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Within-litter sibling aggression in spotted hyaenas: effect of maternal nursing, sex and age

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Models that address facultative siblicide in avian species predict that the costs and benefits of sibling aggression will change in relation to the level of food provisioning by parents. In spotted hyaenas, *Crocuta crocuta*, one of the few mammalian species in which facultative siblicide occurs, aggression rates between siblings were highest when cubs competed for access to maternal milk. In the Serengeti National Park, Tanzania, nursing of cubs by spotted hyaena mothers was influenced by the migratory movements of herbivores and the social status of the mother. Consistent with predictions from avian models, rates of sibling aggression among spotted hyaena littermates were inversely related to levels of maternal input in terms of lactation. Long-distance foraging trips by mothers (commuting trips) resulted in low cub growth. Rates of aggression were higher in years when cub growth rates were low than in years when cub growth rates were medium or high. Rates of aggression between littermates belonging to high-ranking mothers, who nursed their cubs more frequently than low-ranking mothers, were lower than those between siblings of low-ranking mothers. Aggression rates in all-female and all-male litters were higher than in mixed-sex litters. Identical payoff expectations of same-sex litters may provide an explanation for this result. In accordance with predictions from life history theory, aggression rates declined with age and increasing reproductive value of siblings.

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In this study we consider competition among littermates in free-ranging spotted hyaenas, *Crocuta crocuta*. Sibling rivalry appears to contradict the biological premise of maximizing inclusive fitness (Hamilton 1964), particularly when it has fatal consequences. Aggressive brood reduction has been defined as the use of fighting amongst siblings to establish a dominance hierarchy with the lowest-ranked member being most likely to die (Mock & Parker 1997). Mortality may result from physical damage and/or socially enforced starvation (Mock 1984); in fact any act of an individual that substantially reduces the survival of one of its siblings is included in this concept of siblicide. Siblicide (both facultative and obligate) has been defined and documented in a variety of avian species (O'Connor 1978; Mock 1984; Drummond & García Chavelas 1989; Mock 1987; Mock & Parker 1997). In mammals, strong sibling rivalry with potentially fatal consequences has rarely been described, mainly in domestic piglets, *Sus scrofa* (Fraser 1990) and in captive

(Frank et al. 1991) and free-ranging spotted hyaenas (Golla 1993; Smale et al. 1995). The period when chicks are confined to the nest and dependent on their parents for food can be compared to the denning period in spotted hyaenas when cubs are stationed at the communal den and are dependent on maternal milk. For example, in two avian species with facultative siblicide (blue-footed booby, *Sula nebouxii*, and great egret, *Casmerodius albus*), the mean age of siblicide occurred after 26 and 43–50% of the nestling phase (Mock & Parker 1986; Drummond & García Chavelas 1989). In the Serengeti National Park, Tanzania, spotted hyaena litter size is one or two, rarely three (Kruuk 1972; Hofer & East 1997), and mothers typically suckle only their own offspring (Hofer & East 1993c). Cubs are dependent on highly nutritious maternal milk during the first 12 months of life when they are stationed at the communal den, and may not be weaned until 14–18 months of age (Hofer & East 1993a,c, 1995). Large (6–10-kg) asymmetries in body mass between dominant and subordinate littermates have been documented in the Serengeti hyaenas when dominant siblings monopolized maternal milk supplies, leading to the enforced starvation of subordinate cubs in 22 of 114 litters, at a mean age of 24% of the denning period (Hofer & East 1997). We therefore

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consider the definition of strong sibling rivalry used for avian nestlings applicable to spotted hyaena sibling aggression during the denning period (see also Mock & Parker 1997 for applications to other taxa).

Numerous models have tried to explain the evolution of fatal competition among siblings by focusing on parental food-provisioning rates in avian species (O'Connor 1978; Parker et al. 1989; Forbes & Ydenberg 1992; McNamara et al. 1994). The majority of models of facultative siblicide consider the manipulation by a dominant sibling of the amount of food that a subordinate sibling receives from the parents (Parker et al. 1989; Forbes & Ydenberg 1992; McNamara et al. 1994). These models predict that the costs and benefits of such manipulation to the dominant sibling will change in relation to the level at which parents supply food to their brood. When provisioning is high, domination of food supplies may yield only a small gain in fitness for a dominant sibling that is outweighed by the potential cost of causing the death of a subordinate sibling. In contrast, when provisioning is low a dominant sibling should enhance its chance of survival by dominating the food supply. An increase in survival may outweigh the cost resulting from the starvation of a weaker sibling. These models have been developed for and tested in avian species, but predictions from these models have not been tested on a facultative siblicidal mammalian species.

The population of spotted hyaenas in the Serengeti National Park, Tanzania, is suitable to investigate whether maternal nursing influences how much the dominant sibling manipulates the amount of milk received by the subordinate sibling. Although Serengeti spotted hyaenas exist in large, stable territorial groups called clans, individuals regularly leave their clan territory on short-term trips to feed on distant concentrations of migratory prey (Hofer & East 1993a,b). This commuting system profoundly influences how often lactating mothers nurse their cubs (Hofer & East 1993c). When migratory herds are inside the clan territory, mothers typically nurse their cubs on a daily basis, but when mothers commute they leave their cubs at a communal den inside the clan territory for periods of 2–9 days, during which cubs usually receive no nourishment (Hofer & East 1993c). Because mothers of high social status have priority of access to food within the clan territory, they commute less frequently than subordinates (H. Hofer & M. L. East, unpublished data) and thus return more frequently to the den to nurse their cubs (East & Hofer 1991a). When mothers have to commute long distances to migratory herds for much of the year, cub growth rates are poor, whereas in years when migratory herds remain closer to the home territory, cub growth rates are high (Hofer & East 1993c). Spotted hyaena cubs use aggressive behaviour to attempt to manipulate their sibling's access to maternal milk supplies (Golla 1993; Hofer & East 1997). If spotted hyaenas conform to the predictions of avian facultative siblicide models, then rates of aggression between littermates should change in relation to maternal nursing rates. Rates of aggression would be predicted to be (1) higher in cohorts where cub growth rates (a reliable index of maternal milk input; Hofer & East 1993c)

are low than in cohorts were growth rates are high, and (2) higher in litters of low-ranked mothers than in those of high-ranked mothers.

Unequal parental investment in offspring of different sex may result in a sex-specific bias in sibling competition (Mock & Parker 1997) as the sex that receives greater parental investment should compete more for the resources provided by parents (Parker 1974; Popp & DeVore 1979). Such sex bias in sibling competition has been reported in a number of species (Williams 1966; Clark et al. 1991; Clutton-Brock 1991; Cronk 1993). Sex-specific bias in sibling competition in some avian species has been considered to be a consequence of sexual size dimorphism enhanced by hatching asynchrony (Werschkul & Jackson 1979; Edwards & Collopy 1983; Bortolotti 1986a,b; Drummond et al. 1991). In spotted hyaenas, singleton female cubs grow at a significantly higher rate than singleton males (H. Hofer & M. L. East, unpublished data), suggesting that female cubs may acquire more maternal resources than males. Frank et al. (1995) found that interbirth intervals among high-ranked mothers in the Maasai Mara, Kenya, were longer after the rearing of a singleton daughter than of a singleton son, suggesting greater maternal investment in daughters than in sons. However, Holekamp et al. (1996) did not find a sex difference in weaning age of singleton daughters and sons in the same population. In this study we considered whether daughters in mixed-sex twin litters compete more vigorously than sons for maternal resources.

Female spotted hyaenas remain in their natal social groups and typically acquire a social rank immediately below that of their mother, whereas natal males normally disperse (Frank 1986; East & Hofer 1991b; Smale et al. 1995). As twin sisters are in direct competition for social rank, we predict that conflict within all-female litters will be higher than that within mixed-sex and all-male litters.

Escalated conflict should be expected when siblings with equal expected payoffs and similar fighting skills compete for a common resource (Maynard Smith 1982). This suggests that in spotted hyaenas, brothers in all-male litters and sisters in all-female litters are likely to have escalated conflicts, if both littermates have similar fighting skills. We thus expect higher rates of aggression in same-sex litters than in mixed-sex litters.

Alternatively, if there is a sex difference in the likelihood of giving up in a conflict and accepting subordinate status, then we predict that: (1) aggression within same-sex litters composed of the sex that is more likely to accept subordination should be lower than in same-sex litters of the opposite sex; (2) aggression in mixed-sex litters should be less than in litters composed of the sex least likely to accept subordination; and (3) subordinate siblings in mixed-sex litters should be the sex most likely to give up in conflicts.

Mock et al. (1990) predicted that a dominant sibling should dispose of a subordinate sibling when the dominant sibling's own viability is secure and resources are inadequate for the survival of both siblings. This suggests that resource availability is a key component in the timing of siblicide. Life history theory predicts that the

current reproductive value (RV) of a sibling should be taken into account by a potentially siblicidal offspring (Roff 1992; Stearns 1992). This theory predicts that siblicide should occur at an early age, when the RV of the subordinate is low, and that aggression should be more intense among younger than older siblings. Since enforced starvation of subordinate siblings in Serengeti spotted hyaenas occurs within the first 2 months of life (Hofer & East 1997), we investigated whether rates of within-litter aggression are highest during this 2-month period and whether aggression declines as the RV of siblings increases with age.

METHODS

We conducted the study in the Serengeti National Park in northwestern Tanzania, East Africa. The study area was situated at the centre of the park, between the dry and wet season refuges of the large migrating herds of ungulates. These ungulates, mainly wildebeest, *Connochaetes taurinus*, Thomson's gazelles, *Gazella thomsoni*, and zebra, *Equus burchelli*, move along a rainfall gradient and pass through the study area biannually (Sinclair & Norton-Griffiths 1979). All three ungulate species are the principal prey of spotted hyaenas (Kruuk 1972; Hofer & East 1993a).

We recognized individual adult hyaenas from their distinctive spot patterns (Frank 1986; Mills 1990; Hofer & East 1993a) and young cubs from ear notches, scars and bald patches. The age of cubs was estimated from the development of locomotory abilities and pelage changes (Pournelle 1965; Kruuk 1972; East et al. 1989). Estimates of age were accurate to within ± 7 days. To determine sex, we used the dimorphic gland morphology of the erect phallus (Frank et al. 1990). Cubs were sexed at the age of ca. 3 months. A litter could consist of two male cubs (all-male litter) or two female cubs (all-female litter) or a female and a male cub (mixed-sex litter). The social rank of mothers was based on an interaction matrix using aggressive actions and submissive reactions in dyadic interactions (East & Hofer 1991b). A cub was classified as the submissive member of a litter if the number of retreats observed for that cub was greater than that recorded for its littermate. This classification did not depend on a significant difference in retreat frequency between siblings.

We collected data from three clans. For most purposes of this paper, we analysed the aggression rates recorded in 29 sexed litters (six litters of the 1992 cohort, 12 litters of the 1993 cohort and 11 litters of the 1994 cohort) during the first 2 months of life (0–2-month data set). We focused on sibling rivalry during the first 2 months of life because aggression in free-ranging litters is at a maximum during this period (Golla 1993; Smale et al. 1995). A second, expanded data set (0–12-month data set) included all observations during the first 12 months of life from the 29 sexed litters plus observations from an additional three unsexed litters (including one in which a probable siblicide occurred). We used this second data set to examine the change in intralitter aggression rates during the first 12 months of life.

Classification of Probable Siblicide

Hofer & East (1997) recorded large asymmetries in body mass between littermates shortly before subordinate cubs died of enforced starvation when maternal milk supplies were monopolized by dominant siblings. Consequently, in the present study, we classified the disappearance of a member of a litter as a probable incidence of enforced starvation (facultative siblicide), if we observed substantial asymmetries in body size (judged by eye) in littermates prior to the disappearance of the malnourished subordinate cub. We could not weigh cubs until they were about 3 months of age.

Observations

The study was conducted between February 1992 and January 1995. We observed the hyaenas at their communal dens or at natal dens during dawn and dusk usually between 0600 and 0900 hours and again between 1630 and 2030 hours from a vehicle to which the hyaenas had been habituated. Biting, lunging, chasing the sibling, pushing, mouth wrestling and supplanting the sibling from one teat were recorded as aggressive behaviour between siblings. Retreating was recorded as submissive behaviour. Serengeti hyaenas nurse their cubs for an average period of about 30 min (H. Hofer & M. L. East, unpublished data). Golla (1993) and the present study found that sibling aggression rates were highest at the beginning of a suckling bout and then declined. In the present study aggression rates were monitored for 38 min from the start of a suckling bout, and aggression rate declined to 0 after the 33rd minute (Spearman rank correlation: $r_S = -0.63$, $N=38$, $P<0.01$). To ensure that we monitored the period of maximum aggression, we conducted 30-min ($\overline{X} \pm SD = 31.8 \pm 9.3$ min) focal samples (Martin & Bateson 1986) of suckling twin litters that were initiated when mothers started to nurse their cubs.

Spotted hyaenas may give birth in private birth dens or at the communal den (East et al. 1989). Litters born in private dens were not transferred to the communal den until they were several days or weeks old. When the location of a birth den was known, or cubs were born at the communal den, sibling rivalry in newborn cubs was observed. Adult hyaenas are too large to enter dens beyond the entrance, thus cubs of all ages, including newborn cubs, emerge from the den entrance to suckle. Mothers with cubs less than 21 days of age ($N=11$ litters) typically nurse their offspring while lying in shallow depressions close to the den entrance or partially submerged in the den entrance. Under these circumstances we could still observe cubs if the research vehicle was positioned close (2–3 m) to the den entrance in the case of steeply sloping den entrances. The close proximity of the vehicle did not disturb mothers that had been habituated to the presence of the vehicles from birth or those used to sheltering from the sun in the shade of the vehicle, nor did it prevent other clan members from visiting the nursing mother and her cubs. Less-habituated mothers were not observed in this manner. Cubs older than 21 days of age were generally nursed outside the den
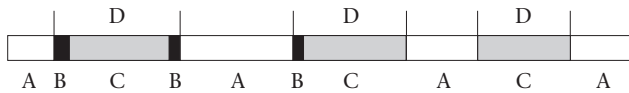
Figure 1. Schematic representation of sections of a focal sample. A: Gap or pause between suckling bouts; B: extension of 'pure' suckling bout (C) to include aggression immediately before or after the 'pure' suckling bout; C: 'pure' suckling bout with both cubs at the teats for at least 1 min; D: suckling bout with aggression extension (B+C) used for the majority of analyses in this study.

entrance, and these were observed from a distance of ca. 15 m.

Aggression Rates and Suckling Bouts

Aggression rates were calculated as the frequency of aggressive behaviours per min. We calculated aggression rates for two situations. (1) Suckling bouts: when cubs attempted to suckle for at least 1 min without a break by either cub of more than 45 s. The 45-s gap criterion was derived by a bout criterion analysis (Sibly et al. 1990). Aggressive or submissive behaviour between siblings that occurred immediately before or after a suckling bout (median 18.0 s, lower interquartile 8.1 s, upper interquartile 45.0 s, N=136) was considered part of the bout and the time period for such behaviours was included in the bout length (Fig. 1). (2) Gaps between suckling bouts: these include periods before the initial start of suckling when a mother returned to the den and all pauses between the suckling bouts during the focal sample.

We recorded a mean ± SD of 6.0 ± 4.3 focal samples per litter in the 0–2-month data set and 11.7 ± 6.2 focal samples in the 0–12-month data set. The 0–2-month data set consisted of 169 focal samples with 341 suckling bouts and a mean ± SD of 2.0 ± 1.4 suckling bouts per focal sample. The 0–12-month data set comprised 375 focal samples with 679 suckling bouts (see Fig. 3a in the Results) and 1.8 ± 1.2 suckling bouts per focal sample.

For the comparison of aggression rates during suckling bouts with those during gaps between suckling bouts, we calculated aggression rates as the sum of aggressive behaviours during all bouts or gaps divided by the sum of bout or gap duration in minutes. Gap data are missing for one litter in this sample (N=28).

Age Structure

The litters we observed varied in age from 4 days to 12 months. We observed five different litters in eight focal samples at ages between 4 and 7 days and 11 different litters in 29 focal samples during the first 14 days after birth. The average ages ± SD at which a litter was first observed were 27.3 ± 18.3 days (range 4–60 days) in the 0–2-month data set, and 25.6 ± 18.0 days (range 4–60 days) in the 0–12-month data set. The last observations were taken at a mean age ± SD of 50.3 ± 14.1 days (range 8–63 days) in the 0–2-month data set, and 136.1 ± 91.6 days (range 8–325 days) in the 0–12-month data set. The mean durations of the periods over which litters were observed ± SD were 23.2 ± 19.4 days for the 0–2-month data set, and 110.0 ± 86.8 days for the 0–12-month data set.

Birth Cohorts

We calculated cub growth rates for the first 6 months of life using the method outlined by Hofer & East (1993c). The mean growth rates of the birth cohorts 1992, 1993 and 1994 were calculated as the average growth rate of all cubs within a cohort. We distinguished between three birth cohorts according to the 3 years in which we observed the cubs. Yearly cohort growth rates provided an index of the impact of migratory movements of herbivores on how often mothers nursed their cubs.

Statistical Analysis

Statistical analysis was performed with SYSTAT 5.0 (Wilkinson 1990), following Sokal & Rohlf (1981) and Lamprecht (1992). Statistics are given as means ± SD (or medians and interquartile ranges where stated), and P values for two-tailed tests. Factors were considered to have a statistically significant influence if P<0.05.

Aggression rates did not differ between subsequent suckling bouts (Friedman test: χ^2_4=3.47, NS), and hence we calculated a mean aggression rate across all suckling bouts within a focal sample. To prevent pseudoreplication with multiple focal samples from individual litters (Hurlbert 1984), and the possible weighting of results in favour of those litters that were most frequently sampled (see Fig. 3a in the Results), we used litters as the independent sampling unit and thus N refers to numbers of litters unless stated otherwise. Because the number of focal samples differed between litters and because it was impossible to standardize the age (see Fig. 3a in the Results) at which litters were observed (as we could not predict on which day mothers would return to nurse their cubs), we could not use the focal sample means in a repeated measures ANOVA. Other procedures that would calculate a mean rate of aggression across several litters for standardized age classes would have prevented us from simultaneously examining the contributions of each of the several factors of interest (see below). Hence, to obtain an overall mean aggression rate per litter we averaged all focal sample means of a litter for the 0–2-month and 0–12-month periods. In the same way we calculated the mean age for each litter and the mean social status for the mother of each litter.

We used a mixed ANOVA model to investigate the influence of several factors on aggression rates during suckling bouts. These factors included maternal social status (rank), birth cohort, age, sex composition of the litter and rate of 'disturbance' by other hyaenas (sniffing of the suckling siblings by other clan members). Plots below show adjusted least squares means, which represent mean values for each category of birth cohort and litter sex composition calculated from the model that take into account the effects of the other factors entered in the model. Birth cohorts and litters with different sex

composition were compared using single-degree-of-freedom contrasts. The mixed ANOVA model explained 76% of the total variance. Residuals were examined using normal probability plots and tested for normality using the Lilliefors test (Wilkinson 1990). For all models examined, residuals were normally distributed.

RESULTS

Circumstantial evidence indicated that the subordinate littermate in four litters (three twin, one triplet) was a probable victim of facultative siblicide caused by enforced starvation. In these litters, subordinate and dominant littermates differed substantially in size before the former disappeared. We could not weigh the subordinate cubs, however, and we did not find their carcasses when they disappeared. The dominant cubs in two of these twin litters were without scars when first observed. However, all members of these litters had developed scars before the demise of the subordinate cub. In the triplet litter, the runt received the majority of the aggressive attacks from both of its larger siblings.

All four incidences of probable siblicide occurred during a period when mothers were commuting (Hofer & East 1993c) to feed on distant migratory herds. The only probable case of siblicide that occurred in the year with the highest cohort growth rate (see below) involved a litter of the lowest-ranked female. In the year of intermediate cohort growth rate, probable cases of siblicide occurred in a triplet litter of a mid-ranked female and a twin litter of a low-ranked female. In the year with the poorest cohort growth rate, a probable case of siblicide occurred in the litter of a mid-ranked female. If we are correct that these reductions in litter size were due to enforced starvation caused by sibling rivalry, then facultative siblicide occurred in three of 29 (10%) twin litters of known sex (two mixed-sex and one all-female litter) during this study, and in a fourth (triplet) litter where the sex of the dead subordinate cub could not be determined before death as it disappeared at the age of 21 days. In one mixed-sex litter the survivor was female, in the other, male.

The majority of cubs in this study (82% of subordinate cubs, 64% of dominant cubs) had scars, typically on the back, neck, shoulders or legs. Scars were chiefly acquired during fights between siblings, when cubs were carried long distances by their mothers or when cubs suffered from skin infections. Wounds that punctured the skin typically became infected, and such infections often spread causing larger wounds and scars. Dominant cubs were as likely to be scarred as subordinates (log likelihood ratio test: $G_1 = 1.306$, NS). There was a trend that subordinate cubs were more heavily scarred than dominants (13 out of 20 litters) but this result was not significant (sign test: $x = 7$, $N = 20$, NS). We have no evidence that wounds inflicted during sibling aggression led directly to the death of a cub.

No incidence of probable death owing to sibling rivalry was recorded in litters less than 2 weeks of age. As litters born in undetected birth dens were not observed during the first few weeks of life, early cases of fatal sibling
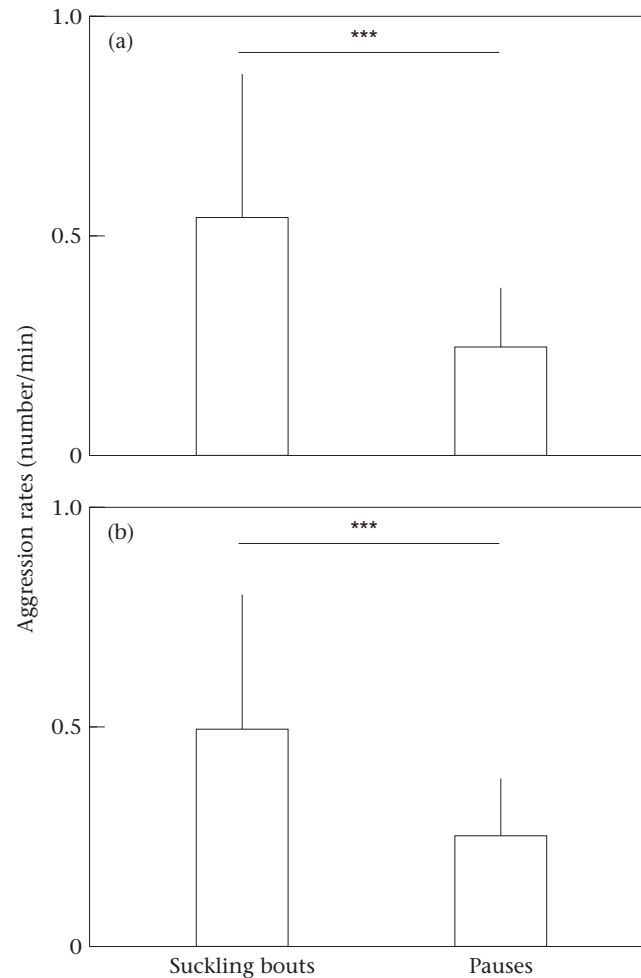

Figure 2. Aggression rates ($\bar{X} + $SD) during suckling bouts and pauses between bouts (periods D and A in Fig. 1) when aggression rates during suckling bouts were calculated (a) with an extension due to aggression (period B in Fig. 1) before and after both cubs were suckling; and (b) without these extensions (period C in Fig. 1). $N = 28$ in both cases. ***$P < 0.001$.

rivalry in these litters might have been overlooked. The mean age of cubs classified as probable siblicides was 59.2 ± 24.0 days when last seen alive, but as enforced starvation in younger litters might have been missed, this value could be an overestimate.

Dominance in Mixed-sex Litters

In 67% (10/15) of mixed-sex twin litters the dominant sibling was female, and in 33% (5/15) the dominant cub was male. The deviation from expected unity approached significance (binomial test: $P = 0.059$).

Aggression Rates and Suckling

Aggression rates during suckling bouts were about twice as high as those during gaps between suckling bouts (Wilcoxon signed-ranks test: $Z = 3.92$, $N = 28$, $P < 0.001$; Fig. 2). To test whether this result was due to the inclusion of aggressive interactions that occurred immediately before
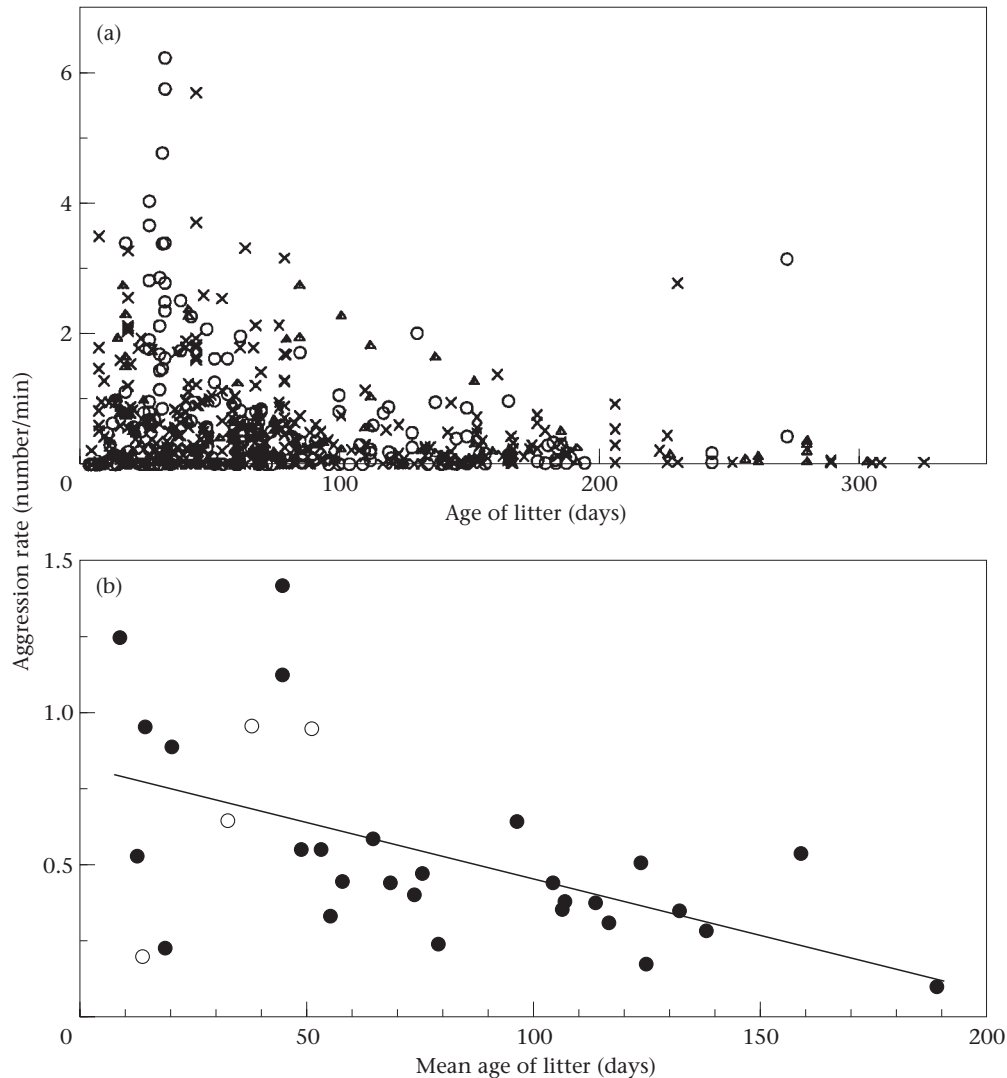
Figure 3. Aggression rates in relation to age during the first 12 months of life. (a) Aggression rates for each suckling bout of all litters. ▲: All-male litter; ×: mixed-sex litter; ○: all-female litter. (b) Mean aggression rates per litter as calculated from multiple samples, as shown in (a), from each litter throughout the period the litter was observed. The mean age of a litter was similarly calculated as the sum of ages of each litter when sampled divided by the number of samples. ○: Litters where siblicide may have occurred; ●: litters with two surviving cubs.

or after the end of a bout, we excluded these (periods marked B in Fig. 1) and repeated the analysis using the periods marked C in Fig. 1. Inclusion of these aggressive interactions in the gap phases (periods marked A in Fig. 1) would have misrepresented the biological function of those aggressive interactions that occurred in the context of suckling behaviour. Rates of aggression remained significantly higher during suckling bouts (0.49 ± 0.31 per min) than during gaps (0.26 ± 0.13 per min; Wilcoxon signed-ranks test: $Z=3.55$, $N=28$, $P<0.001$), even when these aggressive interactions were removed (Fig. 2b).

Aggression Rates of Dominant and Subordinate Cubs

The mean aggression rate of dominant cubs was about three times that of subordinate cubs (dominants: 0.48 ± 0.33 per min; subordinates: 0.15 ± 0.13 per min; Wilcoxon signed-ranks test: $Z= -4.17$, $N=28$, $P<0.001$).

Aggression Rates and Age

Throughout the initial 12 months of life, when Serengeti cubs are dependent on milk from their mother (Hofer & East 1993a), within-litter aggression declined. Figure 3a shows the raw data for each suckling bout for each litter. From these data a mean aggression rate and mean age were calculated for each litter, as outlined above. Figure 3b shows this mean aggression rate for each litter for the corresponding mean litter age. The decline with age was significant ($F_{1,30}=11.82$, $P=0.002$, $r^2=0.28$, $Y=0.81 - 0.0037X$). Rates of aggression remained high during the first 50 days of life (Fig. 3b).

Figure 4. Adjusted least-squares means of aggression rates ±SD for birth cohorts of the years 1992, 1993 and 1994. Adjusted means show the differences in mean aggression rates between cohorts and thus illustrate the contribution of the factor cohort after the effects of other factors in the mixed ANOVA model (maternal rank, sex composition, age, disturbance by third party) had been taken into account. *N* is the number of litters. For test statistics see Table 1. **P<0.01; ****P<0.0001.

Cohort Growth Rates

Growth rates were highest among the 1992 cohort (76.3 ± 17.3 g/day, $N=19$ cubs), lowest for the 1993 cohort (61.2 ± 14.2 g/day, $N=9$ cubs), and intermediate for the 1994 cohort (71.6 ± 19.4 g/day, $N=14$ cubs). The mean growth rates of the 1992 and 1993 cohorts were significantly different (Mann–Whitney U test: $U=128$, $P=0.04$).

Factors Influencing Aggression

A mixed ANOVA model simultaneously considered the influence of cohort growth rate, maternal social status, age, litter sex composition and rate of disturbance by a third party on aggression rates in the first 2 months.

Mean cohort growth rates were a good predictor of aggression rates within litters ($F_{2,17}=13.02$, $P=0.0004$). In years when growth rates were high or intermediate, aggression between littermates was significantly lower than in the year of low growth rates (Fig. 4, Table 1). Aggression between siblings also increased as the social status of mothers declined (Fig. 5; $F_{1,17}=16.52$, $P=0.0008$).

Aggression rates of cubs were influenced by the sex composition of a litter ($F_{2,17}=5.18$, $P=0.017$). Aggression rates of mixed-sex litters were significantly lower than those of all-male litters and of all-female litters (Fig. 6, Table 1). However, there was no significant difference between the aggression rates of all-male and all-female litters (Table 1). We also tested whether the effect of sex

composition depended on prey availability as represented by yearly cohort growth rate. There was a trend for same-sex litters to have substantially higher aggression rates in years with low cohort growth rate compared with mixed-sex litters. The interaction between sex composition and yearly cohort growth rate was, however, not significant ($F_{4,17}=1.94$, $P=0.15$). Within-litter aggression rates also declined with age ($F_{1,17}=8.11$, $P=0.01$) and increased with rate of disturbance ($F_{1,17}=4.69$, $P=0.045$).

DISCUSSION

Hyaena siblings were most aggressive when both members of twin litters attempted to suckle from the mother. This indicates that aggression between littermates was primarily linked to competition over access to maternal milk. In contrast to previous studies (Frank et al. 1991; Smale et al. 1995; Drea et al. 1996), we simultaneously assessed the contributions of several factors that may influence aggression rates during the first 2 months of life when facultative siblicide is most likely in spotted hyaenas (Hofer & East 1997). Significant factors included yearly cohort growth rate and maternal social status, both an index of maternal input of milk, sex composition of a litter, the age of competing siblings and the rate of disturbance by other clan members.

Physical Damage and Starvation

Intralitter aggression is important in the establishment and maintenance of the dominance hierarchy within hyaena litters (Frank et al. 1991; Glickman et al. 1993; Golla 1993; Smale et al. 1995). The present study and previous studies of sibling rivalry in free-ranging hyaenas (Golla 1993; Smale et al. 1995; Hofer & East 1997) have found no evidence that wounds inflicted during sibling aggression were the direct cause of cub mortality. However, sibling rivalry in Serengeti hyaenas can cause large asymmetries in body mass between littermates, leading to enforced starvation of subordinate cubs (Hofer & East 1997). Such facultative litter reduction is the most commonly observed cause of cub mortality in the Serengeti population (Hofer & East 1995), and was the most likely cause of mortality of four subordinate littermates in the present study.

Although the wounds we observed were not directly life threatening, they may have debilitated cubs and reduced their competitive abilities. As enforced starvation was not observed in those litters with the highest aggression rates (see Figs 3b, 5), individual tactics of siblings competing for maternal milk supplies rather than direct aggression may be important in determining the likelihood of facultative siblicide in spotted hyaenas. Smale et al. (1995) reported that in the Mara, only subordinate cubs were scarred during sibling aggression. In contrast, dominant Serengeti cubs were as likely to be injured as subordinate cubs. As wounds on dominant cubs were not exclusively due to skin infections or damage sustained when they were carried, this result suggests that subordinate Serengeti cubs wounded the dominant sibling. More

Table 1. Single-degree-of-freedom contrasts from a mixed ANOVA model of factors influencing rates of aggression (AR) between siblings in litters during the first 2 months of life

	Hypothesis	$F_{1,17}$	P
Birth cohort	AR in cohort with high growth rate < in cohort with low growth rate	9.79	0.006
	AR in cohort with medium growth rate < in cohort with low growth rate	25.89	0.0001
	AR in cohort with high growth rate < in cohort with medium growth rate	1.95	NS
Sex composition	AR in all-male litters > in mixed-sex litters	5.88	0.027
	AR in all-female litters > in mixed-sex litters	7.43	0.014
	AR in all-female litters > in all-male litters	0.02	NS
Model coefficients			
Maternal rank:	0.038; AR increased as maternal rank declined		
Mean age:	−0.013; AR decreased with age		
Disturbance:	1.300; AR increased as rate of disturbance by other clan members increased		

Table 2. Sex composition of spotted hyaena twin litters in ecological systems with different levels of prey availability, and sex composition of twin/triplet litters in a captive colony

		Sex composition of litters				
Ecosystem	Relative prey availability	Mixed-sex %	All-male %	All-female %	No. of litters	Reference
Kalahari	Low	89 P=0.002 Too many	11 NS	0 P=0.075 Too few	9	Mills 1990
Serengeti	Medium	61 P=0.001 Too many	25 NS	14 P=0.003 Too few	114	Hofer & East 1997
Mara	High	61 P=0.081 Too many	15 NS	24 NS	33	Holekamp & Smale 1995
Captivity	ad libitum	56 NS	17 NS	28 NS	18	Frank 1996
Binomial expectation		50	25	25	—	

Relative prey availability was based on resident prey base (sources summarized in Hofer & East 1993a). Binomial expectation calculated with the assumption of an even sex ratio. P values indicate significance of deviation from binomial expectation.

extreme aggression by subordinate Serengeti cubs may be the result of higher levels of hunger, owing to longer periods of absence of commuting Serengeti mothers than resident Mara mothers (see below). Food deprivation is known to increase sibling aggression in certain bird species, and has been considered a logical proximate stimulus for sibling aggression leading to facultative siblicide, as it provides a potentially reversible mechanism should food availability improve (Mock et al. 1987; Drummond & García Chavelas 1989).

Sibling Aggression and Resources

During the long lactation period, Serengeti spotted hyaena cubs receive milk that has a high nutrient content in comparison with that produced by other terrestrial carnivores. This milk has the highest recorded protein content for terrestrial carnivores except for bears, a high fat content and a higher gross energy density than that of

most terrestrial carnivores (Hofer & East 1995). If dominant littermates acquire more milk than do subordinate littermates, then their growth rate is likely to be greater. The discrepancy in growth rate and body mass between dominant and subordinate littermates will depend on the degree to which dominant siblings monopolize maternal milk supplies. If subordinate siblings are prevented from obtaining sufficient milk by dominant siblings, they will die of enforced starvation (Hofer & East 1997). Such despotic behaviour by dominant cubs provides fitness benefits as the mean growth rate of singleton cubs is significantly higher than that of cubs in twin litters (Hofer & East 1993c), and cubs with higher growth rates are more likely to survive to independence (Hofer & East 1993c).

Do changes in food supply alter levels of aggression between spotted hyaena siblings in accordance with the predictions derived from models of avian facultative siblicide (Parker et al. 1989; Forbes & Ydenberg 1992;
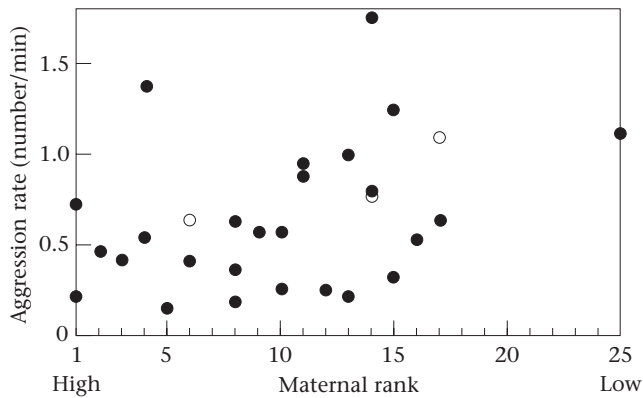
Figure 5. The effect of maternal rank on the mean aggression rate of litters of known sex combination during the first 2 months of life. For test statistics see text and Table 1. ○: Aggression rates from litters where siblicide may have occurred; ●: litters with two surviving cubs.
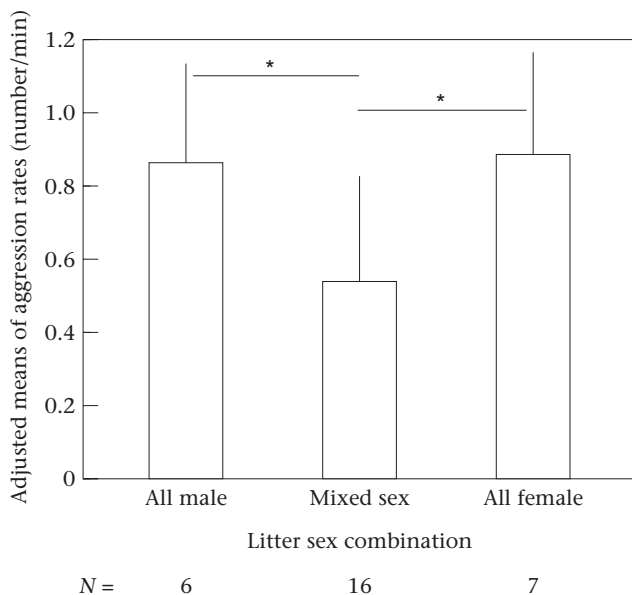

Figure 6. Adjusted least-squares means of aggression rates ±SD for litters of different sex composition. Adjusted means show the differences in mean aggression rates between litters of different sex composition and thus reveal the contribution of the factor sex composition after the effects of other factors in the mixed ANOVA model (maternal rank, cohort, age, disturbance by third party) had been taken into account. For test statistics see Table 1. *$P<0.05$.

McNamara et al. 1994)? The commuting system of Serengeti hyaenas (Hofer & East 1993a, b) dramatically affects how often mothers can nurse their cubs (Hofer & East 1993c). In this study we used yearly cohort growth rates as an index of annual changes in the impact of migratory movements of herbivores on the ability of mothers to nurse cubs. In years when cub growth rates were high, levels of sibling aggression were lower than in years when growth was moderate or poor. These results are consistent with predictions from avian models of fatal sibling competition.

Rates of sibling aggression increased as maternal social status declined (Fig. 5). As mothers of high social status have priority of access to food within the territory, they commute to feed on migratory herds only when their territory contains solely resident herbivores (H. Hofer & M. L. East, unpublished data), that is, when prey are scarce in the territory (Hofer & East 1993a). When prey abundance in a territory is moderate owing to the presence of gazelle herds, then mothers of high social status rarely commute (H. Hofer & M. L. East, unpublished data). In contrast, subordinate females regularly feed within the clan territory only when large migratory herds of wildebeest and zebra are present (Hofer & East 1993c). This means that mothers of low social status forage outside the territory more often and leave their cubs for longer periods than socially dominant mothers (East & Hofer 1991a). Thus, in accordance with our predictions, both of these results indicate that sibling aggression is an inverse function of maternal nursing rates. Smale et al. (1995) used peak monthly rates of intralitter aggression to assess the effect of maternal rank on sibling aggression in Mara litters. Higher rates of intralitter aggression were correlated with low maternal rank, but their analysis did not check whether this relationship persisted when the effects of litter sex composition, age, or disturbance were taken into account.

Smale et al. (1995) studied Mara litters of a similar age to those we observed, but employed critical-incident sampling to measure peak monthly rates of aggression by dominant siblings. In contrast to our study, which focused on periods of maximum aggression when littermates competed for access to milk, Smale et al. (1995) did not restrict their observations to these periods. Their aggression rates may thus be diluted by long periods of no aggression between suckling bouts. This may explain why aggression rates during suckling bouts in our study were 10 times higher than the highest aggression rates (0.043 per min) recorded for dominant female cubs by Smale et al. (1995). Another contributing factor may be the difference in ecological conditions between the Serengeti and the Mara. Owing to higher densities of resident prey in the Mara than in the Serengeti (Hofer & East 1993a), Mara females principally forage within their territories (Frank 1986) and thus Mara cubs may endure less nutritional stress than Serengeti cubs that depend on commuting mothers. Even so, Holekamp & Smale (1995) suggested that severe competition for food in Mara clan territories occurred when the number of competing female clan members was high. Extreme competition for food is likely to impair the ability of mothers to lactate, leading to increased intralitter competition for milk and probability of siblicide. Using data from Holekamp & Smale (1995), East & Hofer (1997) showed that before the fission of a Mara clan, when competition among females was high, the incidence of all-female litters was lower (8%) than after clan fission (41%) when there were fewer competing females. This result is consistent with the idea (Hofer & East 1997) that facultative siblicide is more likely to occur in all-female than all-male or mixed-sex twin litters when food available to lactating females is limited. Comparison of the sex composition of twin litters in

ecosystems with varying levels of available prey also supports this idea, as the proportion of observed all-female twin litters increases as the availability of resident prey increases (Table 2). Predictably, the highest incidence of all-female litters (twins/triplets) was observed in a well-fed captive colony (Frank 1996).

In studies of sibling aggression in newborn captive spotted hyaenas (Frank et al. 1991; Drea et al. 1996), mothers were continually housed with their offspring. Our results suggest that when cubs have constant access to their mother, within-litter aggression should be low. Drea et al. (1996) considered two categories of aggression: stereotypic bite shake attacks and all other categories of aggression (including bites, bite attempts, displacement at the nipple, pushes, shadows and threats). They reported a marked decline in the frequency and duration of bite shakes from week 1 to week 2 after birth, whereas all other categories of aggression occurred at an equal frequency across all 4 weeks of their study. The mean hourly aggression rates reported by Drea et al. (1996) from a sample of five all-female, two mixed-sex and one all-male litter were lower than those we report in this study, even though their sample was biased in favour of all-female litters, a sex composition of littermates where high aggression rates would be expected (see below). We suggest that low aggression rates in captive, all-female litters might be explained by the ability of well-fed captive mothers to nurse their cubs frequently. Frank et al. (1991) reported duration (not frequency) of aggression in three all-female litters, one mixed-sex litter and an all-male triplet litter. Duration of aggression was higher in the triplet than twin litters. As spotted hyaenas normally have only two functional teats, competition for access to milk would be greater in triplet than in twin litters. Frank et al. (1991) found that aggression duration in their twin litters declined from about 70 s/h during the first 24 h of life to ca. 10 s/h in the following days. As the decline in duration of aggression reported by Drea et al. (1996) was due to a decline in bite shake behaviour, but not other forms of aggression, the decline in aggression duration reported by Frank et al. (1991) was also probably due to a decline in bite shake behaviour, and not a general decline in aggression. In contrast to the claim by Frank et al. (1991) that levels of aggression dramatically decline within the first week of life, our results (Fig. 3), and those of Smale et al. (1995) and Drea et al. (1996), demonstrate that intralitter aggression rates do not decline until several weeks after birth in both captive and free-ranging hyaenas. If elevated levels of androgens are associated with aggression, then elevated levels of androgens observed throughout the first month of life (Frank et al. 1991) appear more closely linked to the persistence of sibling aggression during these weeks than the substantial reduction in bite shake behaviour within the first week of life.

Sibling Aggression and Age

Mock et al. (1990) predicted that resource availability is a key component in the timing of siblicide, whereas life history theory suggests that high levels of aggression with potentially fatal consequences should occur at an early age, and that aggression should decline with age. Results from the present and a previous study (Hofer & East 1997) indicate that both the RV of siblings and resource availability influence the timing of high levels of aggression with potentially fatal consequences in Serengeti spotted hyaenas.

The RV of siblings of a given age is directly measured by the probability of survival to independence, since fecundity is held constant prior to their first reproductive attempt (Pianka & Parker 1975). The mortality rate of siblings in their early developmental period is thus the reciprocal of their RV. Hofer & East (1995) observed a steep decline in Serengeti hyaena cub mortality after the first 3 months of life, followed by a more shallow decline during later periods, indicating an increased RV after 3 months of age. In our study, subordinate siblings disappeared at a mean age of 2 months when the RV of siblings is low. The high aggression rates observed in the first 2 months of sibling life demonstrate that (1) the conflict between littermates is highest when the potential cost of sibling mortality in terms of RV is small, and (2) as the RV of siblings increased with age within-litter competition declined (Fig. 3).

Resource availability can also influence the timing of enforced starvation. Hofer & East (1997) showed that if mothers failed to nurse sufficiently to sustain a twin litter, enforced starvation of the subordinate cub can occur even when cubs are 6–7 months of age.

Sibling Aggression and Sex Composition of Litters

We found that aggression rates in all-female and all-male litters were higher than in mixed-sex litters. Higher levels of aggression within same-sex litters may be a consequence of identical interests amongst competitors, and a lack of asymmetry in payoffs and fighting abilities (Maynard Smith 1982). There was a nonsignificant trend for sisters to dominate brothers in mixed-sex litters, a result compatible with the prediction of a sex-specific bias in acceptance of subordinate status. However, high aggression rates in all-male litters argue against a sex bias in the acceptance of subordination.

Theory suggests that the sex that receives greater parental effort should compete more for the resources provided by parents (Parker 1974; Popp & DeVore 1979). As investment in daughters appears to be greater than in sons in spotted hyaenas (see Introduction), we would expect daughters in mixed-sex litters to compete more vigorously for access to milk than sons and for competition among daughters in all-female litters to be greater than among sons in all-male litters. Furthermore, female philopatry, the acquisition by daughters of a social rank below their mother, and the link between dominance rank and access to food resources within the clan territory (Frank 1986; Hofer & East 1993c) would also predict that competition within all-female litters should be greater than within all-male litters. Yet the preponderance of females as the dominant sex in mixed-sex litters only approached significance, and we did not detect any

difference in aggression rates between all-male and all-female litters. Our results may be explained by aggression rates reflecting the combined aggressive behaviour of both siblings. Aggression rates do not necessarily reveal the tactics used by dominant and subordinate siblings during agonistic encounters and the costs and benefits of different tactics. Another reason why we may not have found a difference between aggression rates in all-male and all-female litters may be the small number of same-sex litters in this study and hence the low statistical power to detect differences. This is a problem that plagues many studies examining life history predictions from sex ratio theory.

Sibling Aggression and Potential Fatal Consequences

In this study we suggest that as a consequence of resource shortage, high intralitter aggression rates may lead to the death of the subordinate sibling through enforced starvation. In contrast, Frank et al. (1991) suggested that this species exhibits a phenomenon called 'habitual neonatal siblicide'. Their description of this phenomenon differs from our concept of resource-based sibling rivalry in three aspects. They stated that habitual neonatal siblicide is not resource based, it occurs in the first few days of life, and it is habitual for same-sex litters. Furthermore, Frank et al. (1991) suggested that the phenomenon of habitual neonatal siblicide was a resource-independent by-product of selection for female androgenization, whereas East et al. (1993) proposed that high levels of maternal investment in spotted hyaenas led to selection for resource-based sibling rivalry that was linked to elevated levels of androgens and aggression in cubs of both sex.

There is no direct evidence for habitual neonatal siblicide from long-term studies of free-ranging populations (Holekamp & Smale 1995; Smale et al. 1995; Hofer & East 1997; this study), circumstantial evidence is limited (Frank et al. 1991), and the occurrence of same-sex litters in free-ranging populations (Table 2) contradicts the idea (Frank et al. 1991) that habitual neonatal siblicide accounts for 25% of all cub mortality.

Frank (1996) responded to observation of same-sex litters in free-ranging populations (Holekamp & Smale 1995) by suggesting that: (1) habitual neonatal siblicide may be sensitive to clan demography and competition, but not linked to resources; (2) females may manipulate neonatal aggression to favour the sex that is most valuable under the prevailing ecological or demographic conditions; but also that (3) high levels of neonatal aggression occur inside the den, away from the influence of the mother, during the first few days of life. These ideas await testing with data from free-ranging populations.

Conclusion

We have shown that aggression rates between spotted hyaena siblings were influenced by a variety of factors, of which the most important seems to be nursing by mothers. Aggression was also highest during the first month of life and same-sex litters had the highest aggression rates. The intriguing question of how changes in the sex composition of a litter affect individual tactics of aggressive behaviour remains to be clarified.

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