

Siblicide in the spotted hyena: analysis with ultrasonic examination of wild and captive individuals

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Integrated field and laboratory studies of long-lived, large-bodied mammals are rare but offer unique opportunities to elucidate the behavioral ecology of these animals. Here, we used this approach to examine whether siblicide in spotted hyenas (*Crocuta crocuta*) is obligate or facultative. First, we tested predictions of obligate and facultative hypotheses by using ultrasonography to compare litter size before and after parturition and identify potential causes of litter reduction. Second, we compared litter size and composition between wild and captive hyenas to assess variation in offspring sex ratios. Third, we used demographic data to compare survivorship among litters of various sizes and compositions. Fourth, we compared sex ratios within twin litters born in the wild under conditions of high population density and intense feeding competition with those born when population density and intensity of feeding competition were reduced. Our data were inconsistent with the obligate siblicide hypothesis. Litter reduction occurred during roughly one-third of pregnancies in both wild and captive hyenas, and all such reductions among captives were due to fetal resorptions or stillbirths. Litter sizes and compositions differed little between wild and captive hyenas. However, sex ratios in twin litters varied in the wild with intensity of feeding competition. In conjunction with captive data, long-term study of a wild hyena population under varying environmental conditions suggests facultative siblicide is most likely to occur when feeding competition is most intense, thus offering an ecological explanation for earlier conflicting reports on siblicide in this species. *Key words:* *Crocuta*, hyenas, siblicide, sibling rivalry, siblings. [*Behav Ecol* 18:974–984 (2007)]

Whereas siblicidal aggression is a common phenomenon in many birds (Mock 1984; Drummond et al. 1986; Mock and Parker 1997; Loughhead and Anderson 1999; Drummond 2001), the topic has been less studied in mammals, with its occurrence reported only among young pigs (*Sus scrofa*: Fraser and Thompson 1991), humans (*Homo sapiens*: Anderson 1990; Gebo 2002), Arctic foxes (*Alopex lagopus*: Macpherson 1969), and spotted hyenas (*Crocuta crocuta*: Frank et al. 1991; Hofer and East 1997; Golla et al. 1999). Reports in the literature disagree regarding whether siblicide occurs at all in spotted hyenas, and if so, whether it is facultative or obligate. Siblicide is considered “obligate” or “habitual” when aggression within a brood or litter is almost always fatal to subordinates, as is true in a number of avian species (e.g., some eagles, herons, egrets, and boobies: reviewed in Mock and Parker 1997). By contrast, in “facultative” siblicide, siblings adjust the intensity of intrabrood aggression as its costs and benefits vary with current environmental conditions (Mock and Parker 1997). In this case, inclusive fitness benefits of permitting sibling survival generally outweigh direct fitness costs of resource competition with siblings except under environmental conditions so challenging that only siblicidal offspring have any chance of survival. Facultative siblicide is more common than obligate siblicide and is known to occur in a wide array of birds (Mock and Parker 1997).

Based on observations of a population of spotted hyenas in the Masai Mara National Reserve, Kenya, Frank et al. (1991)

inferred that habitual neonatal siblicide occurred within litters of twin spotted hyenas when the siblings were of the same sex. Although the denning habits of spotted hyenas preclude direct observation of siblicide in nature, their inference was based on 1) direct observation of intense fighting, occurring within minutes of birth, between highly precocial hyena siblings born in captivity; 2) highly skewed sex ratios in litters of twin hyenas in nature, with a statistical paucity of same-sex litters when cubs were first observed above ground at 2–6 weeks of age; and 3) similar patterns of wounding on captive hyena neonates subjected to the attacks of their dominant siblings and on some infant hyenas collected at natal dens in nature. Although the latter wounds were not viewed as lethal, it was suggested that dominant siblings could prevent their littermates from nursing and that infected wounds might contribute to the demise of food-deprived infants. In addition, 4) 43% of litters born to multiparous females in the field presented as singletons when first seen above ground rather than twins or triplets, whereas only 8% of comparable captive litters yielded singletons. This finding was compatible with the notion that litter reduction due to siblicide was occurring in the field but not in captivity.

By contrast, data documenting behavior and litter sex ratios among cubs born in other study populations suggested that siblicidal aggression in *Crocuta* is facultative rather than obligate. Neonatal fighting behavior in these populations was found to conform to predictions derived from facultative models of avian siblicide (Mock and Parker 1997). For example, Golla et al. (1999) found that rates of sibling aggression increase as rates of maternal provisioning decline, and Wachter et al. (2002) found no evidence at all of siblicide among *Crocuta* inhabiting the prey-rich Ngorongoro Crater. Furthermore,

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other workers observed offspring sex ratios consistent with the idea either that mothers can actively adjust offspring sex ratios (e.g., Rosenfeld and Roberts 2004) or that the probability of siblicide in this species depends on the sexes of the cubs involved (Hofer and East 1997; James and Hofer 1999). Similarly, studying the same *Crocuta* clan as the one originally observed by Frank et al. (1991), Smale et al. (1999) failed to observe skewed sex ratios in twin litters and found that proportions of male and female cubs varied with the number of adult females in the population (Holekamp and Smale 1995). They concluded that siblicide was "... far less common than previously supposed and that it occurs only when resources are insufficient to sustain 2 cubs (Smale et al. 1999, p. 545)"; therefore, they suggested that siblicide was facultative rather than habitual even in this study population.

The present report extends the period of observation of spotted hyenas in the Masai Mara through 2003. Having the same group of animals under continuous observation for more than 24 years provides an unusual opportunity for obtaining temporal perspective on covariation of ecology and behavior. In particular, the clan originally observed by Frank et al. (1991) from 1979 to 1987, fissioned in 1989–1990, thereby substantially reducing competitive pressures associated with food acquisition (Holekamp et al. 1993). If siblicide were facultative and occurred under conditions of high population density when food was relatively scarce, but not under conditions of food abundance, siblicide might be anticipated when the clan was large, but not after clan fission, when hyena population density was greatly reduced in the study area. The possibility that clan fission might affect rates of siblicide among spotted hyenas was also suggested by earlier workers (East and Hofer 1997; Golla et al. 1999; Wachter et al. 2002). One major goal of the present report was the analysis of neonatal siblicide, as inferred from the appearance of highly skewed sex ratios, before and after clan fission.

A second major goal of the present report was dependent on the use of ultrasonic examination of pregnant females. We emphasize that neonatal siblicide by spotted hyenas has never actually been viewed in nature, as wild females bear their litters in isolated natal dens (East et al. 1989) where they are often very difficult to observe even with remote-controlled cameras (White 2005). Spotted hyenas typically give birth to singletons or twins, and more rarely, to triplets. Female *Crocuta* only have 2 nipples, and triplets have never been reported to survive in the natural habitat. When infant hyenas are first glimpsed in the wild, after spending their first days of life out of view of observers, it is often not clear whether singletons are the surviving members of twin litters or whether twins are the surviving members of triplet litters (Frank et al. 1991). Moreover, if attrition has indeed occurred, simple observational methods provide no opportunity for distinguishing between the number of fetuses carried by the mother and the number of cubs first viewed by the researcher. Here, we used ultrasonography to overcome these problems.

Place et al. (2002) described how ultrasonography can be used in captivity and in the field to determine whether hyenas are pregnant, how many fetuses are present, and their approximate gestational age. If singleton litters in the field were the result of litter reduction, either during the late stages of gestation or early in postnatal life, then this would be revealed by comparing the results of ultrasonic examination of individual females with numbers of infants first observed at dens. Ultrasonography also facilitates anticipation of the date of birth and thus allows observers to direct attention to particular females and their offspring early in the postnatal period. Because ultrasonic tracking of pregnancy is a routine feature of husbandry in the captive hyena colony at the University of California at Berkeley, here we were able to compare rates

of litter reduction in nature, where siblicide might occur, with the captive situation, where siblicide cannot occur due to human intervention.

The data set from the Berkeley colony is now substantially larger than was the case when Frank et al. (1991) prepared their report. Field and captive populations can now be compared with respect to litter size, and sex ratios within twin litters, using much more extensive data sets than those available even to Smale et al. (1999). Although densities of hyenas and available prey varied considerably in the field during the periods under observation (Holekamp et al. 1993; Smale et al. 1999; Wahaj and Holekamp 2006), each captive female received a stable and adequate allotment of food throughout. If litter size or composition fluctuates with availability of food, then average litter size might be reduced relative to captivity in wild populations that confront prey shortages, and intra-population variation in litter composition might also be expected in the wild as socioecological conditions change (e.g., Holekamp and Smale 1995).

Use of ultrasonography allowed us to compare litter size in utero with litter size after parturition in both wild and captive hyenas, evaluate causes of litter reduction, and test predictions of habitual and facultative models of siblicide in the spotted hyena. These 2 models generate different suites of predictions regarding what we should observe when we examine litters in wild and captive populations of spotted hyenas. First, the habitual model predicts that 25% of offspring born should die shortly after birth in the wild (Frank et al. 1991). However, if siblicide is facultative, then litter reduction should be far less common than the 25% predicted by the habitual model. Second, if as suggested by Frank et al. (1991), twin litters result from habitual siblicide within triplet litters and singletons routinely result from siblicide within same-sex twin litters, this should become apparent by comparing litter sizes in utero with those after parturition. By contrast, the facultative model predicts that siblicide should only occur routinely when a mother produces more offspring than she can support, so we should be more likely to observe siblicide during periods of intensive feeding competition than when competition is relaxed. Furthermore, the facultative model predicts that, except under circumstances associated with food shortage, we should observe siblicide only when a female produces a larger number of cubs than her number of functional teats, such as when females give birth to triplet litters or when females with only one intact teat bear twins. Third, according to the habitual siblicide hypothesis, hyena litter sizes in captivity should be larger than in wild populations because researchers and/or captive mothers (because they have access to cubs) can intervene to prevent litter reduction during siblicidal interactions. The facultative model, however, predicts that litter sizes and frequencies of litter reductions should be similar between captive and well-fed wild populations in which prey abundance is consistently high.

Finally, each hypothesis makes contrasting predictions about offspring sex ratios and survivorship among cubs from litters of different sex compositions, and these predictions vary depending on whether or not outcomes of intralitter conflict are influenced by littermate sex. Frank et al. (1991) argued that siblicide was occurring in same-sex litters but not in mixed-sex litters; their habitual model of siblicide therefore predicts that litter reduction among same-sex twins should result in sex ratios in singleton litters that differ from chance expectations and that mixed-sex twin litters should be observed disproportionately more often than expected by chance relative to same-sex twin litters. By contrast, if intralitter conflict is independent of littermate sex, the facultative model predicts that, under conditions of food shortage severe enough to promote siblicide in same-sex litters, litter

reduction should also be observed in mixed-sex litters as well, and litter reduction should therefore result in offspring sex ratios and litter compositions that do not differ from chance expectations. On the other hand, if outcomes of facultative intralitter conflicts depend on the sexes of the combatants, as suggested by earlier workers (Hofer and East 1997; James and Hofer 1999), then offspring sex ratios under conditions of food shortage should be biased; the sex ratio in twin litters surviving siblicide should be skewed in the opposite direction to the sex ratio among singletons. That is, "the sex more likely to achieve siblicide should be overrepresented among singletons, whereas twin litters should contain more litters in which both cubs are of the sex less likely to achieve siblicide because both littermates would survive" (Hofer and East 1997, p. 309). Finally, the habitual model of siblicide predicts that cubs from mixed-sex litters should have higher survivorship than cubs from same-sex litters and that cubs whose littermates survive should have lower survivorship than cubs whose siblings die very young. The facultative model predicts difference in survivorship neither between cubs from same- and mixed-sex twin litters nor, except under very challenging ecological conditions, between cubs from reduced litters and those from litters in which both cubs survive.

METHODS

Field study

Field data were collected between July 1988 and May 2004 from 1 large social group, or clan, of spotted hyenas inhabiting the Talek region of the Masai Mara National Reserve. Hyena clans contain multiple adult males and several matrilineal groups of adult female kin with their offspring. Members of both sexes are capable of breeding at approximately 24 months of age, although most individuals delay first reproduction for several more months (Matthews 1939; Holekamp et al. 1996). Males disperse from their natal groups after puberty (Boydston et al. 2005), whereas females are usually philopatric (Frank 1986a; Henschel and Skinner 1987; Mills 1990; Smale et al. 1997). Adults can be ranked in a strict linear dominance hierarchy within the clan, and female *Crocuta* are dominant to all immigrant males (Kruuk 1972). Rank relations remain stable for extended periods and across a variety of contexts (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986b; Smale et al. 1993). An individual's position in the group's hierarchy strongly determines its priority of access to food (Kruuk 1972; Frank 1986b).

The Talek clan defended a group territory of approximately 65 km² (Boydston et al. 2001) and usually contained 50–70 hyenas. Talek hyenas were monitored daily at least 23 days per month in 1988–2004 except during April 1991, when observers were present on only 14 days. All adult hyenas were identified by their unique spot patterns, and young cubs that had not yet developed spots were identified by unique scarring, bald patches, ear notches, size differences, molt patterns, or a combination of these features. Sex was determined from the dimorphic glans morphology of the erect phallus (Frank et al. 1990). By 2 months of age, the glans of the male's phallus assume a distinctly different shape from that of the female (Drea et al. 1998). Cubs regularly develop erections during greeting ceremonies, which occur virtually every time a new hyena arrives at the den (East et al. 1993). Here, young hyenas were sexed repeatedly by multiple experienced observers, and sex could be assigned with complete certainty by the time cubs were 2–3 months old, although some cubs died before they could be sexed.

Spotted hyenas breed throughout the year with a gestation period of 110 days (Schneider 1926; Kruuk 1972). We estimated cub birth dates (to ± 7 days) by using their pelage, size,

and other aspects of their appearance and behavior when cubs were first observed above ground (Holekamp et al. 1996), and this date was assigned as the "date first seen" for each cub, although its actual date of birth might have been several weeks earlier. A disappearance date for each cub was assigned as the date on which it was last seen if it did not survive to adulthood; hyenas disappearing at ages younger than 24 months were assumed to have died.

Mother-offspring relations were established on the basis of regular nursing associations and molecular genetic analysis (Van Horn et al. 2004). Females that had given birth at least once (multiparous females) could be distinguished from nulliparous females (who had never previously given birth) based on the presence of pink scar tissue on the posterior surface of the erect phallus (Frank and Glickman 1994). This scarring results from tearing of the phallus at first parturition, and it remains visible throughout the lifetime of the animal. Social ranks were determined based on wins and losses in dyadic agonistic interactions. Outcomes of these interactions were organized into a matrix from which each female hyena could be assigned a social rank in the clan's dominance hierarchy (Martin and Bateson 1988).

Because very little is known about the length or timing of the estrous cycle in female spotted hyenas and because pregnancy cannot be identified by observation of the female's physical state, we relied on the abrupt cessation of male courtship behavior to provide behavioral indicators as to when females became pregnant. That is, Talek females are usually followed by an entourage of adult males for some weeks before estrus, but this entourage abruptly disappears when a female conceives (Szykman et al. 2007). Each pregnant female was immobilized with an intramuscular injection of Telazol (6.5 mg/kg) delivered from a CO₂-powered rifle in a lightweight plastic syringe. When anesthetized, females underwent a transabdominal ultrasound using a real-time HITACHI EUB-405 scanner with a 5-MHz curved-array transducer. Animals were scanned while lying on their backs after we removed the fur from the lower abdomen with electric clippers. Ultrasound data were collected in the field from August 1999 through May 2004. Multiple ultrasounds within a single pregnancy were not possible in wild hyenas due to both the difficulty of darting any particular female repeatedly within a narrow window of time and our reluctance to stress pregnant females with multiple dartings.

Fetuses and their heartbeats were identified using methods described by Place et al. (2002). Briefly, using the bladder as a landmark, we located the bifurcation of the uterine body and followed each of the 2 horns anteriorly to search for the presence of fetuses. Fetuses were recognized during early pregnancy by the presence of a gestational sac within a thickened endometrial cavity (Figure 1a) together with fetal cardiac activity, which can be clearly discerned as a rapid fluttering within the fetus as early as 24 days after mating. Thirty days after mating, development of spine, cranium, and long bones begin, and skeletal elements can be easily discerned on sonographic images (Figure 1b). Circumference of the gestational sac (in young fetuses) and fetal femur lengths (in older fetuses) were measured to estimate gestational age (Place et al. 2002). All immobilized females were radio collared (Telonics Inc., Mesa, AZ) and tracked daily to facilitate discovery and observation of neonatal cubs. Monitoring of each pregnant female was intensified during a narrow window of time around her expected date of parturition. Two different datasets documenting litter size in wild female hyenas are reported here: 1) litter size in the subset of female hyenas that were examined via ultrasonography and 2) litter size in all female hyenas, regardless of whether or not their litters were observed in utero with ultrasound.



Figure 1
 Sonographic images of (a) early pregnancy (gestational age here was 43 days) indicated by the presence of a gestational sac and thickened endometrial cavity. The gray donut-shaped outer circle is the endometrial wall of the uterine horn and the dark hypochoic center represents the amniotic fluid and the developing fetus. (b) late pregnancy (gestational age here was 97 days) indicated by skeletal development. The vertebrae (arrow) and ribs of the fetus are indicated by the hyperechoic white bands across the screen.

Detailed demographic data from the Talek hyena clan were collected by Frank et al. (1991) from 1979 to 1987 and by us from 1988 to 2003. These data were used to generate survivorship tables during the first 2 years of life for individuals in 1) litters of varying size, 2) twin litters of varying sex compositions, and 3) twin litters in which 1 sibling died before 3 months of age compared with those in which both siblings lived at least 3 months. Survivorship data were not censored. In addition, we used demographic data to determine whether sex ratios varied in twin litters born to multiparous females during 3 consecutive periods, each characterized by different conditions of population density and feeding competition (Holekamp et al. 1993). Specifically, size of the Talek clan was reduced by approximately 30% during a clan fission event that occurred in 1989–1990 (Holekamp et al. 1993). Therefore, we compared twin sex ratios among 1) the period prior to clan fission (1979–1987), 2) the period during which clan fission took place (1988–1990), and 3) the period after fission (1991–2003).

Captive study

Pregnant spotted hyenas were studied at the Field Station for the Study of Behavior, Ecology, and Reproduction at the

University of California, Berkeley, from October 1987 through March 2003. A description of the Berkeley hyena colony is presented in Frank et al. (1989), and captive husbandry is described in Berger et al. (1992). Long-term goals of the Berkeley hyena project include experimental treatments of pregnant spotted hyenas with antiandrogens and aromatase inhibitors to study development of the external genitalia. Here, however, only untreated females and females on which amniocentesis had been performed were included in our data set; litter size did not differ significantly between these 2 groups of females (5 amniocentesis females 1.60 ± 0.51 ; 22 untreated females 1.41 ± 0.18 ; $t = -0.425$, degrees of freedom [df] = 25, $P = 0.647$). Together females in these groups were referred to here as “untreated” females. Pregnancies in captivity were monitored by transabdominal ultrasonography using a real-time Aloka SSD-500 scanner with a 5-MHz curved-array transducer. Prior to each examination, animals were immobilized with an intramuscular injection of Ketaset (4–6 mg/kg) and xylazine (1 mg/kg) administered via blowdart. Detection of fetuses was as in our field study, although captive hyenas often underwent multiple (mean \pm standard error of the mean = 1.96 ± 0.15) ultrasounds per pregnancy, whereas wild hyenas underwent only one. When more than one ultrasound was performed during a particular captive pregnancy but the number of fetuses observed varied among examinations, the ultrasound showing the greatest number of fetuses was used in calculating litter size in utero. Exact dates on which conception occurred were often known for captives because mating usually occurred in the presence of human observers. Staff members are almost always present during captive births to aid or intervene in the event of birth complications. Therefore, in contrast to the situation in the field study, neonatal litter sizes reported for captive hyenas were true litter sizes at birth as there was no time or opportunity for mortality to reduce litters after parturition. Captive mothers give birth in pens (2×2 m) with straw bedding. Mothers are accessible to the infants 24 h a day, which is not the case in nature. Although severe fighting between sibling neonates has been observed in captivity, siblicide has never been observed there because cubs are always separated before they can inflict serious injury on one another.

Terminology

The number of fetuses observed “in utero” refers to the number of fetuses detected via ultrasonography during pregnancy in both captive and wild hyenas. The term “neonatal” refers to the postpartum number of neonates in captivity, but in the wild, this term refers to the number of cubs present when a litter was first seen above ground. In both cases, neonatal litter size indicates the number of cubs observed alive as soon after parturition as possible. Resorptions or miscarriages of fetuses were detected when either a second ultrasound during a particular pregnancy confirmed a reduction in the number of fetuses in utero (captive study only) or a second or third trimester fetus lacked a heartbeat (both captive and wild studies). Stillbirths could only be positively identified in captive hyenas because sources of early mortality are difficult to identify in the field. In both wild and captive studies, “litter reduction” was defined as a decrease in litter size from the number of fetuses observed in utero to the number of living “neonatal” cubs observed. The term “litter composition” refers throughout to whether individual litters were comprised of singletons, twins, or triplets.

Data analysis

Results are reported here for both primiparous and multiparous females. However, to make our results comparable with

those of Frank et al. (1991), in some analyses, we restricted our data set to multiparous females. Sample sizes of litters observed in utero and those observed as neonates occasionally differed in the wild because some ultrasounded females kept their litters so well hidden that we never had opportunities to observe these cubs as neonates. In addition, some captive litters were born to females that were never ultrasounded. Independent sample *t*-tests were used to compare litter sizes between captive and wild populations and between primiparous and multiparous females. Chi-square tests were used to compare litter compositions, and these were adjusted for small sample sizes as necessary using Yates' correction. Litter reductions were assessed by matched comparison of number of fetuses observed in utero with the number of cubs observed alive at the end of the same pregnancy either at parturition (captive) or when cubs were first observed above ground (field study: mean = 42.9 ± 6.8 days of age, $n = 27$ cubs from 15 litters). For these matched comparisons, we used dependent sample *t*-tests. We used a Spearman's Rank correlation to assess the relationship between mean litter sizes born to females in the wild and the social ranks of those females. A one-way analysis of variance was used to determine whether litter size varied with age at which litters were first seen above ground in the wild. Binomial tests were used to determine whether observed sex ratios differed from those based on chance expectations. In survivorship analyses, proportions of individuals surviving were compared among multiple groups using a multiple sample test in which a score was assigned to each survival time (Mantel 1967) and then a Chi-square value was computed based on the sum of these scores for each group. Cox's *F* tests were used in survivorship analyses to compare survival between only 2 groups. Despite small sample sizes and low statistical power, differences between groups were considered significant when $P \leq 0.05$. Throughout the paper, means (\pm standard error) are reported. All statistical tests were 2 tailed and performed using Statistica 6.1 software.

RESULTS

Sample sizes

Field study

Twenty-two females were immobilized and ultrasounded during pregnancy in the wild, including 2 primiparous and 20 multiparous females. For 18 of these 22 females, we were able to observe their litters above ground within the first several weeks of life (mean = 41.3 ± 3.0 days), but 4 ultrasounded females maintained their litters for extended periods in dense thickets or otherwise made it impossible for us to observe their cubs as neonates. Of the 18 observable females, 2 were primiparous and 16 were multiparous. In the larger sample of all wild females for which litter size was known (including both those who were ultrasounded and those who were not), we had 241 litters, of which 44 were from primiparous females and 192 from multiparous females. On average, cubs from these 241 litters were first seen at 38.7 ± 2.1 days of age. For mothers of 5 of the 241 litters, parity was unknown.

Captive study

Twenty-seven untreated females were immobilized and ultrasounded during pregnancy, including 11 primiparous and 16 multiparous captive females. All but 4 of these were ultrasounded more than once per pregnancy. Thirty-two litters were born in the captive colony, but mothers of 5 of these litters were not ultrasounded prior to birth. Of these 32 captive litters, 15 were born to primiparous females and 17 to multiparous females. The paucity of litters born to multiparous females in captivity was due to their experimental drug

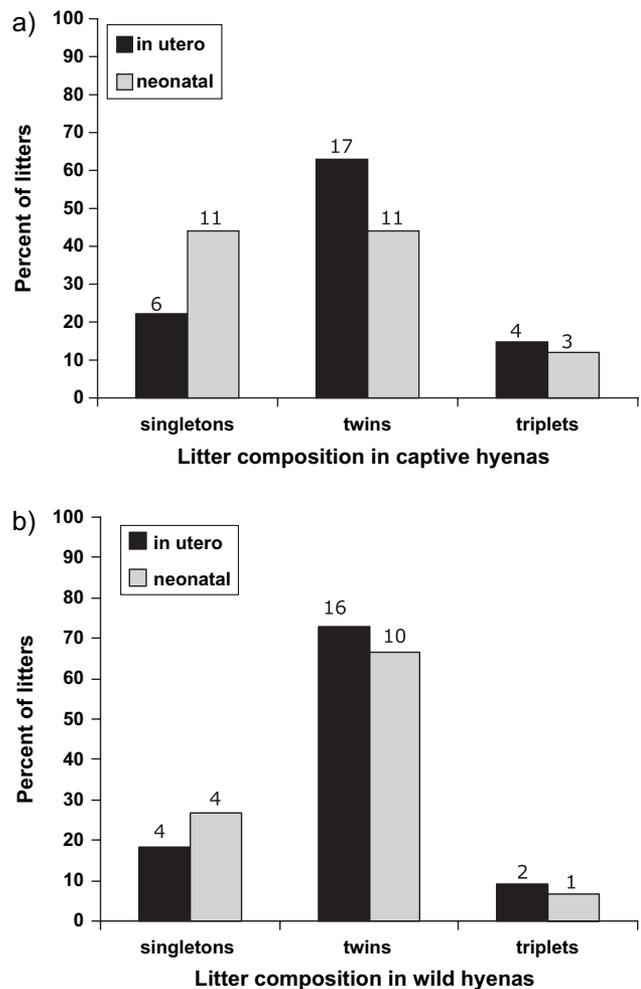


Figure 2

Percentage of all litters that contained 1, 2, or 3 cubs when observed in utero and again as neonates in (a) captive and (b) wild hyenas examined during pregnancy with ultrasonography. Numbers above bars represent numbers of litters of each type.

treatments for the study of genital development in their offspring.

Litter composition and litter size

Litter composition in utero did neither differ overall between captive and wild hyenas (Yates' $\chi^2 = 0.265$, $df = 2$, $P > 0.8$) nor differ when we compared litter composition in utero between captive and wild hyenas that had been examined during pregnancy with ultrasonography (Figure 2; Yates' $\chi^2 = 0.884$, $df = 2$, $P > 0.5$). When we compared the ratios of singleton:twins:triplet litters at birth between untreated captive females (litter composition at birth was 11:11:3), and our larger sample of all wild hyenas (litter composition at emergence was 123:126:2), we found a significant difference between these litter compositions (Yates' $\chi^2 = 11.78$, $df = 2$, $P < 0.01$). However, when triplet litters were eliminated from the neonatal data set, we found no difference between captive and wild hyenas with respect to the proportions of singletons and twin litters observed (Yates' $\chi^2 = 0.03$, $df = 1$, $P > 0.98$). These data suggest that perhaps captive hyenas have disproportionately large numbers of triplet litters compared with wild hyenas, but triplets are rare in both environments. We observed no significant difference in composition between litters observed

in utero and those observed again later as neonates in either captive (Figure 2a; Yates' $\chi^2 = 1.84$, $df = 2$, $P > 0.30$) or wild hyenas (Figure 2b; Yates' $\chi^2 = 0.39$, $df = 2$, $P > 0.80$).

Considering both primiparous and multiparous females together that were examined via ultrasonography, we found no difference between captive and wild hyenas in mean size of litters in utero (captive: $n = 27$, mean = 1.93 ± 0.12 ; wild: $n = 22$, mean = 1.91 ± 0.11 ; $t = 0.102$, $P = 0.92$) or in mean size of neonatal litters (captive: $n = 32$, mean = 1.31 ± 0.16 ; wild: $n = 18$, mean = 1.50 ± 0.20 ; $t = -0.702$, $P = 0.49$). In order to fairly compare neonatal litter size between captive and wild hyenas that were never examined via ultrasonography, we limited the data set of captive hyenas to only those 25 cases in which litter size was greater than zero. That is, we excluded cases in which ultrasonography indicated occurrence of stillbirths or resorptions such that no cubs were born alive to captive females because we were unable to perform multiple ultrasounds within pregnancies in the wild and stillbirths cannot be observed there. Here again mean neonatal litter size in captive females ($n = 25$ litters, mean = 1.68 ± 0.14) did neither differ significantly from that observed in the larger sample of all wild females ($n = 241$ litters, mean = 1.52 ± 0.03 ; $t = 1.34$, $P = 0.18$) nor differ between wild females that were ultrasounded ($n = 18$ litters, mean = 1.50 ± 0.20) and wild females that were not ultrasounded ($n = 241$ litters, mean = 1.52 ± 0.03 ; $t = 0.09$, $P = 0.92$). Finally, because the age after birth at which cubs were first observed differed between captive and wild hyenas, we compared mean neonatal litter size born to the 25 captive hyenas with that observed in a subset containing the 25 wild hyenas whose cubs were seen soonest after birth (i.e., the earliest dates first seen), but we found no difference in litter size; mean age first seen in the wild for this subset was 4.12 ± 0.52 days, and mean litter size for both wild and captive populations was 1.68 ($t = 0.0$, $P = 1.0$). Thus, aside from a greater tendency of captive females to produce triplets, we detected no differences between wild and captive hyenas with respect to either mean litter size or composition.

Litter composition and litter size among multiparous females

We next restricted our analyses to multiparous females to compare our findings with those reported earlier by Frank et al. (1991), but we found no difference in litter composition between captive and wild hyenas either in utero (captive litter composition = 2:11:3, wild litter composition = 2:16:2; Yates' $\chi^2 = 0.185$, $df = 2$, $P > 0.9$) or among neonates (captive litter composition = 4:8:3, wild litter composition = 2:10:1; Yates' $\chi^2 = 0.60$, $df = 2$, $P > 0.7$). Here again litter composition differed between captives and our larger sample of all wild hyenas (captive litter composition = 4:8:3, wild litter composition = 87:103:2; Yates' $\chi^2 = 16.93$, $df = 1$, $P < 0.001$), but this difference vanished when triplets were excluded from the data set (Yates' $\chi^2 = 0.29$, $df = 2$, $P > 0.8$). We found no difference in litter composition between uterine and neonatal observations of multiparous females either in captivity (Yates' $\chi^2 = 0.57$, $df = 2$, $P > 0.70$) or the wild (Yates' $\chi^2 = 0.31$, $df = 2$, $P > 0.80$).

Among ultrasounded multiparous females, we also failed to find any significant difference between captive and wild hyenas in mean litter sizes observed either in utero (captive: $n = 16$, mean = 2.06 ± 0.13 ; wild: $n = 20$, mean = 2.00 ± 0.10 ; $t = 0.36$, $P = 0.72$) or as neonates (captive: $n = 17$, mean = 1.61 ± 0.23 ; wild: $n = 16$, mean = 1.50 ± 0.22 ; $t = 0.45$, $P = 0.65$). Thus, our results here differed from those obtained earlier by Frank et al. (1991). However, in accord with the results obtained by those earlier workers, when we compared multiparous captive females with our larger sample of wild

Table 1

Neonatal litter sizes born to multiparous females that were directly observed but not examined with ultrasound in this study compared with those observed earlier by Frank et al. (1991)

Population	Mean litter size \pm standard error	N
Frank et al. (1991)—captive	2.08 ± 0.14	13
Frank et al. (1991)—field	1.58 ± 0.05	99
This study—captive	1.93 ± 0.18	15
This study—field	1.56 ± 0.04	192

"N" indicates the number of litters born.

multiparous females that were not ultrasounded, we found neonatal litter size among multiparous females to be significantly larger in captivity than in the wild (Table 1; $t = -2.63$, $P = 0.009$).

Litter reduction

Significantly more fetuses were observed in utero than as neonates in captivity (Figure 3; $t = 2.8$, $n = 27$, $P = 0.01$). Specifically, 9 of 27 litters were reduced in captive females. Among captive multiparous females, 5 of 16 litters were reduced, and here again we observed significantly more fetuses in utero than after parturition ($t = 2.41$, $n = 16$ pairs, $P = 0.03$). Thus, nearly one-third of captive litters were reduced, and none of those reductions were due to siblicide.

Among wild multiparous females, 5 of 18 litters were reduced, and more fetuses were observed than neonates within pregnancies ($t = 2.41$, $n = 16$ pairs, $P = 0.03$). Thus, as in captivity, we found that significantly more fetuses were observed in utero than as neonates in the wild (Figure 3; $t = 2.36$, $n = 18$, $P = 0.03$). Although siblicide is not permitted in captivity, the proportion of litters in which reduction occurred did not differ between captive and wild hyenas (Yates' $\chi^2 = 0.004$, $df = 1$, $P > 0.95$). Because siblicide could not

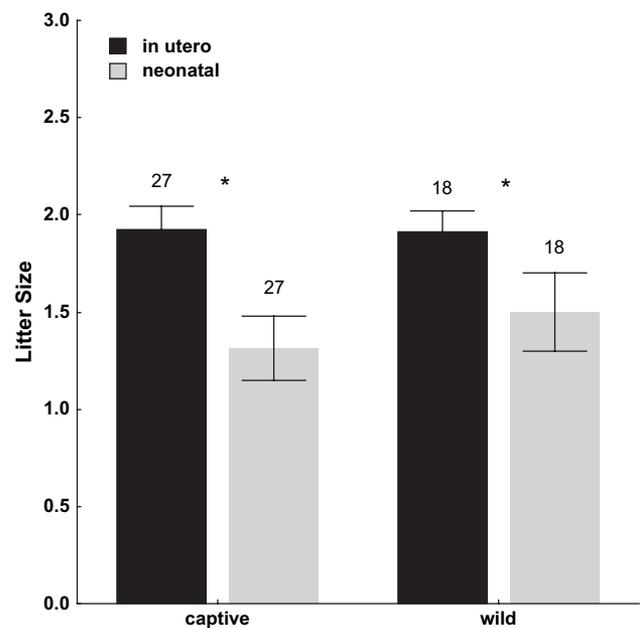


Figure 3

Matched pairs comparisons within pregnancies of litter size before and after birth in captive and wild hyena populations. Numbers above bars represent numbers of pregnant females examined via ultrasonography. Significant differences are indicated with asterisks.

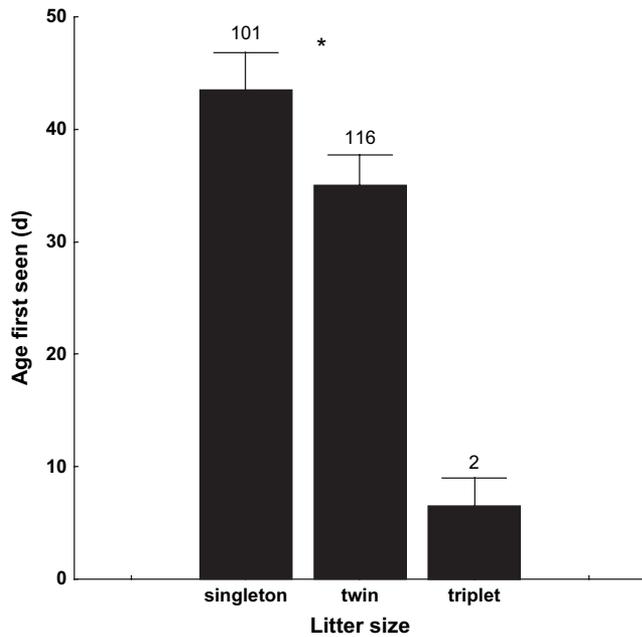


Figure 4

Mean age at which cubs were observed above ground in wild litters for which we had an opportunity to see cubs. Numbers above bars represent litters in each group. Significant differences are noted with an asterisk.

account in the wild for reductions in either litters observed in utero as singletons or litters from which all cubs disappeared, only 2 of the 5 cases of litter reduction we observed in ultrasounded wild hyenas possibly could have been attributable to siblicide. In both these cases, twin litters seen in utero during the last month of gestation appeared above ground as singletons.

Causes of litter reduction

In captivity, 80% of litter reductions were due to stillbirths and 20% were due to resorptions. Of 32 captive pregnancies, 9 (28%) produced at least one stillborn cub, and fetal resorptions occurred in 2 (6.3%) of the 32 pregnancies.

In the wild, litter reductions might be due to stillbirths, resorptions, predation, disease, maternal abandonment, infanticide, or siblicide. Although it was impossible for us to detect stillbirths in nature, we did observe one fetus being resorbed in a wild female. There was substantial variation in the age at which cubs were first observed above ground, and the longer it took us to see wild litters, the smaller the litters tended to be (Figure 4; $F_{2,216} = 3.18$, $P = 0.04$). On average, singleton litters were first observed above ground substantially later than twins (43 singleton litters at 43.5 ± 3.3 days vs. 34 twin litters at 35.1 ± 2.7 days; LSD post hoc test, $P = 0.04$) or triplets (6.5 ± 2.5 days), though the small sample of 2 triplet litters did not differ significantly in age at first sighting from smaller litters.

In our large sample of wild females, we observed 32 cases of litter reduction from twin to singleton litters in 102 twin litters, and half of these 32 cases occurred before cubs were 3 months old. Although it is possible that all these 32 litter reductions were attributable to other causes, at most, 8 of these reductions might conceivably have been due to siblicide. Specifically, each of 2 adult females in our study population sustained severe damage to one of her teats during fights, leaving only one functional teat intact. Each time either of these females produced twins (3 times for each female), the

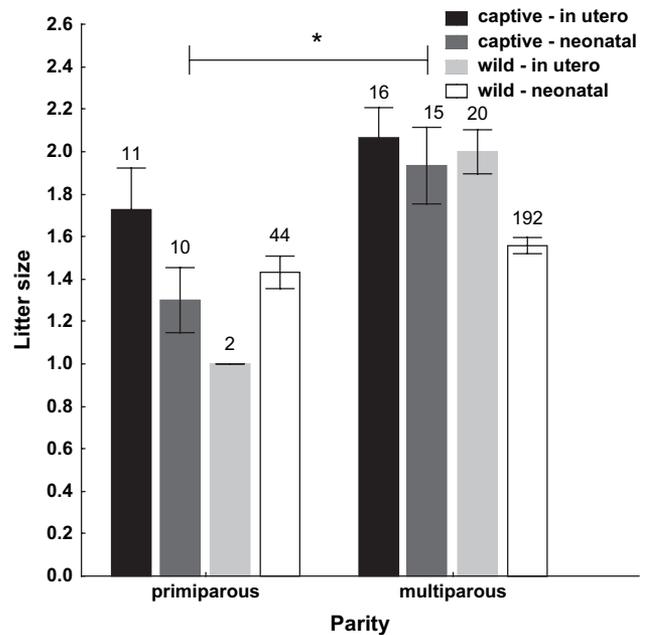


Figure 5

Mean litter sizes before and after birth compared between primiparous and multiparous hyenas in captivity and in the wild. Neonatal litter sizes are reported for both ultrasounded and nonultrasounded hyenas. Numbers above bars represent litters in each group. Significant differences are indicated with asterisks.

subordinate cub was viciously attacked by the dominant whenever it attempted to nurse. These subordinate cubs exhibited many wounds and scars and grew far more slowly than their dominant siblings. Subordinate cubs in 2 of the 8 litters were eventually separated from their siblings by their mothers, but they were already battered and emaciated at this point, and like all other subordinate cubs in this sample, they inevitably disappeared within the first few months of life (mean age at death for the 6 cubs from twin litters was 118.4 ± 39.8 days). Similarly, in both triplet litters born in the wild, the third-ranking cub disappeared at a very young age (at 4 and 29 days after birth, respectively) after being severely attacked by both its dominant littermates.

Effects of maternal parity and social rank

In captivity, litter size in utero did not vary significantly with parity ($t = 1.50$, $P = 0.15$), but neonatal litter sizes were larger among multiparous females than among primiparous females (Figure 5; $t = 2.48$, $P = 0.02$). Among primiparous females in captivity, 7 of 15 pregnancies produced stillborn cubs. Among captive multiparous females, 2 stillbirths and 2 resorptions were observed in 17 pregnancies. Primiparous females tended to have more stillbirths and resorptions than multiparous females, but this difference was not significant among captives (Yates' $\chi^2 = 1.0$, $df = 1$, $P > 0.7$).

Only 2 primiparous females were ultrasounded in the wild and each contained only one fetus in utero, whereas mean litter size in utero for multiparous females was 2.0 ± 0.10 ($n = 20$ females). Among ultrasounded wild hyenas, the 2 primiparous females had neonatal litter sizes of only one cub, whereas mean neonatal litter size among multiparous females was 1.92 ± 0.14 ($n = 13$ females). Because only 2 primiparous females were ultrasounded in the wild, we could not use statistical tests to compare mean litter size in utero between primiparous females in the wild and captivity. However, among our larger sample of 236 wild hyenas, we observed

Table 2
Sex ratios among litters born to wild and captive hyenas

Population	Number of males	Number of females	N	P (binomial test)
Wild (overall)	140	128	268	0.25
Captive (overall)	21	20	41	0.50
Wild (in singleton litters)	38	43	81	0.66
Captive (in singleton litters)	5	4	9	0.50
Wild (in twin litters)	89	97	186	0.61
Captive (in twin litters)	11	13	24	0.42

no significant difference in neonatal litter sizes between primiparous and multiparous females (Figure 5; $t = 1.46$, $P = 0.147$). Mean litter size did not vary with maternal social rank in our large sample of wild hyenas ($F_{23,219} = 0.65$, Spearman $r_s = 0.033$, $n = 24$ ranks, $P = 0.875$).

Sex ratios

We observed no significant difference between proportions of male and female cubs produced in all litters considered together, in singletons considered alone, or in twin litters considered alone among either captive or wild hyenas (Table 2). The ratio of all-male:mixed-sex:all-female twin litters born in captivity was 3:5:4, and this did not differ from chance expectations (Yates' $\chi^2 = 0.21$, $df = 1$, $P > 0.5$). Similarly, sex ratios in twin litters born to wild hyenas did differ from neither chance expectations (Figure 6a; Yates' $\chi^2 = 0.95$, $df = 1$, $P > 0.5$) nor the ratios observed in captive hyenas (Yates' $\chi^2 = 0.55$, $df = 2$, $P > 0.7$).

Sex ratios in 112 twin litters born to multiparous wild females between 1979 and 2003 varied significantly before, during, and after clan fission (Figure 6b; Yates' $\chi^2 = 8.58$, $df = 4$, $P < 0.03$). Whereas only 2 of 19 twin litters were same sex before fission (both all male), as soon as hyena population density began to decline during the period of clan fission, both all-male and all-female twin litters began to appear. Twin litter sex ratios in the period during which fission occurred did not differ significantly either from those during the pre-fission period (Yates' $\chi^2 = 0.216$, $P > 0.8$) or from those during the postfission period (Yates' $\chi^2 = 0.520$, $P > 0.7$). However, comparing only the pre- and post-fission periods, we observed a significant difference (Figure 6b; Yates' $\chi^2 = 7.20$, $df = 2$, $P = 0.006$). Furthermore, whereas observed twin litter composition differed significantly from binomial expectation in the wild before fission (Yates' $\chi^2 = 9.20$, $df = 2$, $P = 0.01$), no difference from binomial expectation was observed after fission (Yates' $\chi^2 = 1.22$, $df = 2$, $P = 0.54$).

Survivorship among wild hyena cubs

Among wild hyenas, we observed significant differences in the proportion of individuals surviving to 24 months of age among 112 singleton cubs, 208 cubs from twin litters, and 6 cubs from triplet litters (Figure 7a; $\chi^2 = 13.34$, $df = 3$, $P = 0.001$). Cubs from twin litters experienced higher survivorship than those from singleton (Cox's $F_{224,416} = 1.29$, $P = 0.01$) or triplet litters (Cox's $F_{12,416} = 7.33$, $P < 0.001$), and cubs born as singletons also survived better than did cubs from triplet litters (Cox's $F_{224,12} = 4.10$, $P = 0.009$). Of 146 cubs from twin litters in which the sex of both siblings could be determined, we found no significant variation in survivorship among individuals from all-female, mixed-sex, and all-male litters (Figure 7b;

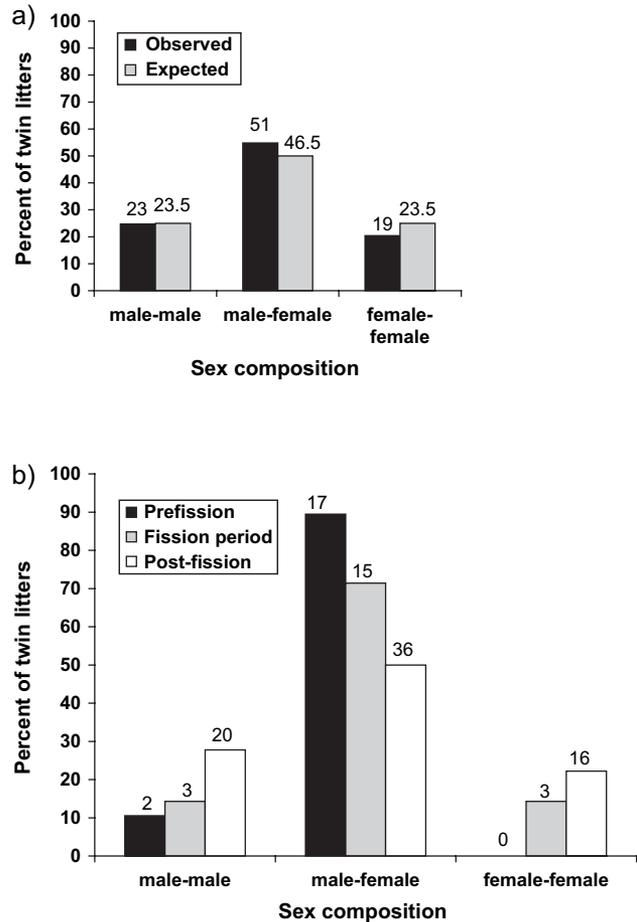


Figure 6
Percentage of wild twin litters of each type born to (a) both multiparous and primiparous females in the current field study compared with expectations based on a binomial distribution and (b) multiparous females from periods before, during, and after clan fission. Data from the pre-fission period are from Frank et al. (1991). Sample sizes above bars represent number of litters of each type observed.

$n = 26$ cubs from all-female litters, 84 from mixed-sex litters, 36 from all-male litters; $\chi^2 = 1.59$, $df = 3$, $P = 0.45$). Within twin litters, individuals experienced better survivorship when their siblings survived to at least 3 months of age ($n = 142$ individuals) than when their siblings disappeared before 3 months of age ($n = 32$ individuals; Figure 7c; Cox's $F_{284,64} = 2.11$, $P < 0.001$). These data strongly suggest habitual siblicide would be maladaptive in these animals.

DISCUSSION

Several results reported here are inconsistent with predictions of the habitual siblicide hypothesis. First, possible siblicide in the wild could account, at most, for reduction of only 2 of 18 (11.1%) ultrasounded litters. Considering that some wild litters may also be reduced by stillbirths, miscarriages, resorptions, and a number of postnatal mortality sources, it seems unlikely to us that this rate of litter reduction represents habitual siblicide. Second, the frequency of litter reduction in captivity, where siblicide could not occur, did not differ from that in our wild study population. Third, habitual siblicide did not reduce triplets to twins before these litters emerged above ground, as all members of both wild triplet litters observed here were seen above ground before they died. Fourth, the

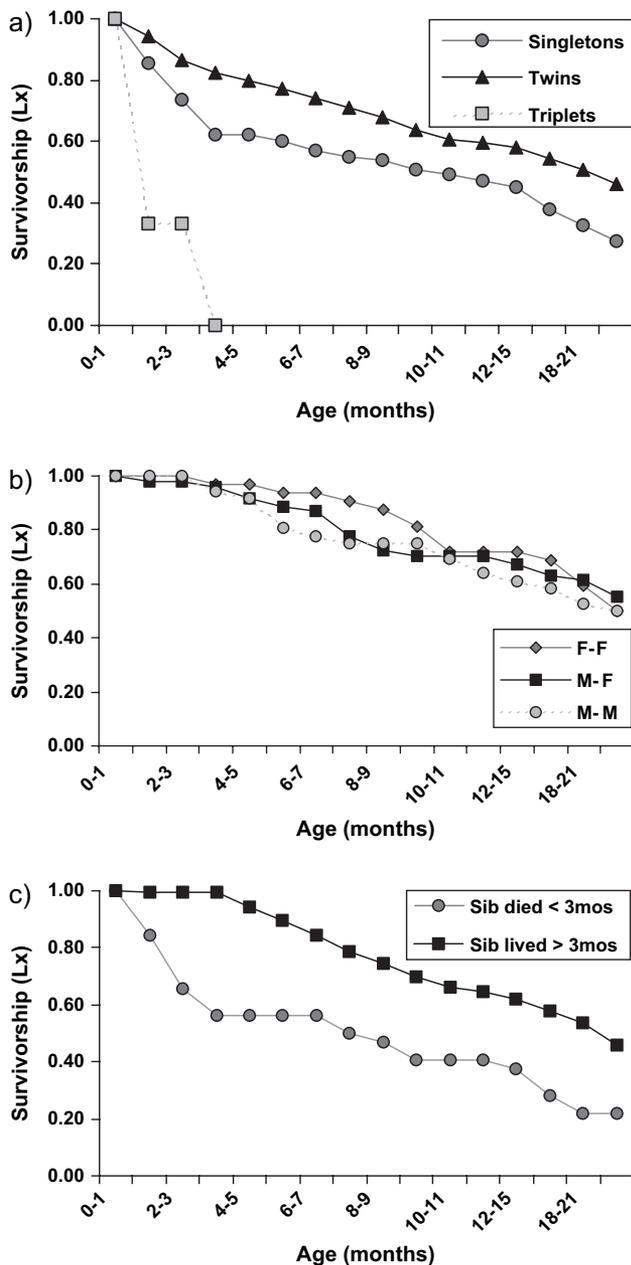


Figure 7
Survivorship to 24 months of (a) 112 singleton cubs, 208 cubs from twin litters, and 6 cubs from triplet litters; (b) 26 cubs from all-female litters, 84 cubs from mixed-sex litters, and 36 cubs from all-male litters; and (c) 142 individuals from twin litters whose littermate lived longer than 3 months and 32 individuals whose twin died before 3 months of age.

lack of sex bias in compositions of twin or singleton litters in either the wild or captivity indicates that litter reductions here were not occurring exclusively or predominantly within same-sex litters in the wild during our recent (after fission) study period. In addition, probability of survival to adulthood among members of wild twin litters did not vary with sex composition of these litters. Finally, habitual siblicide could not possibly be adaptive in spotted hyenas because, not only did cubs from twin litters experience better survivorship than those from singleton or triplet litters, but also twins whose siblings died early experienced significantly poorer survivorship than did those whose siblings survived for at least 3

months. Thus, our results fail to support the habitual siblicide hypothesis.

In both wild and captive study populations, larger numbers of cubs were observed in utero than after parturition. Litter reduction occurred during roughly one-third of all pregnancies in both environments, and captive observations helped shed light on the causes of these litter reductions. First, litter reduction can clearly occur prenatally through resorption of fetuses, as we observed this in both wild and captive females. Litter reduction can also occur during the parturition process and result in stillbirths. Female spotted hyenas are unique among mammals in having external genitalia that are highly masculinized (Matthews 1939; Neaves et al. 1980). Because the female hyena gives birth through her peniform clitoris, complications during the birth process can result in fetal mortality (Frank and Glickman 1994; Frank et al. 1995). In addition, female *Crocuta* possess abnormally long birth canals and their fetuses have short umbilical cords, so infants not born immediately after placental detachment will die of anoxia in the birth canal (Frank et al. 1995). Because captive females get less exercise than wild animals and near-term fetuses may also be slightly larger in captivity, birth complications might occur more frequently among captive than wild females (Kranendonk et al. 1982; Frank and Glickman 1994; Frank et al. 1995). Thus, litter reductions might conceivably be equalized between captive and wild populations by more frequent operation of post-natal mortality sources in the wild and relatively high rates of dystocia among captives (Frank and Glickman 1994).

Whereas in captivity only resorption and stillbirth can account for litter reduction, litter reduction in the wild might also be due to predation, disease, maternal abandonment, infanticide, or siblicide. Our observation that the average number of cubs per litter tended to decline in nature with time since parturition suggests that these other mortality sources probably contribute to early postnatal litter reduction in the wild. Between 1979 and 1988, Frank et al. (1991, p. 703) observed 4 cases of early litter reduction in the field from twins to singletons. Between 1988 and 2003, we observed 32 cases in which cubs originally seen as twins were reduced to singletons within the first 3 months of life. Both these 32 cases and the 4 observed by Frank et al. (1991) might have involved siblicide, but they also might have involved other mortality sources.

Several lines of evidence from this and earlier studies are consistent with the notion that facultative siblicide occurs among free-living spotted hyenas. One member of each triplet litter we observed in the field died very young, as did one member of each twin litter born to females with only one functional teat. In each of these cases, the cub that succumbed became badly scarred and emaciated before it vanished, which strongly suggests siblicide as the mortality source (Frank et al. 1991; Hofer and East 1997). Golla et al. (1999) found that rates of aggression between littermates increased as maternal rank and cub growth rates decreased, suggesting that success in feeding competition among adult females affected aggression rates among their offspring. Similarly, Smale et al. (1995) observed that rates of aggression within twin litters increased as maternal rank decreased. Smale et al. (1999) found that offspring sex ratios in Talek varied as environmental conditions changed over a 10-year study period but that mean litter size remained constant, a result consistent with the facultative model of siblicide. Wachter et al. (2002) found no evidence that siblicide occurs in the prey-rich habitat of Ngorongoro Crater, and Wahaj and Holekamp (2006) observed that sibling aggression increased as local prey abundance declined in the Masai Mara. Thus, intensity of sibling fighting is strongly affected in multiple populations by both local prey abundance and priority of access to food, and the

facultative model predicts that intensity of sibling aggression and sibling mortality should covary.

Hofer and East (1997) inferred that facultative siblicide might be taking place in all-female twin litters in Serengeti based on occurrence of significantly fewer all-female litters than expected by chance, and a female bias within singleton litters. Thus, in addition to supporting a facultative model of siblicide, the observations of Hofer and East (1997) are in accord with the notion originally proposed by Frank et al. (1991) and later modeled by James and Hofer (1999) that siblicide may be sex biased in this species. Frank et al. (1991) observed a bias toward mixed-sex twin litters, and they attributed this finding to habitual siblicide within same-sex litters. If sex-biased siblicide is independent of local environmental conditions, then sex composition of twin litters in hyena populations should deviate from binomial expectations, yielding an overabundance of mixed-sex litters and too few same-sex litters. Although secondary sex ratios in *Crocuta* can apparently be adjusted according to socioecological conditions (Holekamp and Smale 1995; Smale et al. 1999; Wachter et al. 2002), there is no known prenatal mechanism by which adult females might increase the probability of producing mixed-sex twins, with one uterine horn containing a male and the other a female. Of course, predation, disease, and other postnatal mortality sources might also differentially affect male and female infants in this species.

Earlier workers developed a simple model predicting that the probability of siblicide among spotted hyenas should depend on the sex of both perpetrator and victim, such that females in all-female litters should be most likely to commit infanticide (Hofer and East 1997; James and Hofer 1999). If so, then singletons should be female biased and twins should be male biased among spotted hyenas (Hofer and East 1997). Frank et al. (1991) presented no data on singleton sex ratios, so we could not compare singletons here before and after fission. However, we found significant differences in sex ratios within twin litters before and after fission. Because the latter results are consistent with the predictions of the model developed by Hofer and East (1997), we suggest that the peculiar sex ratios in the twin litters observed by Frank et al. (1991) might have been caused not by obligate siblicide but by frequent occurrence of facultative siblicide within same-sex litters during their study period, particularly within all-female litters. Documented sex differences in initiation and persistence of early fighting in *Crocuta* are also consistent with this model. That is, like adult female hyenas (Szykman et al. 2003), juvenile females initiate aggressive interactions at higher rates than do males (Frank et al. 1989), and young females are also less likely than males to give up during fights (Smale et al. 1993), so they might possibly fight to the death more often than males during early sibling rivalry. These sex differences in early aggression suggest a mechanism that might account for the presence of male-biased twin sex ratios during the study period of Frank et al. (1991).

Striking differences among *Crocuta* populations have been observed in both rates of sibling aggression and offspring sex ratios (Wachter et al. 2002), consistent with the notion that these animals engage in facultative, but not obligate, siblicide in some populations. However Frank et al. (1991) observed the same hyena population from late 1979 to 1987 as that monitored in the current study between 1988 and 2004. Whereas Frank et al. (1991) clearly observed a strong bias toward production of mixed sex twin litters, we found no such bias after clan fission. During the years in which Frank et al. (1991) observed Talek hyenas, it appeared that this population was continuously at or near the carrying capacity of the clan's territory (Holekamp and Smale 1995) and that competition for food within the clan was quite intense (Holekamp

et al. 1993). The clan fission event was associated with a sudden and dramatic switch in overall offspring sex ratios from male biased before fission to female biased immediately after fission (Holekamp and Smale 1995). Before fission, hyena population density in our study area was high and prey resources were being partitioned among 30% more hyenas than after fission; because prey availability did not change in the Talek area at fission, competition for food was much less intense after than before fission (Holekamp et al. 1993).

In accord with an hypothesis forwarded by earlier workers (East and Hofer 1997; Golla et al. 1999; Wachter et al. 2002), our data suggest the possibility that splitting of the Talek clan and the ensuing reduction in competition for food might have eliminated the need for fatal sibling rivalry, particularly within female–female litters. Production of all-female litters began during the period of clan fission and became commonplace during the first years after clan fission (Holekamp and Smale 1995). If sibling rivalry is particularly intense in all-female litters, then the likelihood of siblicide in all-female litters should be high in environments where prey are often scarce, and this appears to be true in both Kalahari (Mills 1990) and Serengeti populations (Hofer and East 1997; Golla et al. 1999). Our current data are consistent with the idea that intensity of sibling rivalry can vary temporally as well as spatially, when feeding competition changes within a single study population.

The current study elucidates the power of an integrated field–laboratory approach in resolving conflicts in behavioral ecology. It also highlights the value of extended study in both the field and in captivity of long-lived, large-bodied mammals. Considered alone, data from various earlier short-term field studies indicated either that siblicide occurs in *Crocuta* commonly (Frank et al. 1991; Hofer and East 1997), hardly at all (Wachter et al. 2002; White 2005) or at intermediate levels (Smale et al. 1995, 1999). By closely monitoring a single *Crocuta* population under a variety of different ecological conditions, we have found that young spotted hyenas do not routinely behave like Cain and Abel (e.g., Alcock 2001), nor are they unique among birds and mammals in habitually killing same-sex siblings. Instead, the siblicidal behavior emitted by juvenile hyenas conforms to the same facultative model that predicts fatal sibling aggression in many avian species (Mock and Parker 1997).

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