive success are linked (e.g. Clutton-Brock, 1988). The costs of co-existence then reflect the fact that low ranking females have a lower fitness than high ranking females. While such effects have been documented in matrilineal societies (Dunbar, 1984; Altmann *et al.*, 1988; Cheney *et al.*, 1988; Clutton-Brock, 1991), very few studies provide empirical quantitative measures that link individual fitness to the intensity of maternal care and explain the mechanism by which social status influences care and fitness (Clutton-Brock, 1991; Hofer and East, 1996).

Here we use data from a long-term study of several hundred individually known spotted hyenas in the Serengeti, Tanzania, to look at the fitness consequences of three behavioral processes among reproductively active adult females mediated via maternal care. These are maternal choice of foraging tactic, the maintenance of individual dominance rank (social status) within the adult female hierarchy, and the behavioral support provided by mothers to their daughters when daughters acquired their position in the adult female hierarchy.

We have previously shown that Serengeti hyenas operate two foraging tactics which determine the level of maternal care, cub growth and the survival of offspring to the age of adulthood at 2 years (Hofer and East, 1993a). We will now extend this analysis by considering the impact of social status (the position within the female dominance hierarchy) on maternal access to food resources and choice of foraging tactic, and its consequences for the growth and survival of progeny. We also examine the role of mothers as coalition partners and

supporters of adult daughters when they establish themselves within the adult female hierarchy and the effect of maternal social status on the age at first parturition of adult daughters, a key life history trait in the evolution of mammalian life histories (Charnov, 1991).

Predicting the fitness consequences of behavioral processes

Serengeti spotted hyenas live in stable, highly structured female-dominated social groups called clans, with separate male and female dominance hierarchies. Clans defend permanent territories in which dominant females have priority of access to large food resources such as carcasses (Frank, 1986; Hofer and East, 1993b). The abundance of food resources within group territories fluctuates throughout the year, due to the movement of migratory herbivores, and thus territories usually do not contain sufficient food resources for all group members (Hofer and East, 1993b). When the abundance of food resources is low, i.e. only low densities of resident prey species are present, all group members, individually or in small groups, undertake costly, long-distance (up to 70 km) short-term foraging trips in a non-synchronized pattern to areas containing large herds of migratory prey such as wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* (Hofer and East, 1993c). Lactating females regularly return to the clan territory to nurse their cubs at the communal den (Hofer and East, 1993a). We have termed this foraging tactic the commuting system. At high prey abundance (large migratory herds inside a clan territory) all clan members forage inside the clan territory (Hofer and East, 1993a, b). For approximately one third of the year, resident prey species are complemented by small, scattered migratory herds, particularly Thomson's gazelles *Gazella thomsoni* and Grant's gazelles *Gazella granti* (medium prey abundance). This is sufficient prey for some but not all clan members (Hofer and East, 1993b, c). In this situation females have a (frequency dependent) choice between the costly commuting tactic and the inexpensive option of foraging at home. We predict that the choice depends on social status: because dominance status determines priority of access to food (Frank, 1986), high ranking females are likely to monopolize kills inside the clan territory whereas low ranking females are likely to commute to the large herds elsewhere. If we apply the logic of optimal parental care (Evans, 1990; Clutton-Brock, 1991; Hofer and East, 1993a) then for females with high foraging costs (low ranking females) the optimal level of maternal input should be shifted downward relative to females with the inexpensive foraging costs (high ranking females). We therefore predict that low ranking females should have cubs that grow more slowly, survive less well and have daughters that give birth to their first litter later than high ranking females.

The Serengeti hyenas

The study was conducted in the Serengeti National Park and the adjacent Ngorongoro Conservation Area in northwestern Tanzania. The major biomass of Serengeti herbivores is dominated by migratory species, chiefly wildebeest, Thomson's gazelles and zebras. These three migratory species are the principal prey of Serengeti spotted hyenas (Kruuk, 1972; Hofer and East, 1993b). For details on the herbivore migration and the Serengeti ecosystem see Kruuk (1972) and Sinclair and Norton-Griffiths (1979). In this paper we analyse information from three spotted hyena social groups called clans that defended permanent territories of approximately 56 km² (Hofer and East, 1993b) in the centre of the Serengeti National Park, an area that lies midway between the dry and wet season ranges of the large migratory herds.

Serengeti clans were stable multi-female, multi-male fission–fusion groups that consisted of approximately 45 members, and contained similar numbers of natal adult females and immigrant adult males (Hofer and East, 1993b; East and Hofer, 2001). All adult females reproduced. Singleton, twin and rarely triplet litters were born throughout the year; maternal input was high with the production of highly nutritious milk during a long lactation period of 12–18 months (Hofer and East, 1995). Males did not contribute to parental care. Cubs were reared at the communal den for at least the first 6 months of their life, and during this period were entirely dependent on maternal milk. Females nursed their cubs at least once a day when migratory herds were present, but were often absent from their cubs for several days when on long distance foraging trips (Hofer and East, 1997; Golla *et al.*, 1999; Wachter *et al.*, 2002). Individuals were considered adults at 24 months of age.

Materials and methods

The methods used in this study have been previously described in detail. Below we summarize the salient details and refer to the original papers in which the methods were first described and applied.

Demography and female reproductive careers

This study presents data from three spotted hyena clans closely monitored for ca. 13 years (May 1987–December 2000), 11 [years!] (November 1989–December 2000) and 10 [years!] (August 1990–December 2000), respectively. The three study clans contained on average 20, 26, and 33 adult females per clan. Clan members were individually known from their spot patterns, natural ear-notches and scars (Hofer and East, 1993b). Females were philopatric, were

aged on the basis of their known birth dates and were assigned a death date when last recorded in the clan's territory. Age at first parturition was recorded as (1) the age when females first gave birth to a surviving litter based on the age of the cubs when first sighted, or (2) the age at which females first gave birth to a litter that was stillborn or died shortly after birth. Because female hyenas lack a vulva and the exit of the vagina passes through the peniform clitoris (Matthews, 1939), females give birth through their clitoris which causes a specific wound to develop where the clitoris ruptures, which clearly indicates that parturition has occurred.

Social status

Social status of adult females was determined from submissive acts (retreat, displacement, cower, tail between legs, ears back, head bobbing, head upside down) in dyadic interactions recorded ad libitum and during focal observations. These dyadic interactions were used to construct an adult female linear dominance hierarchy. For the comparison of rank positions across clans, individuals within dominance hierarchies were assigned a standardized rank. This measure distributed ranks evenly between the highest rank (standardized rank +1) and the lowest rank (standardized rank -1), with the median rank being scored as 0. We refer to the standardized rank below as social status (Goymann *et al.*, 2001).

Unless specified otherwise, maternal social status was evaluated for the date of birth of offspring. The social status of adult daughters was evaluated for the date of birth of their first litter. Because mothers formed coalitions with their daughters during conflicts with other females (Engh *et al.*, 2000) and mother-daughter coalitions extended into the adult life of the daughter, we evaluated the association between maternal social status and the social status of the daughter by calculating an average rank for the mother between the date of birth of her daughter and the date on which the daughter gave birth to her first litter, or until the date of maternal death if the mother died prematurely. We also calculated the proportion of a daughter's life that her mother was present and alive to support her daughter.

Cub development, growth and survival

Cub age was determined to an accuracy of 1 week on the basis of pelage, size, locomotory abilities and behavioral development when first sighted, and in two cases because the birth of the cub was observed (Pournelle, 1965; Golding, 1969; Kruuk, 1972; East *et al.*, 1989). We measured the body mass of cubs when they stood on an electronic scale (Soehnle 7750 and 7751) covered by a wooden platform which was positioned near the research vehicle in the vicinity

of the communal den (Hofer and East, 1993c). We calculated long-term growth rates for the first 6 and 24 months of a cub's life. Mean linear growth rates were calculated using the mean of the three weights measured closest to the age of 6 or 24 months minus the average birth mass (1.5 kg, Pournelle, 1965), and divided by the mean age (in days) at which the three weights were taken.

Survival was determined only for those cubs whose fate was known in that they either died or survived and whose life could have been monitored for at least 2 years ($n = 674$ cubs). To assess survival of cubs as a function of maternal social status, the number of cubs born and survived were summarized for each decile of maternal social status from all three clans, plus the values for alpha and omega females (who have a status value of +1 and -1, respectively), providing a total of 22 status categories. Each decile had a sample size of on average 30.6 ± 1.6 cubs (range 17–44).

Maternal attendance

Maternal attendance at the communal den was recorded between 1987 and 1991 during more than 3000 h of observations. Observations were made at dawn and dusk and during all-night watches. During each observation period all individuals present within a radius of 100 m of the den were recorded. Only cubs can enter the narrow tunnels of spotted hyena communal dens (Kruuk, 1972), thus activities involving mothers and their cubs occur above ground and can be monitored (Golla *et al.*, 1999). As mothers that returned to the communal den fed their cubs during long nursing bouts (Golla *et al.*, 1999), we could assess maternal care by calculating a 'relative provisioning rate' as the number of observation periods a mother was present at the communal den divided by the total number of observation periods she could have been present (Hofer and East, 1993a). We also calculated the corresponding absence intervals from the communal den using the methods described in Hofer and East (1993a).

Prey abundance

Prey abundance was scored as described in Hofer and East (1993a) where further details can be found. Based on repeated transect counts, we distinguished three categories of prey abundance: (1) low abundance: only resident herbivore prey species present, all migratory prey species either absent or present only in very low numbers; (2) medium abundance: in addition to the resident prey species, gazelle herds present; (3) high abundance: in addition to resident prey species, major migratory herds of wildebeest and zebra (typically numbering in the thousands) present. Changes between these levels of abun-

dance occurred repeatedly throughout the year; the approximate dates of these changes were used to delineate periods of equal prey abundance.

Lifetime reproductive success

Lifetime reproductive success was defined as the rate per year at which females raised cubs to the age of 2 years. This rate was calculated by dividing the total number of cubs they raised by the period spanned by their reproductive careers. As the youngest age at which a female conceived a litter was 2 years and 3 months, we set the potential start of reproduction at 2 years of age and included in the analysis only the 36 females that were monitored for at least 4 years after adulthood (i.e. those that survived until 6 years of age or older), since the oldest primiparous female was 5.9 years of age when she gave birth to her first litter.

Statistics

Statistical and graphical analyses were performed using SYSTAT 10.0 (Wilkinson, 2000), following the procedures recommended by Conover (1980) and Sokal and Rohlf (1981). Statistics are given as means \pm standard deviations, and probabilities are for two-tailed tests. Wherever appropriate, we summarized values to means per individual to avoid pseudo-replication. We assessed the impact of maternal social status on early cub growth in a general linear model after we corrected for the influence of litter size (one or two), maternal experience (i.e. inexperienced if it was a cub belonging to the first two litters, experienced if in a later litter), the sex of the cub, and its membership in a particular cohort and clan (and thus the spatial and temporal variation in prey accessibility). In all general linear models we confirmed the normal distribution of residuals with the Lilliefors test.

Results

Lifetime reproductive success

Mean lifetime reproductive success was 0.29 ± 0.17 cubs raised to adulthood per year (range 0–0.64 cubs/year). The mean duration of lifetime reproductive period was 7.48 ± 2.52 years (range 4.15–14.54 years), and the mean total number of cubs raised was 2.36 ± 1.90 (range 0–7 cubs). Lifetime reproductive success increased with social status ($F_{1,31} = 8.84$, $p = 0.006$) and the total duration of the reproductive period ($F_{1,31} = 5.66$, $p = 0.024$), which was a likely measure of maternal experience, but was similar across clans ($F_{2,31} = 0.68$,

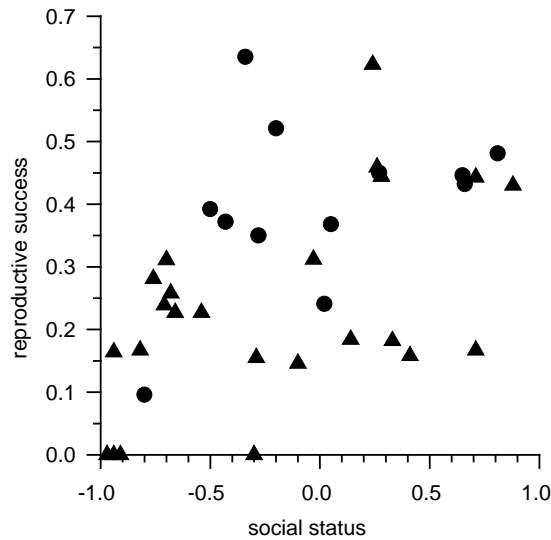


Figure 1. Lifetime reproductive success increases with mean lifetime social status and the total duration of the female's reproductive period. Lifetime reproductive success is here expressed as the annual rate of cubs raised to adulthood at 2 years of age. Triangles: females monitored for 4–8 years after adulthood; circles: females monitored for more than 8 years after adulthood.

$p = 0.51$, $r^2 = 0.43$, $n = 36$ females, Fig. 1). The distribution of the total number of cubs raised did not follow a random (Poisson) distribution (Kolmogorov–Smirnov test, $d_{\max} = 0.31$, $p = 0.002$).

Maternal provisioning rates

Low ranking females and high ranking females differed in their provisioning rates only during periods of medium prey abundance (Table 1). Here, provisioning rates of low ranking females were equivalent to provisioning rates of both low and high ranking females during low prey abundance. In contrast,

Table 1. Mean relative provisioning rates (and the corresponding absence intervals from the communal den) as a function of maternal social status at three levels of prey abundance

| Prey abundance | Relative provisioning rate | | | | Mean absence interval (days) | | | | Statistical comparison | | |
|----------------|----------------------------|------------|-------------|------|------------------------------|----------|-------------|------------|------------------------|----------|----------|
| | Low status | | High status | | Low status | | High status | | | | |
| | Mean | \pm SD | <i>n</i> | Mean | \pm SD | <i>n</i> | Mean | \pm SD | <i>n</i> | <i>U</i> | <i>p</i> |
| Low | 0.37 | \pm 0.13 | 8 | 0.40 | \pm 0.09 | 8 | 1.19 | \pm 0.48 | 8 | 29.5 | 0.79 |
| Medium | 0.38 | \pm 0.12 | 9 | 0.53 | \pm 0.18 | 10 | 1.25 | \pm 0.42 | 9 | 20 | 0.04 |
| High | 0.56 | \pm 0.08 | 6 | 0.67 | \pm 0.21 | 9 | 0.86 | \pm 0.14 | 6 | 15 | 0.16 |

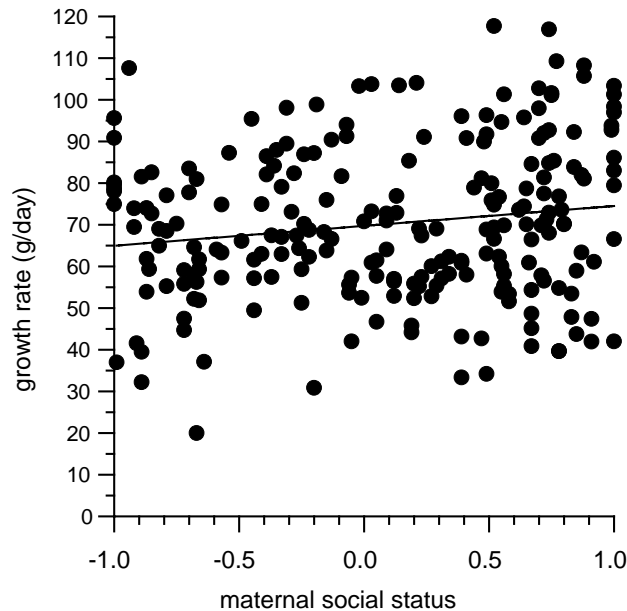


Figure 2. Early cub growth (first 6 months) as a function of maternal social status.

high ranking females accomplished provisioning rates at medium prey abundance that corresponded to provisioning rates of low ranking females at high prey abundance (Table 1).

Social status and the success of maternal care

Early cub growth (first 6 months) increased as maternal social status increased ($F_{1,181} = 14.2$, $p = 0.0002$, $n = 200$ cubs, Fig. 2). Survival of cubs to the age of adulthood at 2 years was 35.6% ($n = 674$ cubs). Survival improved with early cub growth (during the first 6 months of cub life, logistic regression, log likelihood ratio test $G = 11.16$, $df = 1$, $p = 0.0008$, $n = 174$ cubs, Fig. 3). As cub growth was a function of maternal input and thus dependent on maternal status, we would expect cub survival also to improve with maternal social status. This was the case (linear regression, % survived = $34.63 + 12.96 \times$ maternal social status, $F_{1,20} = 10.81$, $p = 0.0037$, $n = 674$ cubs, Fig. 4).

Age at first parturition

Females gave birth to their first litter at the age of 3.87 ± 0.60 years, range 2.60–5.86 years ($n = 76$ females). The faster daughters grew during their first 2 years of life, the younger they were when they gave birth to their first litter

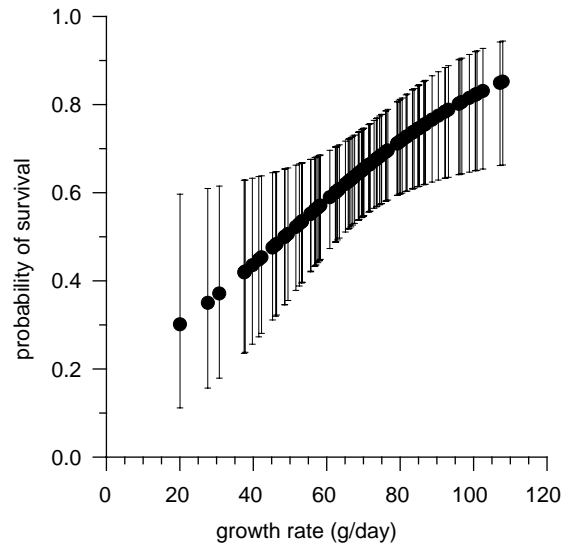


Figure 3. Survival of cubs to the age of adulthood at 2 years as a function of early cub growth (first 6 months).

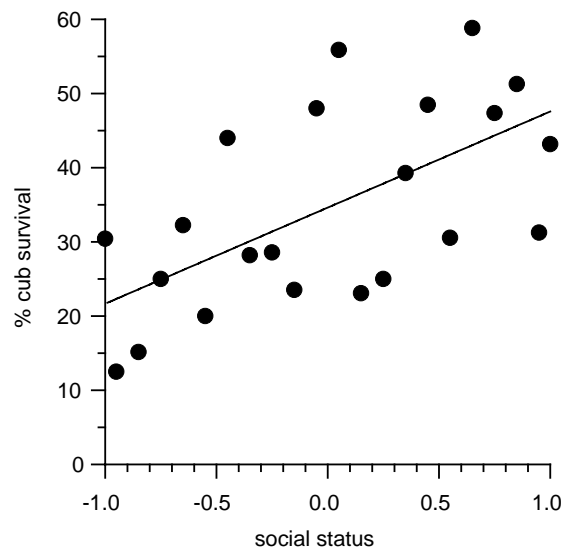


Figure 4. Survival of cubs to the age of adulthood at 2 years as a function of maternal social status. Note that each data point is an aggregate of on average 30.6 ± 1.6 cubs for each decile of maternal social status (total $n = 674$ cubs).

(linear regression, age [years] = $6.3 - 0.042 * \text{growth rate [g/day]}$, $F_{1,28} = 13.94$, $p = 0.00085$, $n = 30$ daughters, Fig. 5). An increase in the growth rate by 1 g/day was equivalent to a reduction in the age at first parturition by 15 days. As

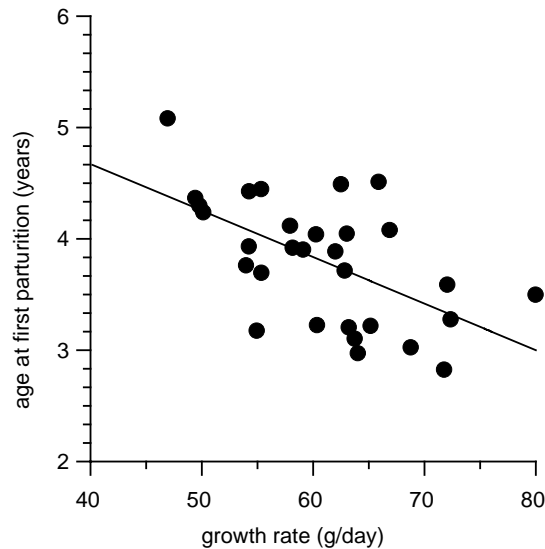


Figure 5. Age at first parturition as a function of growth rate during the first 2 years.

cub growth was primarily a function of maternal foraging intake and thus status-dependent (see above), age at first parturition of daughters was also reduced as maternal social status increased (general linear model, $F_{1,71} = 4.07$, $p = 0.047$, Fig. 6) and the proportion of daughter life when her mother was alive increased (see below, $F_{1,71} = 6.37$, $p = 0.014$) but did not vary across clans (effect of clan $F_{2,71} = 0.034$, $p = 0.97$; overall regression equation: age [years] = $4.51 - 0.22 \times \text{maternal social status} - 0.69 \times \text{proportion of time mum was alive to support her daughter}$; $n = 76$ daughters). There was no correlation between age at first parturition and longevity (Spearman's $\rho = 0.15$, $n = 41$ females, NS).

Daughter social status

Daughter social status increased with average maternal social status (Spearman's $\rho = 0.880$, $n = 76$ daughters, $p < 0.0001$). Figure 7 demonstrates the phenomenon of 'rank inheritance' as daughters typically assumed a rank just below their mother, at a mean of -0.19 ± 0.36 social status units below her. Some spectacular deviations of daughter ranks from maternal rank occurred in both positive and negative directions. Some daughters achieved a social status higher than that of their mother by joining a coalition of high ranking females of another matriline and thus enjoying the support of the members of that matriline in conflicts with other females (Fig. 7). Others achieved a rank well

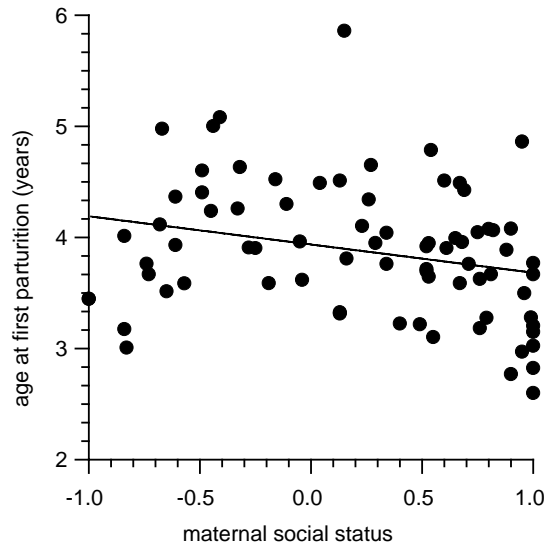


Figure 6. Age at first parturition of daughters as a function of maternal social status.

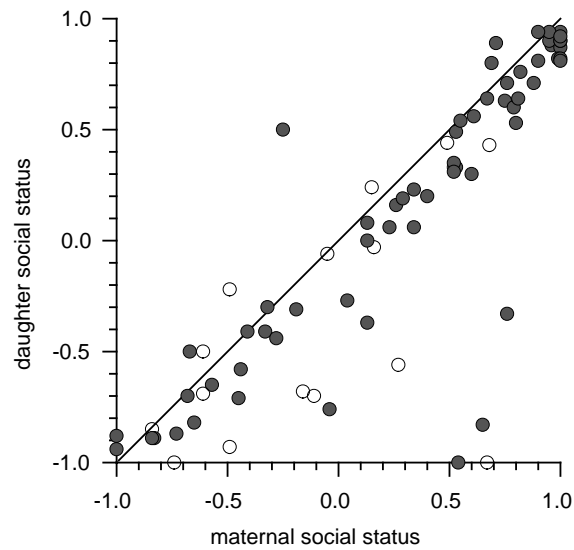


Figure 7. Daughter social status at the age of first parturition as a function of the average maternal social status during the life of her daughter until this moment or until the mother died. The identity line shows equality of maternal and daughter social status. Filled circles: daughters with mothers that were alive and present for at least 75% of their daughter's life; open circles: daughters with mothers alive and present for less than 75% of their daughter's life.

below maternal status because the mother died prematurely, causing a significant delay in the age at first parturition (for statistics see results above).

Discussion

Our study shows that social status has a substantial effect on cub growth, cub survival to adulthood and hence lifetime reproductive success, and also influences the reproductive careers of adult daughters. The mechanism through which maternal status operates is status-dependent differential access to food resources, and transgenerational behavioral support of daughters when they acquire their dominance rank in the adult female hierarchy. As a consequence, there is a strong positive phenotypical correlation between the quality (and the likely reproductive value) of mothers and daughters (Trivers and Willard, 1973; Leimar, 1996). This status-dependent correlation determines the likely *relative* fitness of daughters and affects key life history parameters of daughters. Thus, the selective forces which shape behavioral tactics that promote social success have profound life history consequences across generations.

Maternal foraging tactics

Females have a choice of two foraging tactics. During commuting trips mothers cover an average distance of 40 km (one way) to the nearest large herds of migratory prey, a distance that is an order of magnitude larger than those of approximately 4 km during foraging trips inside the clan territory (Hofer and East, 1993b, c). Our observed status-dependent differences in relative provisioning rates at medium prey abundance reflect different choices in foraging tactics by low and high ranking females: low ranking females commuted whereas high ranking females foraged at home. We call these choices frequency-dependent because in the fission–fusion society of hyenas, each female makes her own decision on foraging tactics and because there is no evidence that high ranking females force low ranking females to commute. We have previously shown that foraging on migratory herds inside the clan territory is less costly and more productive in terms of cub growth rate than commuting to distant migratory herds elsewhere (Hofer and East, 1993a). It therefore seems likely that, even if both classes of females make the optimal choice under status-specific expectations, low ranking females do no better than making the best of a bad job.

Maternal care and life history

Hofer and East (1993a) showed that relative maternal provisioning rate was the key aspect of maternal care that determined cub growth rate and as a consequence cub survival. Furthermore, Hofer and East (1997), Golla *et al.* (1999) and Wachter *et al.* (2002) showed that higher provisioning rates decreased levels of aggression between litter mates within twin litters and reduced the

chance of facultative siblicide, the most important known cause of cub mortality in Serengeti hyenas (Hofer and East, 1995). We therefore conclude that the increased provisioning of cubs with milk by high ranking mothers improved cub growth, survival to adulthood and advanced the age at first parturition compared to low ranking mothers.

The transgenerational effects of maternal care in Serengeti hyenas are demonstrated by the positive contribution of cub growth and maternal social status to the advancement of age at first parturition in adult daughters. Our study also shows that the period of maternal support during adulthood is important, because the age at first parturition decreased as maternal presence throughout her daughter's life increased. Similar long-term and sometimes even life-long maternal support to adult daughters in various guises has been observed in matrilineally organized primates (Combes and Altmann, 2001).

Costs of co-existence in matrilineal societies

Where social status is a key determinant of female lifetime reproductive success (e.g. Altmann *et al.*, 1988; Clutton-Brock, 1988; Pusey *et al.*, 1997), the traits that assist individuals in acquiring and maintain social status become important. In matrilineal societies such as hyenas and cercopithecine primates, female hierarchies are 'nepotistic' in that status depends on family membership, social skills, or networks rather than physical characteristics or age (Hrdy and Hrdy, 1976; Engh *et al.*, 2000; Combes and Altmann, 2001). Unlike many matrilineal primate species, where the mechanism by which social status influences reproductive success remains unclear, our studies have identified individual maternal foraging tactics as such a mechanism (Hofer and East, 1993a, this study). In hyenas, the link between dominance status and priority of access to food resources has perhaps particularly clear consequences for the fitness consequences of maternal care, because spotted hyenas are the species in the order Carnivora with the highest per litter investment in parental care (Hofer and East, 1993a, 1995).

If the cost of co-existing with socially superior clan members is substantial, why do low ranking hyena females remain in their natal clan? Dispersal would only be beneficial if low ranking females would improve their social status and thus their expected reproductive success. This is unlikely if they join another clan, as the behavioral processes that permit high ranking matrilineal females in their natal clan to maintain a privileged position are likely to operate everywhere. In stable populations habitats are likely to be saturated with clan territories, as is usually the case in social breeders (Stacey and Koenig, 1990; Emlen, 1997). Thus, low ranking females willing to disperse would have to wait until another clan became extinct, creating a gap in the network of territories. When such

gaps occurred, low ranking hyena females have indeed dispersed and established new clans (Mills, 1990; Holekamp *et al.*, 1993; Hoener, 2001).

Hyena life history

Age at first parturition is an important parameter in the life history of species such as spotted hyenas that combine a long reproductive period and long interbirth intervals with small litters (Clutton-Brock, 1988). The observed variation in the age at first parturition in this study has substantial fitness consequences: the youngest female (who first gave birth at 2.6 years) could have raised 0.95 cubs more to adulthood than the oldest female that gave birth at 5.86 years, a difference of 40% given the average total lifetime output of 2.36 cubs in this study, since females who gave birth at an early age did not suffer decreased longevity.

The range of values in this study were very similar to those measured in a small sample in a Kenyan clan in the Masai Mara by Holekamp *et al.* (1996). The effect of social status appears to be more severe in the Mara clan than in the Serengeti clans. Low ranking Serengeti females may partly compensate their lower social status by spending extended periods foraging on large migratory herds outside their clan territory, whereas in the more strictly territorial Mara clan such commuting trips have not been recorded and low ranking females might experience stricter resource limitations.

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