



Siblicide revisited in the spotted hyaena: does it conform to obligate or facultative models?

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Aggression among spotted hyaena, *Crocuta crocuta*, siblings is often intense, and sometimes lethal. Frank et al. (1991, *Science*, **252**, 702–704) proposed that siblicide routinely occurs in half of all spotted hyaena litters, namely those composed of same-sex twins. We propose an alternative to this ‘obligate’ model. In our ‘facultative’ model we suggest that siblicide is far less common than previously supposed, and that it occurs only when resources are insufficient to sustain two cubs. According to this facultative model, intense neonatal aggression functions to establish intralitter dominance rather than to kill siblings. Furthermore, differences in litter size and composition between captive and field settings previously used to support the obligate model are assumed in the facultative model to be due to prenatal factors rather than to postnatal siblicide. Here we tested the predictions of these two hypotheses with 10 years of field data from hyaenas inhabiting the Masai Mara National Reserve, Kenya. We found that, although sex compositions of hyaena litters averaged over the entire 10-year period did not differ from those predicted by chance, they did vary with environmental conditions. Litter sizes, by contrast, remained constant. These data are inconsistent with the widely accepted hypothesis that spotted hyaenas in same-sex litters routinely engage in siblicide.

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Cooperation between siblings has received much attention in the 35 years since Hamilton (1964a, b) introduced the concepts of inclusive fitness and kin selection. Competition between siblings has received far less attention, even though Hamilton’s rule also makes explicit the conditions under which selfish interactions between siblings should prevail (Mock & Parker 1997). Sibling rivalry has been investigated extensively in birds, but is relatively poorly understood in other classes of vertebrates (Mock & Parker 1997). In some avian species, aggression between nestmates is almost always fatal to subordinates, and in these species, siblicide is said to be ‘obligate’. In most siblicidal birds however, the consequences of intrabrood aggression are highly variable, and dependent on environmental conditions (Mock et al. 1987). In these species siblicide is said to be ‘facultative’. Variables known to influence the probability of avian siblicide include food availability (Drummond et al. 1986; Drummond & Chavelas 1989), brood size (Mock & Lamey

1991), prey size (Mock 1984; Mock et al. 1987) and the degree of competitive asymmetry between nestmates (Fujioka 1985; Mock & Ploger 1987).

Although sibling rivalry has been a relatively neglected topic in the study of mammalian social development, it has been documented among juvenile pigs, goats, primates, marsupials and carnivores (reviewed in Mock & Parker 1997). In contrast to siblicidal birds, few mammals are equipped at birth with the weapons needed to engage in successful combat with siblings, nor can mother’s milk generally be as easily monopolized as can food items delivered to nestlings by avian parents. However, intralitter aggression can be very intense in some mammals. For example, young pigs, *Sus scrofa*, are armed at birth with erupted canine teeth which they use during intralitter fights that leave siblings bloodied and scarred. Each newborn piglet establishes a ‘territory’ around a nipple from which it effectively excludes its littermates (De Passile et al. 1988). A teat order is established within the first few hours of life, after which intralitter aggression drops dramatically (Hartsock & Graves 1976). However, if there are more piglets than teats, the losers in this early competition are likely to starve to death (Fraser 1990). Thus porcine siblicide is best described as facultative. Another mammal in which siblicide has been observed is

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the spotted hyaena, *Crocuta crocuta*, (Frank et al. 1991; Hofer & East 1997). Frank et al. (1991) suggested that 'siblicide appears to kill nearly 25% of spotted hyaena offspring: at birth 50% of litters are same-sex and half of those individuals succumb' (Frank et al. 1991, page 704). According to this hypothesis, siblicide is only assumed to occur within the subset of litters composed of same-sex twins. However, within that subset, siblicide is assumed to occur routinely in nature, regardless of environmental circumstances. Therefore, according to this model siblicide within same-sex litters is 'obligate' (Mock & Parker 1997, page 318).

In the wild, neonatal hyaenas spend most of their time underground (East et al. 1989) and have therefore rarely been observed. Thus, evidence supporting the obligate model of hyaena siblicide has been primarily indirect. (1) Aggression between captive littermates is exceptionally intense immediately after birth, suggesting that this early aggression might function to kill siblings (Frank et al. 1991). (2) Litter sizes observed in the wild are significantly smaller than those observed in captivity, suggesting to Frank et al. (1991) that litter reduction occurred routinely in the wild. Specifically, for multiparous females the ratio of singletons:twins:triplets was 1:10:2 in captivity at birth (mean litter size=2.08), and 42:57:0 in the field when cubs were first brought from the natal den to the clan's communal den at 2–4 weeks of age (mean litter size=1.58). (3) The ratio of same-sex:mixed-sex twin litters was 5:5 in captivity, but only 5:28 and 1:8 in wild populations in eastern Africa (Frank et al. 1991) and the Kalahari (Mills 1990), respectively. Frank et al. (1991) concluded that this difference between captive and field observations resulted from selective loss of cubs in the wild due to siblicide within same-sex litters. Frank et al. (1991) suggested further that those same-sex twin litters that had been observed in the wild were probably born as triplets and then reduced to twins through siblicide. One direct observation of apparently siblicidal behaviour was reported from a litter that was captured at a natal den during the neonatal period (Frank et al. 1991). Whereas the obligate model does not preclude the possibility of additional siblicide in response to diminished food supplies, it does maintain that 25% of cubs are routinely killed by their littermates in a manner that cannot be explained by competition for nutritional resources (Frank et al. 1991). If the obligate hypothesis is correct, then the spotted hyaena would be unique among vertebrates in exhibiting sex-biased obligate siblicide (Mock & Parker 1997). However, the 'facultative' model may be better able to account for existing data.

According to the facultative model proposed here, the intense fighting among neonatal hyaenas does not habitually result in siblicide, but functions instead to establish intralitter dominance relations. Once intralitter dominance is established, within the first 48 h after birth (Smale et al. 1995), levels of aggression drop dramatically (Frank et al. 1991). Intralitter rank is important because it determines priority of access to resources among littermates, and because this rank relationship persists as long as both siblings remain in the natal clan. If environmental conditions deteriorate such that the mother

becomes unable to provide adequate nourishment to support two cubs, then the significance of intralitter dominance becomes starkly apparent. Under these conditions, the dominant may monopolize the available milk, leading the subordinate cub to starve. Because most early intralitter aggression occurs in the isolation of the natal den, which older hyaenas cannot enter, the only factor determining intralitter dominance appears to be a highly escalated form of all-out sibling-directed aggression.

According to the facultative model, siblicide should also occur in all triplet litters. That is, although triplets are extremely rare in the wild, they should always engage in siblicidal behaviour because female *Crocuta* normally have only two teats (Kruuk 1972) and one of three cubs would inevitably go hungry. The lowest-ranking triplet is the target of attacks initiated by its two dominant siblings, and thus may be effectively excluded from access to the mother's teats. Finally, according to this model, the discrepancies between litter sex ratios and sizes in captive and field settings exist because these parameters differ at birth, most likely in response to differences in prenatal stress and/or maternal nutrition. For example, maternal nutrition may be substantially better, and litter size at birth larger, in captivity than in the wild. Such prenatal influences on sex ratios and litter sizes have been documented in a variety of mammalian species (litter sex ratios: Verme 1965; Rivers & Crawford 1974; Charnov 1982; Austad & Sunquist 1986; litter size: Verme 1965; Pratt & Lisk 1989; Tardif & Jaquish 1994).

According to the obligate model, neonatal siblicide always occurs in same-sex litters, leading to a disproportionately large number of mixed-sex twins among surviving litters. Furthermore, the obligate model is based on the assumption that compositions of litters produced in different environments (e.g. captive versus field settings) should be the same. By contrast, the facultative model does not expect disproportionately high rates of siblicide among same-sex litters, nor does it assume that litter-sex compositions at birth cannot vary with environmental conditions. We present field data collected over 10 years that bear on these contrasting predictions of the two models.

METHODS

This study was conducted in the Talek region of Masai Mara National Reserve, Kenya, between 1 July 1988 and 1 July 1998. The subject population was the large *Crocuta* clan originally described by Frank (1986a, b) and discussed by Frank et al. (1991). In the current study, observers were present in the Talek area 23–31 days/month throughout the study period, except during April 1991, when observers were present on only 14 days. We conducted daily observations at all active dens and travelled daily throughout the home range of the Talek clan searching for new dens. All hyaenas in the study clan were known individually by a host of distinctive characteristics including their unique spot patterns, ear damage, patterns of scarring and stage of moult. Males were distinguished from females on the basis of the dimorphic glans morphology of the erect phallus (Frank et al. 1990).

The glans of the male is distinctly larger than that of the female by 2 months of age, if not earlier (Drea et al. 1998). To sex cubs, observers parked their vehicles 8–10 m from the den and examined the erect phallus of each cub through 10 × binoculars or a 40 × spotting scope. Cubs get erections during greeting ceremonies which occur virtually every time a new animal arrives at the den. Animals were sexed repeatedly by multiple observers to verify results. Sex could be assigned with complete certainty when cubs were 2 months old. However, on several occasions (as noted below) cubs died before they could be sexed. Mother–offspring associations were established on the basis of observations of regular nursing associations. Females that had given birth at least once could be distinguished from nulliparous females on the basis of observations of scar tissue on the posterior surface of the erect phallus (Frank & Glickman 1994).

Data were examined for Pearson's correlations using SYSTAT version 8.0, and these were considered significant when $P < 0.05$; all percentages were arcsine transformed prior to correlational analyses. A sign test was used to evaluate overall sex ratios, and chi-square statistics were used to evaluate litter compositions.

RESULTS

Demographic Changes

Figure 1a presents the number of adult female members of the Talek clan observed each year of the study. Between July 1988 and July 1990 the Talek clan contained 22 reproductive females. This number is similar to that reported for each of the 6 years in which this population was examined between 1979 and 1987 (range 20–23; Frank et al. 1995). Between November 1989 and June 1990, a group of seven adult females and their eight offspring left the Talek clan during a fission event (Holekamp et al. 1993). The number of adult breeding females returned to its pre-fission level in July 1994, then rose above the number originally present in the clan, and finally dropped again in the last year of the study (Fig. 1a). The number of adult females in the clan plays a major role in determining overall clan size. The ratio of adult immigrant males to breeding females in the Talek clan remains relatively constant at around 1:1.5 across a wide range of demographic and ecological conditions (Holekamp et al. 1993; Frank et al. 1995). Changing numbers of adult females also produce variation in overall clan size by influencing the number of juveniles, and juveniles represent significant competitors for food because they can often dominate adult females (Smale et al. 1993). Total clan size is positively correlated with intensity of competition for food (Holekamp et al. 1993), and thus presumably also with the stress levels experienced by competitors. Therefore, to evaluate the influence of demographic parameters on litter compositions and sizes, we examined the relationship between the number of adult females present in the clan and a variety of reproductive parameters in the analyses that follow.

Litter Compositions

Over the 10-year study period, 218 cubs in 139 litters were observed at 66 natal dens as well as numerous communal dens. When first observed above-ground, 61 litters were singletons, 77 were twins and one was a triplet. Of these 218 cubs, the sexes of 183 were reliably determined and the remaining 35 died prior to being sexed. The number of unsexed cubs was distributed randomly across the study period, and did not vary as a function of the number of adult females in the clan (Bartlett test: $\chi^2_1 = 0.216$, NS). The overall ratio of male:female cubs observed was 93:90; this did not differ from 1:1 (sign test: NS). The ratio of male:female (M:F) cubs was 66:62 among twins in which both cubs survived to be sexed, and this ratio was 21:23 among cubs that were singletons when we first observed them; these ratios did not differ from 1:1 (sign test: NS). However, on an annual basis, sex ratios (% of cubs that were male) declined at clan fission, and increased again as the number of adult females increased (Fig. 1b). Overall, the sex ratio among cubs produced each year was significantly correlated with the number of adult females in the clan (Fig. 1c; Bartlett test: $\chi^2_1 = 4.762$, $P < 0.05$).

Sex composition was obtained for 64 of the 77 twin litters recorded. Among these litters, the overall ratio of MM:MF:FF twins did not differ from that expected by chance (15:36:13; $\chi^2_1 = 1.125$, NS). Whereas FF twins were rare during the first and last years of the study, before clan fission and after recovery, they were common during the middle years immediately after the clan had fissioned (Fig. 1d). The percentages of twin litters that were FF was inversely correlated with the number of adult females in the clan (Fig. 1e; Bartlett $\chi^2_1 = 4.387$, $P < 0.05$). The proportion of twin litters produced per year that were MM did not vary systematically over the course of the study period, and was not correlated with the number of adult females in the clan (Bartlett $\chi^2_1 = 1.060$, NS). Similarly, the proportion of twin litters that were MF was not correlated with the number of adult females in the clan (Bartlett $\chi^2_1 = 0.129$, NS). However, during the first 2 years of the study a very high proportion of twin litters were of mixed sex (13/16), as Frank et al. (1991) had observed in previous years. This pattern was not maintained during the last 8 years of the study, during which only 23 of 49 twin litters were of mixed sex.

Litter Sizes

Mean litter sizes over the 10-year period were 1.59 for multiparous females ($N = 109$ litters) and 1.50 for primiparous females ($N = 30$ litters). Annual mean litter size did not change in a systematic manner over the course of the study period, and was unrelated to the number of adult females in the clan (Bartlett $\chi^2_1 = 0.850$, NS). The same result was obtained when we restricted this analysis to multiparous females (Bartlett $\chi^2_1 = 0.058$, NS).

The high proportion of twin litters that were of mixed sex during the first 2 years of this study was consistent with the pattern that had led Frank et al. (1991) to conclude that siblicide occurred within same-sex twin

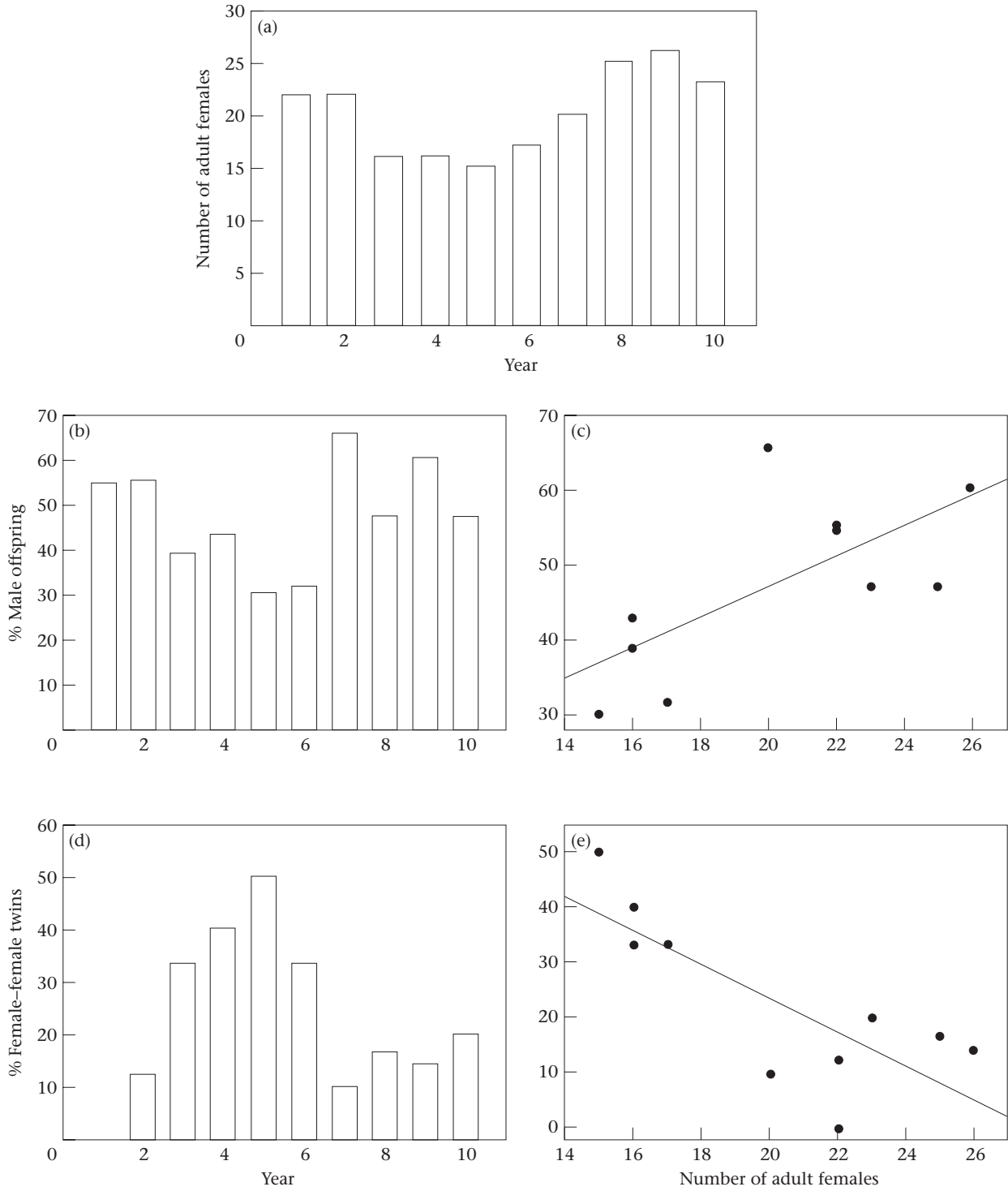


Figure 1. (a) Numbers of adult females in the Talek clan for each year of the 10-year study beginning 1 July 1988. Percentages of offspring that were male (b) for each year of the study and (c) as a function of the number of adult females in the clan. Percentages of twin litters that were female (d) for each year of the study and (e) as a function of the number of adult females in the clan.

litters. This finding raised the possibility that an obligate form of siblicide had been occurring in this population, but ended in 1990. However, such a change should have led to an increase in litter size, but this was not observed. Litter sizes during the first 2 years of the study were 1.58

($N=26$ litters) and 1.63 ($N=19$ litters) for all females, and for multiparous females, respectively. Litter sizes during the next 8 years were 1.57 for all females ($N=113$ litters), as well as for the subset that was multiparous ($N=90$ litters).

Siblicide

One clear observation of events that appeared to lead to siblicide was recorded. In December 1994 our assistants discovered the natal den of the first and only triplet litter observed during the study period. The cubs appeared to be less than 3–4 days old, on the basis of their size, coordination, and the fact that their ears were still flattened against the head, a characteristic of very young hyaenas. Over the ensuing 3 weeks, the two top-ranking members of the litter attacked the subordinate, and prevented it from nursing effectively. It became progressively weaker until it vanished at 21 days of age.

DISCUSSION

The sex ratio data presented here are inconsistent with predictions of the obligate model of siblicide in two respects. First, whereas the obligate model maintains that neonatal siblicide should occur within all same-sex litters, we observed as many same-sex twin litters well beyond the neonatal period as would be predicted by chance (15:36:13, MM:MF:FF). Our data set included over twice as many twin litters of known sex as reported by Frank et al. (1991) from the same population during a different time period. Second, our correlational data challenge an important assumption of the obligate model, that litter sex compositions at birth do not vary with environmental conditions (e.g. captivity versus field). Over the 10-year period of this study, changes in litter composition coincided with changes in the numbers of adult females in the Talek hyaena clan. Specifically, there was a positive relationship between the number of adult females in the clan and the proportion of offspring produced that were male (Fig. 1c), and an inverse relationship between the number of adult females and the percentage of twin litters containing two females (Fig. 1e). Mean litter size did not change over the course of the study and was unrelated to the number of adult females in the clan. Changes in litter composition are thus unlikely to have resulted from changing levels of siblicide because this should have altered litter size. These data suggest instead that in hyaenas, as in a variety of other species, environmental influences before or during pregnancy can affect offspring sex ratios (Verme 1965; Rivers & Crawford 1974; Charnov 1982; Austad & Sunquist 1986). Food availability increased, and stress presumably decreased, when the Talek clan underwent a dramatic decrease in size at the time of clan fission (Holekamp et al. 1993; Holekamp & Smale 1995), and these processes appear to have reversed themselves when clan size later increased.

An important line of evidence invoked by Frank et al. (1991) in support of the obligate siblicide hypothesis was that litter sizes observed at birth in the captive setting were larger than those recorded in the wild when cubs were first brought to the communal den. Litter sizes at birth were assumed to be the same under field and laboratory conditions, and siblicide in the wild was offered to explain the observed differences in litter size. Here we suggest instead that differences in litter size between captive and field populations might be due to

prenatal factors rather than to siblicide. The influences of prenatal variables, such as stress, diet quality and energy availability, on litter size have been well documented in many different species representing several orders of mammals (e.g. rodents: Pratt & Lisk 1989; artiodactyls: Verme 1965; primates: Tardif & Jaquish 1994) and spotted hyaena litter sizes may be similarly labile. In various wild populations of *Crocuta*, mean litter sizes at the time cubs were first observed above-ground have been reported to be 1.91 ($N=21$, Chobe: Cooper 1993), 1.70 ($N=20$, Kalahari: Mills 1990), 1.58 ($N=99$, Masai Mara: Frank et al. 1991) and 1.56 ($N=205$, Serengeti: Hofer & East 1997). These data suggest that, in most populations, litter sizes are similar to those reported here for Talek, but that some variability exists. The data collected by Cooper (1993) present a special problem for the obligate siblicide hypothesis. In her study population, 19 litters observed over a 3-year period were twins and two were singletons; sex compositions were unknown. Cooper's (1993) large mean litter size suggests either that prenatal factors can influence litter size in this species, or that siblicide did not occur in this population. Both interpretations are inconsistent with the obligate model of siblicide.

Lindeque (1981) reported on prenatal litter sizes in South Africa where nine pregnant spotted hyaenas were shot before the third trimester. Eight of these females were carrying twins and one carried a singleton litter (mean litter size=1.89). Had the pregnancies been carried to term, some fetuses might have been resorbed. Litter reduction in utero is common among mammals, including carnivores (Hayssen et al. 1993). Unfortunately, neither the litter size nor the sex ratio of cubs at the time they emerge from the den were known for this population (Lindeque 1981). At the time of Lindeque's 1981 study, hyaenas were being culled from the population, raising the possibility that the density of the population was unusually low. Exploited carnivore populations may respond by increasing litter size (Knowlton 1972).

Hofer & East (1997) recently reported on siblicide in a population of spotted hyaenas in the Serengeti National Park where, over a 7-year period, siblicide killed 22 out of 228 cubs observed between 12 and 273 days of age (average=87 days). Sex compositions of these litters were not specified. Body weights were reported for three litters in which subordinate cubs, prior to their deaths at 160–220 days of age, were approximately half the size of dominants. The pattern of siblicide reported for the Serengeti is consistent with the facultative model in that siblicide was not concentrated during the neonatal period, but occurred at widely varying ages when the mother was unable to provide milk sufficient to sustain two cubs. Facultative siblicide may be far less likely to occur at Talek than in the Serengeti, where hyaenas routinely leave their cubs unattended for extended periods while they commute considerable distances from their territories to feed on migratory prey (Hofer & East 1995). In the Talek area, resident populations of prey persist year-round (Holekamp et al. 1997). Interestingly, Hofer & East (1997) found a slight but nearly significant tendency towards a female bias among singletons, and a significant male bias among twins. Based on this pattern,

they suggested that rates of siblicide are higher in FF than in MF or MM litters, a pattern they attributed to higher levels of resource competition between sisters (Hofer & East 1997). While this interpretation is certainly plausible, other factors might also have promoted this pattern. Specifically, the relatively harsh ecological conditions of the Serengeti may have led to decreased production of FF twins. A female bias among singletons might have occurred if dangerously low food supplies led to facultative siblicide, both because females are more likely to dominate their male littermates than vice versa (Smale et al. 1995), and because of an increased probability of siblicide among FF litters as suggested by Hofer & East (1997).

Many birds manipulate competitive asymmetries between their offspring by altering the length of laying intervals between successive eggs, or by depositing different titres of testosterone in successive eggs (e.g. Mock & Ploger 1987; Schwable 1993, 1996; Wiebe & Bortolotti 1994a, b). If female hyaenas similarly attempt to modify competitive asymmetries between their offspring, then we should observe differences within hyaena litters with respect to variables likely to affect fight outcomes between littermates. Two possible variables are intralitter differences in cub body size and cub sex. Smale et al. (1995) reported no significant size differences between captive littermates at birth, although the sample size was small. However, the possibility also exists that females adjust competitive asymmetries by manipulating the sex composition of their litters before parturition. Because young hyaenas are sexually dimorphic in their aggressive behaviour (Frank et al. 1989; Smale et al. 1993), same-sex twins are likely to be more evenly matched in their fighting ability, and their fighting could thus last longer and involve greater risk of injury for both littermates than would be likely in mixed-sex litters. In the early years of observation of the Talek clan, numbers of mixed-sex twin litters were disproportionately high (Frank et al. 1991; this study). One possible explanation for this is that obligate siblicide occurred among same-sex twins (Frank et al. 1991). An alternative view is that females produced disproportionately large numbers of mixed-sex twins. This might have been due to chance, or it may have been a means for females to produce competitive asymmetries between their cubs that would minimize intralitter aggression.

In their presentation of data pertaining to siblicide, Frank et al. (1991) stated that 'this is the first report of habitual siblicide in a mammal'. The conclusion that neonatal siblicide routinely kills 25% of spotted hyaena cubs was presented as though it had been firmly established, and has been subsequently presented as fact in a variety of other contexts (e.g. Frank 1996, 1997; Mock & Parker 1997; Alcock 1998). The new data presented here pose a serious problem for this obligate hypothesis, and instead support a facultative model of siblicide in spotted hyaenas. We suggest that the facultative hypothesis accounts for existing data in a manner that is more parsimonious and more plausible than does the obligate model. The only evidence left to support the obligate hypothesis is that, in captivity, litter sizes of spotted

hyaenas at birth differed from those observed in the field after cubs had emerged from the den (Frank et al. 1991). However, this evidence is also compatible with the facultative model; that is, the difference between litter sizes observed in captive and field settings could be due to differing circumstances before birth. The only way to distinguish definitively between these interpretations will be with direct observation of spotted hyaena litters in the field either just prior to birth using ultrasound techniques, or via intensive behavioural observations of den-dwelling cubs during the days immediately after birth.

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