
Conflict and Cooperation in a Female-Dominated Society: A Reassessment of the “Hyperaggressive” Image of Spotted Hyenas

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I. INTRODUCTION

The spotted hyena (*Crocuta crocuta*) displays a suite of unusual traits that include female dominance, the masculinization of female genitalia (virilization), and sibling rivalry that can lead to the death of one sibling (siblicide). There has been much speculation about the evolution of these traits, probably because the assumed links between androgens, aggressive behavior, and masculinized traits in spotted hyena females point to fundamental issues concerning the evolution of sex-specific (aggressive) behavior (Gowaty, 1997; Hrdy, 1999). The prevailing assumption has been that elevated levels of androgens in female spotted hyenas produce large, hyperaggressive females that are able to outcompete males in feeding situations and thus acquire absolute dominance over males (Gould, 1981; Glickman *et al.*, 1993; Frank *et al.*, 1995; Frank, 1997; Hrdy, 1999). Some authors have even suggested that the assumed high levels of androgens in adult female spotted hyenas may induce pathological problems during reproduction such as difficulties in completing pregnancies or a delay in the onset of reproduction (Packer *et al.*, 1995). Female spotted hyenas have an enlarged clitoris that is erectile and resembles the penis of the male (Matthews, 1939). The prevailing opinion on the evolution of this “pseudo-penis” has been that it was acquired as a by-product of selection for androgenized, aggressive females (Gould, 1981; Hamilton *et al.*, 1986; Frank *et al.*, 1991; Frank, 1996, 1997). Similarly, a phenomenon described as “habitual neonatal siblicide” in spotted hyenas has also been viewed as a by-product of selection for androgenized, aggressive females (Frank *et al.*, 1991; Frank, 1996, 1997).

TABLE I
EVIDENCE THAT SPOTTED HYENAS EVOLVED BEHAVIORAL AND LIFE HISTORY TRAITS IN THE CONTEXT OF CONFLICT RESOLUTION THAT ARE FLEXIBLE, RESOURCE-DEPENDENT, INDEPENDENT OF BODY SIZE, OR RELY ON CONFLICT AVOIDANCE

Behavioral or life history trait or context	Manifestation	Remarks	References
Behavioral response to territorial intruders	Highly context-specific, ranging from tolerance of intruders in transit to quickly escalated aggressive attacks on intruders at carcasses or kills	One of the few vertebrates where such flexibility has been demonstrated; consistent with game theoretical arguments	Hofer and East, 1993b
Territorial defense through encounters with neighboring clans	Territorial encounters are won by the side that recruits the largest number of clan members after the encounter begins	Group size, not the physical qualities of the participants, decides the outcome of the encounter	Hofer and East, 1993b
Acquisition of social status (females)	Linear dominance hierarchy based on aggressive and submissive interactions in female dyads	Independent of body mass, muscular measures, or skeletal body size, but dependent on coalition quality (i.e., the social status of the mother)	Frank, 1986b; Hofer and East, 1995a; Holekamp <i>et al.</i> , 1996
Acquisition of social status (immigrant males)	Immigrant males queue for social status: social status is based on tenure, agonistic encounters usually consist of submissive avoidance responses rather than aggressive dominance actions, and social status is independent of body size	Queues contain a much higher number of members and last for a substantially longer period of time than other mating queues in vertebrates, yet queuing discipline is strict in comparison to queues described for other species	East and Hofer, 2001
Acquisition of social status (nondispersing natal males)	Natal males acquire top rank in the immigrant male social hierarchy when they start competing with immigrant males for access to females	"Nondispersal" natal males do not queue for high social status probably due to the status they acquired from their mothers when cubs. All nondispersal natal males submit to all females, irrespective of their mother's rank	East and Hofer, 2001

Maintenance of social status (males)	Position in queue mostly maintained by coalitions among males and between high ranking males and females	Independent of measures of body size	East and Hofer, 2001
Rate of aggression between siblings	Most intense sibling rivalry occurs during suckling bouts; depends on food availability and maternal social status, which determines access to food resources in the territory	Consistent with avian models of facultative sibling rivalry	Golla <i>et al.</i> , 1999
Age at first reproduction (females)	Increases as social status declines	Dependent on coalition quality (maternal social status) when daughters acquired their rank	Hofer and East, 1996; Holekamp <i>et al.</i> , 1996
Reconciliation	Affiliative behavior after an agonistic encounter is more likely after escalated conflicts; winners of conflicts regularly initiate affiliative behavior with losers of conflicts	One of the few nonprimate species where reconciliation has been documented after conflicts	Hofer and East, 2000
Commuting system	Clan members regularly forage outside the territory in areas containing large concentrations of migratory herds when such herds are absent from the clan territory	Avoidance of conflict with high-ranking clan members inside the territory	Hofer and East, 1993a,b,c
Acoustic defense of resources	Rate of loud calling (whoops) by females is related to social status, prey abundance, level of intrusion and food competition, and expected benefits in terms of increased food intake and improved cub survival	The rate of acoustic defense of the territory and the resources it contains vary with both intrusion pressure and expected fitness benefits through the resources that are being defended	East and Hofer, 1991a,b
Greeting ceremonies	Ritualized greeting in which the erect "penis" is used as a signal of submission and clan members compete for "valuable" greeting partners	Individuals value these affiliative interactions and those greeting partners likely to provide maximum social benefits in accordance with primate models of optimal partner choice	East <i>et al.</i> , 1993

Given the volume of literature that has promoted the idea that female dominance in spotted hyenas evolved due to selection favoring androgenized, large, hyperaggressive females, it is perhaps surprising that this idea has received little critical assessment. In this review we will use data from our long-term research on a population of several hundred individually known spotted hyenas in several social groups in the Serengeti National Park, Tanzania to examine this prevailing view. Using current knowledge of the behavior, ecology, and endocrinology of free-ranging spotted hyenas, we will present an alternative evolutionary scenario for the occurrence of habitual male submission resulting in female dominance in this species. We will outline a scenario that links elevated levels of androgens in neonates of both sexes with selection for early sibling rivalry leading to resource-dependent, facultative siblicide (East *et al.*, 1993; Hofer and East, 1995a, 1997; Golla *et al.*, 1999) and producing as a side effect virilized genitalia in female offspring (East *et al.*, 1993; Hofer and East, 1995a).

During our discussion of these scenarios we will consider some of the conflicts that exist within spotted hyena society and the mechanisms used to resolve them. Throughout our review we aim to highlight how both conflict and cooperation shape hyena society and to emphasize that spotted hyenas most likely use social relationships with other group members as an important resource (Table I). This view of social relationships coincides with a major paradigm shift among many animal behavior researchers (Aureli and de Waal, 2000) who view aggression not as the driving force that determines the fabric of social life, but rather as one of several forms of conflict resolution that are in an evolutionary balance with mechanisms of conflict avoidance and with affiliative behaviors that encourage the maintenance of social relationships. This argument is particularly pertinent for long-lived, slowly reproducing, and highly social mammals, such as spotted hyenas, where the social environment may exert as strong a selective force as the natural environment. We thus hope that our review of the evidence relating to the assumed links between aggressive behavior, androgens, and masculinization in spotted hyenas leads to a more balanced appraisal of this topic.

II. SERENGETI HYENA SOCIAL ORGANIZATION

Similar to spotted hyenas elsewhere (Kruuk, 1972; Frank, 1986a; Henschel and Skinner, 1987; Mills, 1990; Hofer, 1998), Serengeti hyenas live in stable social groups called clans that defend territories against neighboring clans (East and Hofer, 1991a,b; Hofer and East, 1993a). Females remain in their natal clan throughout their life. As in other spotted hyena populations (Hofer, 1998), there is a strong social hierarchy among female Serengeti

clan members (East and Hofer, 1991b; East *et al.*, 1993), with high-ranking females maintaining priority of access to food resources (Hofer and East, 1996). Coalitions among Serengeti females are important for the acquisition and maintenance of social status (Table I). As a consequence of such coalitions, the social status of adult females is highly positively correlated with that of their mother (most daughters acquire a social status just below that of their mother). Also, adult females may dramatically decline in social status after the death of a strong coalition partner, such as a mother or adult daughter (Hofer and East, 1996; Hofer and East, unpubl. data). All adult females breed and their cubs are typically reared in a communal den inside the clan territory (Hofer and East, 1995b). Serengeti males normally disperse from their natal clan after reaching sexual maturity at about 2 years of age (Hofer and East, 1995b). When males disperse into a new clan, they join the immigrant male dominance hierarchy at the bottom. Immigrant males do not fight for social status, but instead low-ranking males with short tenure increase in rank as higher ranking, longer tenured males die or leave the clan (Table I). Thus, immigrant males can be considered to queue for social status (East and Hofer, 1991b; East *et al.*, 1993; East and Hofer, 2001). All immigrant males are subordinate to all female clan members; males do not participate in parental care.

III. CONFLICT OVER ACCESS TO FOOD

A. THE COMMUTING SYSTEM

In the Serengeti National Park, the herbivore biomass is dominated by migratory species, chiefly wildebeest (*Connochaetes taurinus*), Thomson's gazelles (*Gazella thomsoni*), and zebras (*Equus burchelli*), and these species are the primary prey of Serengeti spotted hyenas (Hofer and East, 1993a). Due to the movements of these migratory herbivores, the abundance of prey within clan territories fluctuates markedly. Large numbers of herbivores are present within any given territory for only 22–30% of any year and, during such periods, the abundance of herbivores is high (mean of 238 animals/km²). Irrespective of social status, all clan members forage within the clan territory when large migratory herds are present (Hofer and East, 1993b). When such herds are absent from a territory, the abundance of prey is dramatically reduced to a mean of 31 animals/km² during periods of medium prey abundance (small herds of migratory and resident herbivores are present) and to a mean of 3.3 animals/km² during periods of low prey abundance when only resident herbivores are present (Hofer and East, 1993a,b).

Conflict between clan members over access to food resources in the clan territory increases as the abundance of herbivores declines. One method of decreasing conflict over access to declining food resources is to leave the clan territory on short-term (6–8 days for nonlactating animals), long-distance (40–80 km) foraging trips to the nearest concentration of migratory herbivores (Table I). The proportion of clan members regularly commuting to forage outside the territory increases as the abundance of herbivores declines (Hofer and East, 1995b). Individuals of low social status regularly commute when there are moderate densities of herbivores in the group territory. In contrast, females of high social status only commute when conditions of low prey abundance prevail. Although commuting decreases conflict with socially dominant group members, commuting dramatically increases foraging effort. For example, nonlactating, low-ranking females undertake approximately 15–18 commuting trips annually, and such trips entail traveling a minimum average distance of 1000–1300 km per year (Hofer and East, 1993c).

B. TERRITORIAL DEFENSE AND INTRUSION PRESSURE

The evolution of the commuting system in Serengeti spotted hyenas does not indicate near-pathological hyperaggression among females. Rather, it demonstrates considerable behavioral flexibility that allows the year-round exploitation of abundant migratory prey, copes with high levels of intrusion by commuters, and permits a larger group size than would be feasible given the low abundance of resident prey in group territories (Hofer and East, 1993a,b). Clan territory owners have a highly context-specific response to intruding hyenas. Intruders in transit, moving swiftly along recognized thoroughfares through a clan territory, are tolerated or ignored by residents, whereas foraging intruders are usually subjected to low-level aggressive challenges by residents when the latter encounter the former. Territory owners escalate aggressive attacks at food resources if intruders do not immediately relinquish the prey they have killed or carcass they have scavenged (Hofer and East, 1993b). Such flexible, context-specific adjustment of the territorial response to intruders is expected from game-theoretical arguments (Hofer and East 1993b) but, to our knowledge, our study of Serengeti hyena territoriality is the only example where such a flexible territorial response has been demonstrated in a carnivore society (Table I).

Territory owners rarely need to resort to physical contests as they invest in olfactory (Mills and Gorman, 1987; Hofer *et al.*, 2001) and acoustic signals to advertise ownership of resources in their territory (East and Hofer, 1991a,b). Clan females “loud call” or whoop most often when their territory contains a high abundance of herbivores. Thus females adjust their vocal defense of resources in their territory in relation to (1) levels of competition from

intruding commuters and other clan members and (2) the expected benefit that an increased abundance of carcasses provides in terms of food and high cub growth rates (Hofer and East, 1993b,c). High-ranking resident females who stand to benefit the most from ensuring that they have priority of access to carcasses also whoop at the highest rates (East and Hofer, 1991b).

C. MATERNAL CARE

Parental effort (the effort required to obtain resources) and parental input (the quality and quantity of resources delivered to offspring that are converted into growth; Evans, 1990) comprise parental care. Benefits of parental care are usually measured in terms of the survival and reproductive success of the offspring. Although the cost of parental care is the reduced fitness obtained from future offspring caused by the level of care invested in current offspring (Trivers, 1972), parental energy expenditure has often been considered an appropriate approximation of parental costs (Clutton-Brock, 1991). Due to fluctuating levels of conflict over access to food resources in Serengeti clan territories, the options available to females with respect to parental effort and parental care differ according to social status.

During periods of high prey abundance, maternal effort is low, maternal input is high as offspring are nursed each day, and thus, cub growth rate is high irrespective of the social status of mothers (Hofer and East, 1993c, 1996; Golla *et al.*, 1999). In contrast, all Serengeti females, irrespective of social status, regularly leave the clan territory to forage on distant migratory prey during periods of low prey abundance. Maternal effort is high because mothers have to travel long distances to foraging areas and return to the clan territory to nurse their offspring at the communal den. Maternal input is low because commuting mothers are absent from their offspring for several (2–9) days. Mothers do not compensate for infrequent nursing of their young by increasing milk quality or volume delivered during nursing (Hofer and East, 1993c, 1996). Consequently, the comparatively low maternal input during commuting periods results in minimum or even negative growth rates of offspring over periods of several weeks (Hofer and East, 1993c, 1996; Golla *et al.*, 1999).

During periods of medium prey abundance, females of high social status monopolize low-cost foraging opportunities inside the clan territory, whereas females of medium and low status continue to exercise the high-cost foraging option of traveling long distances to feed on migratory prey. By remaining “at home,” females of high status ensure that their parental effort is kept as low as possible, and they continue to nurse their offspring frequently. By comparison, commuting medium- and low-ranking females have a substantially higher maternal effort and lower maternal input. Medium- and low-ranking lactating females undertake between 42–51 commuting trips

annually, traveling a minimum average distance of 2900–3700 km, whereas high-ranking mothers may travel only half this distance (Hofer and East, 1993c, and unpubl. data). These commuting distances exceed the total distance covered by the migratory herds throughout their annual migratory cycle by a factor of 3 or more (Hofer and East, 1995b).

The two foraging options available to Serengeti mothers substantially differ in their consequences for maternal effort (costs to the mother) and maternal input (benefits to the cubs). For instance, the average one-way distance of a commuting trip of 40 km exceeds by an order of magnitude the distance of 4 km that is equivalent to the approximate radius of territories defended by clans in our study (Hofer and East 1993b, 1995b). Similarly, commuting mothers nurse their cubs on average at intervals of 3.4 days, which is substantially less often than mothers feeding inside the clan territory who nurse their cubs typically twice a day (Hofer and East, 1993c). Thus, commuting is clearly the worse option, yet low- and mid-ranking females spend most of the year commuting to avoid conflict over food with high-ranking clan members.

Offspring of high-ranking females generally grow faster and survive better than those of low- and mid-ranking mothers because their mothers only commute during periods of low prey abundance (Hofer and East, 1996; Golla *et al.*, 1999). These effects have far-reaching consequences for the reproductive careers of daughters. Parental input by Serengeti mothers, measured in terms of cub growth rate to independence, is a significant predictor of adult mass, adult skeletal size, and age at first parturition of daughters (Hofer and East, 1996). Age at first parturition is considered a key life history trait (Roff, 1992; Stearns, 1992) because it determines, among other things, the expected duration of the lifetime reproductive period. In species such as spotted hyenas, with small litter size and long interbirth intervals due to their long period of offspring dependence, total duration of the reproductive period is a significant predictor of lifetime reproductive success (Clutton-Brock, 1988). Since daughters of high-ranking Serengeti mothers grow faster, obtain a higher social status, and reproduce earlier than daughters of low-ranking mothers, offspring quality in Serengeti hyenas is strongly and positively correlated between generations (Hofer and East, 1996).

IV. SIBLING RIVALRY: A BY-PRODUCT OF ANDROGENIZATION OR AN ADAPTATION TO FLUCTUATING LEVELS OF PREY?

Intense sibling rivalry, leading to the death of a sibling, has been observed in numerous avian species (Mock and Parker, 1997). Such siblicide has been described as obligate if rivalry invariably results in the death of a sib and

facultative if brood reduction only occurs when parental food provisioning falls below that required to sustain the entire brood (Mock and Parker, 1997). Spotted hyenas are one of the few mammalian species that exhibit sibling rivalry leading to siblicide. Frank *et al.* (1991) and Frank (1996, 1997) considered siblicide in spotted hyenas to be independent of resources, "habitual" (i.e., presumably obligate) in twin litters composed of cubs of the same sex, and a by-product of selection for large, aggressive, androgenized females that could dominate males.

In contrast, we have described in detail cases of resource-dependent, facultative siblicide in Serengeti spotted hyenas (Hofer and East, 1997). Variation in the intensity of sibling rivalry within Serengeti litters conforms to predictions derived from avian models of facultative siblicide (Golla *et al.*, 1999), and facultative siblicide in Serengeti litters normally occurs within the first 2 months of life (Hofer and East, 1997; Golla *et al.*, 1999). "Habitual" siblicide in same-sex twin litters has not been observed during our long-term study (East and Hofer, 1997; Hofer and East, 1997). Smale *et al.* (1999) also argued that siblicide in spotted hyenas was unlikely to be "habitual," and more likely to be facultative, due to the low incidence of siblicide in their study clan in the Masai Mara of Kenya.

In the Serengeti, litter size is one or two, rarely three (Hofer and East, 1997), and cubs are born throughout the year (Hofer and East, 1995b). Mothers normally nurse only their own offspring, and cubs are stationed at the communal den for approximately 12 months (Hofer and East, 1993c). Due to a long period of lactation (12–18 months), Serengeti mothers experience large fluctuations in prey abundance in their territory irrespective of the timing of parturition (Hofer and East, 1995b). The milk of spotted hyenas is highly nutritious (protein content 14.9%, fat content 14.1%, gross energy density 9.70 kJ/g), with a protein content higher than that recorded for any other land carnivore, a fat content only exceeded by Palearctic bears and sea otters (*Enhydra lutris*), and a gross energy density higher than that of most other land carnivores (Hofer and East, 1995b). Given the considerable maternal investment of spotted hyenas in terms of high-quality milk and long lactation period, the existence of siblicide in this species might be expected, as a siblicidal survivor would gain exclusive access to highly nutritious maternal milk during the prolonged period of lactation.

Although a siblicidal cub might gain an additional share of the maternal milk supply, a cub should only sacrifice a littermate when the increase in fitness acquired by such an act is greater than the fitness cost incurred (Parker *et al.*, 1989; McNamara *et al.*, 1994). Such a situation will occur when maternal food supply is insufficient to sustain the entire litter (Table I), and under such circumstances, the dominant offspring should seek to improve its chance of survival by monopolizing maternal resources (Mock *et al.*, 1990).

Severe sibling rivalry between spotted hyena siblings results in the exclusion by the dominant cub of the subordinate cub from access to maternal teats. This results in large asymmetries in body mass between littermates and the eventual death due to starvation of the subordinate offspring (Hofer and East, 1997). If, as theory predicts, insufficient parental provisioning causes despotic behavior by the dominant offspring (Mock *et al.*, 1990; McNamara *et al.*, 1994; Mock and Parker, 1997), then escalated sibling rivalry within spotted hyena twin litters should be expected when mothers fail to provide sufficient milk to sustain a litter. Consistent with this prediction, rates of aggression among Serengeti littermates increased as levels of maternal input, measured in terms of cub growth, decreased (Golla *et al.*, 1999). Rates of aggression were calculated as the frequency of aggressive behaviors per minute during suckling bouts derived by a bout criterion analysis (Sibly *et al.*, 1990). Also in accordance with this prediction, littermates belonging to high-ranking mothers and receiving high levels of maternal input (see earlier) had lower rates of aggression than those belonging to lower ranking mothers that provided less adequate levels of input (Golla *et al.*, 1999).

Thus all the evidence currently available suggests that siblicide in spotted hyenas is facultative and resource-driven, just as in any other species with facultative siblicide, and not a pathological by-product of selection for another trait.

V. SIBLICIDE AND BIASES IN THE SEX COMPOSITION OF TWIN LITTERS

Facultative siblicide in spotted hyenas is an interesting phenomenon, as enforced starvation does not appear to occur randomly with respect to the sex composition of twin litters. Twin litters may be composed of cubs of the same sex (i.e., both male or both female) or of mixed sex (male and female cubs). Considering the sex composition of 114 twin Serengeti litters at the age of 3 months, when cubs can first be sexed in the field by the shape of their phallic glands (Frank *et al.*, 1990), mixed-sex litters occurred significantly more often than expected, whereas there were too few all-female litters (Hofer and East, 1997). This suggests that facultative siblicide is more likely to occur in all-female than all-male or mixed-sex twin litters. If facultative siblicide most often occurs in all-female twin litters, then many all-female twin litters will be represented by a singleton female after siblicide has occurred (Hofer and East, 1997). The overall sex ratio expressed as the proportion of males in singleton Serengeti litters was 0.429 ($N=91$ cubs), a significant female bias consistent with the idea that females are more likely to commit siblicide (Hofer and East, 1997).

If females are more likely to commit siblicide, then the twin litters that survive intact to the age of 3 months should show a male bias. In the Serengeti, the proportion of males in twin litters at this age was 0.557, a bias toward male cubs. James and Hofer (1999) showed that siblicide could only account for the subbinomial variance of the sex composition of Serengeti twin litters at the age of 3 months if the probability of siblicide depended on the sex of the victim, or if it was caused by preparturition processes, as suggested by Smale *et al.* (1999).

East and Hofer (1997) suggested that if facultative siblicide is most common in all-female litters, then the sex composition of twin litters in spotted hyena populations should alter with the amount of food available to lactating mothers. If so, the low incidence (8%) of all-female litters in a Masai Mara clan, when group size was considered at carrying capacity, and the higher incidence of such litters (41%) after fission reduced group size to below carrying capacity (Holekamp and Smale, 1995), may have been caused by a decline in facultative siblicide after fission (East and Hofer, 1997). A comparison of the sex composition of twin litters in ecosystems with large differences in prey abundance shows that the proportion of all-female twin litters increased as the availability of resident prey increased (Table II, Spearman's $\rho = 0.886$, $N = 6$, $P < 0.05$). The highest incidence of all-female (twin/triplet) litters was observed, as predicted, in a well-fed captive colony of spotted hyenas.

Sex-specific biases in sibling competition may result from unequal investment in offspring of different sex (Clutton-Brock, 1991), causing more extreme competition for parental resources by the sex that receives more parental investment (Mock and Parker, 1997). In Serengeti spotted hyenas, singleton female cubs grow at a higher rate than singleton males, suggesting that investment in females is higher than in males (H. Hofer and M. L. East, unpubl. data). Also, as previously mentioned, females remain in their natal groups and normally acquire a social rank immediately below that of their mother, with social status directly influencing access to food resources. Thus, due to philopatry among females, higher levels of competition may be expected within all-female litters than within all-male litters (Holekamp and Smale, 1995; Golla *et al.*, 1999). Aggression rates among Serengeti cubs within all-male and all-female litters were higher than in mixed-sex litters, but did not differ between all-male and all-female litters (Golla *et al.*, 1999). These results may be due to escalated contests between competitors with identical interests (Maynard Smith, 1982). More likely, they reflect the combined aggressive behavior of both siblings and not the tactics used by dominant and subordinate contestants during competition for access to maternal milk supplies (Golla *et al.*, 1999).

TABLE II
RESIDENT PREY DENSITIES (IN ANIMALS/KM²), AGGRESSION RATES WITHIN TWIN LITTERS (AGGRESSIVE MOVES/MIN), OCCURRENCE OF SIBICIDE, AND SEX-RATIO BIASES IN DIFFERENT ENVIRONMENTS^a

Ecosystem	Prey density	Aggression rate	Facultative sibicide	Sex composition of litters			References
				% Mixed-sex	% All-male	% All-female	
Kalahari	2.6 ^b	?	?	89**	11	0 [§]	9 Mills, 1990; Hofer and East, 1993a
Serengeti	3.3	0.49 ± 0.31	Yes	61**	25	14**	114 Hofer and East, 1993a, 1997; Golla <i>et al.</i> , 1999
Masai Mara ^c	?	?	Yes	85***	12 ^{§§§}	3***	33 Frank <i>et al.</i> , 1991
Masai Mara ^d	153 ^e	0.035 ^{e,i}	Possible	81**	13	6 ^{§§}	16 Holekamp <i>et al.</i> , 1993; Holekamp and Smale, 1995; Smale <i>et al.</i> , 1995, 1999
Masai Mara ^b	163 ^e	0.035 ^{e,i}	No ^g	48	27	25	48 Holekamp <i>et al.</i> , 1997; Smale <i>et al.</i> , 1995, 1999
Ngorongoro	184.2	0.023 ± 0.06	No	49	31	20	35 B. Wachter and O. P. Höner, unpubl. data
Captivity	<i>Ad libitum</i>	0.05 ^e	Possible ^h	56	17	28	18 Drea <i>et al.</i> , 1996; Frank, 1996

Note: [§] $p = 0.075$; ^{§§} $p = 0.063$; ^{§§§} $p = 0.058$; ** $p < 0.005$; *** $p < 0.001$.

^aSex composition of twin litters from binomial expectations is 50% mixed-sex, 25% all-male, and 25% all-female litters.

^bMinimum estimate.

^cStudy period 1979–1987.

^dStudy period 1988–1990 before clan fission, high competition between females.

^eDerived from graphs or data published in the original citations.

^fStudy period 1990–1998 after clan fission, low competition between females.

^gNo evidence for sibicide in twin litters but one case in a triplet litter.

^hThe subordinate in a twin litter and the runts in all four triplet litters sustained serious injuries and observers intervened.

ⁱAggression rates may have been recorded before and after clan fission.

VI. FEMALE DOMINANCE AND VIRILIZATION

The female genitalia of spotted hyenas are virilized and resemble the genitals of the males. The clitoris is enlarged and forms an erectile pseudo-penis, the labia are fused to form a pseudo-scrotum, and the urogenital tract passes through the pseudo-penis (Matthews, 1939; Neaves *et al.*, 1980; Frank *et al.*, 1990). Female spotted hyenas thus urinate, copulate, and give birth through their clitoris. Several hypotheses have been advanced to explain the virilization of female genitalia in spotted hyenas. The nonadaptive theories view female virilization as an incidental by-product of selection for elevated prenatal androgen levels. Such elevation occurred because (1) it led to large size, increased aggression, and social dominance of adult females over males (Gould, 1981; Frank *et al.*, 1991; Frank, 1997); it was (2) a consequence of a punctuated genetic translocation (van Jaarsveld and Skinner, 1987); it was (3) favored in the evolution of sibling rivalry (East *et al.*, 1993, Hofer and East, 1995a). Adaptive theories considered the enlarged clitoris to have the direct selective advantage of a conspicuous structure used to facilitate the reestablishment of social bonds (Wickler, 1965; Kruuk, 1972). Another theory, which is an adaptive extension of the nonadaptive theory of Gould (1981), suggests that the virilization of female genitalia evolved as a by-product of selection for androgen-facilitated dominance and that the virilized clitoris was incorporated into greetings, favoring selection for its enlargement and erectile nature (Hamilton *et al.*, 1986).

What evidence is there to support the idea that virilization of the female external genitalia was driven by selection for androgen-facilitated dominance? We will look at the evidence on androgen concentrations in the next section and concentrate here on the behavior. Adult female spotted hyenas are commonly assumed to be highly aggressive (Hamilton *et al.*, 1986; Frank *et al.*, 1991, 1995; Glickman *et al.*, 1993; Monaghan and Glickman, 1992; Packer *et al.*, 1995), even though levels of aggression among female spotted hyenas have not been compared with those of females in other mammalian species living in a similar social context of multimatrilineal groups that live in a fission-fusion society (Goymann, 1999). Rates of aggression among competing immigrant males are low, and males are rarely aggressive to females (East and Hofer, 2001). Thus, females may appear to be aggressive because the aggressiveness of immigrant males is so low (East *et al.*, 1993). In mammalian species other than the spotted hyena (e.g., European mole *Talpa europaea*: Matthews, 1935; platyrrhine monkeys: Ploog and MacLean, 1963) virilization of female external genitalia is rare but where it occurs it is not associated with female dominance (East *et al.*, 1993; Hofer and East, 1996; Teltcher, 1996). In mammalian species, female dominance is uncommon, but does occur in a variety of taxa (Ralls, 1976; Hrdy, 1981) and is typical for

Lemuriformes (Jolly, 1984; Kappeler, 1990; Young *et al.*, 1990). However, extreme masculinization of female external genitalia has not been recorded in any female-dominated species except for the spotted hyena (Teltscher, 1996). Female dominance in other mammals is not dependent on females being larger than males, and dominance is not a function of aggressiveness (Rowell, 1974). Even in spotted hyenas, females are not necessarily larger than males (Hamilton *et al.*, 1986; East and Hofer, 1997, unpubl. data), and body size in males and females is not related to social status in our Serengeti population (East and Hofer 1997, 2001), nor in a clan in the Masai Mara of Kenya (Holekamp *et al.*, 1996). In several primate species (*Saimiri*, *Cebus*, *Cercopithecus talapoin*, *Macaca mulatta*, *Erythrocebus patas*), coalitions of females can successfully challenge larger males (Harvey *et al.*, 1987; Smuts, 1987), and in spotted hyenas coalitions are important in the maintenance of female rank (East *et al.*, 1993; Hofer and East, 1996).

VII. VIRILIZATION AND ANDROGENS

It has been argued that spotted hyena females have androgen profiles that are unusual for female mammals. On an interspecific level, they are thought to have higher androgen levels than other female mammals (e.g., Glickman *et al.*, 1993; Packer *et al.*, 1995; Frank, 1996). On an intraspecific level, the quoted "aggressiveness" of females is assumed to be caused by elevated levels of androgens. What is the evidence?

Comparative data demonstrate that testosterone and androstenedione levels in nonpregnant free-ranging spotted hyena females are below or similar to those in a variety of other nonpregnant female mammals, including those in female brown and striped hyenas (Tables III and IV).

In intraspecific comparisons, some studies reported similar testosterone levels in male and female spotted hyenas, whereas others reported significantly higher testosterone levels in males than in females (Table V). Androstenedione levels were similar in females and males in some studies and significantly higher in females than in males in other studies (Table VI). Confusion about androgen levels in spotted hyenas probably stems from three sources (Goymann *et al.*, 2001). First, some studies have not considered the impact of reproductive status on androgen levels in males. This is a problem because androgen levels in young, nonbreeding natal males ("predispersal" males) are significantly lower (Holekamp and Smale, 1998) than levels in older, mostly immigrant, reproductively active males ("post-dispersal" males) (Table V and VI). Second, since the challenge hypothesis (Wingfield *et al.*, 1990) predicts that androgen levels should increase when individuals experience elevated levels of social challenge, androgen levels in

TABLE III
 EXAMPLES OF PUBLISHED DATA ON PLASMA TESTOSTERONE (ng/ml) IN NONPREGNANT
 FEMALE CARNIVORES AND OTHER MAMMALS

Species	Plasma concentration (ng/ml)	References
Spotted hyena (<i>Crocuta crocuta</i>)	0.32	Goymann <i>et al.</i> , 2001
Brown hyena (<i>Hyaena brunnea</i>)	0.52	Racey and Skinner, 1979
Striped hyena (<i>Hyaena hyaena</i>)	0.64	Racey and Skinner, 1979
Domestic dog (<i>Canis familiaris</i>)	0.05–0.29	Concannon and Castracane, 1985
Human (<i>Homo sapiens</i>)	0.30–0.60	Feder, 1985
Chimpanzee (<i>Pan troglodytes</i>)	0.35–0.73	Nadler <i>et al.</i> , 1985
Baboon (<i>Papio hamadryas</i>)	0.15–0.23	Feder, 1985
Talapoin monkey (<i>Miopithecus talapoin</i>)	2.2–4.0	Batty <i>et al.</i> , 1986
Syrian hamster (<i>Mesocricetus auratus</i>)	0.06–0.09	Feder, 1985
Musk shrew (<i>Suncus murinus</i>)	0.20	Rissman <i>et al.</i> , 1990
European mole (<i>Talpa europaea</i>)	0.79–1.44	Whitworth <i>et al.</i> , 1999

captive (e.g., Glickman *et al.*, 1987, 1992) and free-ranging spotted hyenas may not be comparable. Unlike free-ranging spotted hyenas that live in fission–fusion societies, captive individuals are housed together, have constant social contact, and have limited opportunities to avoid interactions. These socially challenging conditions are likely to result in elevated levels of androgens. Following the same line of argument, Serengeti spotted hyenas that are caught in wire snares set by game meat hunters, but escape by biting through the tethering wire (Hofer *et al.*, 1993), experience an elevated level of social challenge. This is because the snare is often embedded in the

TABLE IV
 EXAMPLES OF PUBLISHED DATA ON PLASMA ANDROSTENEDIONE (ng/ml) IN NONPREGNANT FEMALE
 CARNIVORES AND OTHER MAMMALS

Species	Plasma concentration (ng/ml)	References
Spotted hyena (<i>Crocuta crocuta</i>)	2.44	Goymann <i>et al.</i> , 2001
Brown hyena (<i>Hyaena brunnea</i>)	4.70	Racey and Skinner, 1979
Domestic dog (<i>Canis familiaris</i>)	0.41–0.79	Concannon and Castracane, 1985
Human (<i>Homo sapiens</i>)	2.25	Cashdan, 1995
Baboon (<i>Papio hamadryas</i>)	1.2–2.0	Feder, 1985
Talapoin monkey (<i>Miopithecus talapoin</i>)	3.6–6.0	Batty <i>et al.</i> , 1986
Syrian hamster (<i>Mesocricetus auratus</i>)	1.0–1.9	Feder, 1985
European mole (<i>Talpa europaea</i>)	1.22	Whitworth <i>et al.</i> , 1999

TABLE V
MEAN TESTOSTERONE CONCENTRATIONS (ng/ml PLASMA) IN MALE AND FEMALE SPOTTED HYENAS
OF DIFFERENT REPRODUCTIVE STATE

Female, neither pregnant nor lactating	Pregnant female	Lactating female	Young, natal male before dispersal	Sexually mature, reproductively active male (usually immigrants)	Male of unknown reproductive state	References
0.76 (5)	1.20 (10)	1.06 (5)	—	—	1.48 (18)	Racey and Skinner, 1979
—	1.33 (4)	—	—	—	—	Lindeque and Skinner, 1982
0.5 ^a (1)	0.5 ^a (1)	—	—	—	—	Gombe, 1985
0.35 (12)	—	—	—	—	3.15 (9)	Frank <i>et al.</i> , 1985
0.46 (16)	1.24 (8)	—	—	—	0.84 (4)	Lindeque <i>et al.</i> , 1986
0.3 ^{a,b} (11)	—	—	—	1.5 ^{a,b} (16)	—	Glickman <i>et al.</i> , 1987
0.75 (12)	—	—	—	—	4.52 (6)	van Jaarsveld and Skinner, 1991a
1.2 ^a (5)	—	0.6 ^a (6)	1.5 ^{a,c} (6)	10.5 ^a (3)	—	van Jaarsveld and Skinner, 1991b
0.4 ^{a,b} (8)	—	—	—	3.6 ^{a,b} (6)	—	Glickman <i>et al.</i> , 1992
0.3 ^{a,b} (5)	0.3–7.0 ^{a,b} (5)	—	—	—	—	Licht <i>et al.</i> , 1992
—	1.7 ^{a,b} (3)	—	—	—	—	Drea <i>et al.</i> , 1998
—	—	—	0.3 ^d (12)	1.30 (30)	—	Holekamp and Smale, 1998
0.32 ± 0.12 (7)	0.29 ± 0.02 (3)	0.16 ± 0.02 (24)	0.51 ± 0.20 (4)	4.26 ± 0.77 (19)	—	Goymann <i>et al.</i> , 2001

Note: Numbers in parentheses refer to "sample sizes" (i.e., some references may contain repeat samples from the same individual, thus, sample sizes are not necessarily identical with the number of individuals sampled).

^aThe original paper did not supply numeric means; thus, mean values have been approximated from published graphs.

^bData from captive individuals.

^cDescribed as "resident natal males," included subadults older than one year.

^dLabeled as "natal males."

TABLE VI
MEAN ANDROSTENEDIONE CONCENTRATIONS (ng/ml PLASMA) IN MALE AND FEMALE SPOTTED HYENAS
OF DIFFERENT REPRODUCTIVE STATE

Female, neither pregnant nor lactating	Pregnant female	Lactating female	Young, natal male before dispersal	Sexually mature, reproductively active male (usually immigrants)	Male of unknown reproductive state	References
—	1.18 ^a (10)	—	—	—	0.66 (18)	Racey and Skinner, 1979
—	11.1 (3)	—	—	—	—	Lindeque and Skinner, 1982
1.92 (16)	6.79 (8)	—	—	—	0.97 (4)	Lindeque <i>et al.</i> , 1986
2.7 ^{a,b} (11)	—	—	—	1.5 ^{a,b} (16)	—	Glickman <i>et al.</i> , 1987
1.67 (12)	—	—	—	—	1.14 (6)	van Jaarsveld and Skinner, 1991a
2.1 ^a (5)	—	1.6 ^a (6)	1.0 ^{b,c} (6)	3.4 ^a (3)	—	van Jaarsveld and Skinner, 1991b
4.5 ^{a,b} (8)	—	—	—	2.5 ^{a,b} (6)	—	Glickman <i>et al.</i> , 1992
3.42 ^b (5)	6.06 ^b (5)	—	—	—	—	Licht <i>et al.</i> , 1992
2.44 ± 1.02 (7)	2.32 ± 1.03 (3)	1.14 ± 0.21 (24)	0.18 ± 0.06 (4)	1.57 ± 0.28 (19)	—	Goymann <i>et al.</i> , 2001

Note: Numbers in parentheses refer to "sample sizes" (i.e., some references may contain repeat samples from the same individual, thus, sample sizes are not necessarily identical with the number of individuals sampled).

^aThe original paper did not supply numeric means, thus, mean values have been approximated from published graphs.

^bData from captive individuals.

^cDescribed as "resident natal males," included subadults older than one year.

flesh and the wound created by the snare, and the wire protruding from the flesh draw the attention of other clan members, including individuals with higher social status than the snared animal, and contact with the wound probably causes pain. Elevated levels of social challenge may explain why nonpregnant females with snares have elevated levels of androgens in comparison to nonpregnant females without snares (Goymann, 1999). Third, studies have applied different analytical techniques for the measurement of androgen levels (Goymann *et al.*, 2001). Often studies purporting to measure testosterone do not distinguish between testosterone and 5- α -dihydrotestosterone, as common antisera against testosterone cross-react highly with 5- α -dihydrotestosterone, and vice versa, and it requires special techniques to prevent these kinds of cross-reactions from biasing the results. For the first time in hyena studies, Goymann *et al.* (2001) measured testosterone, 5- α -dihydrotestosterone, and androstenedione concentrations in plasma samples from Serengeti spotted hyenas after partial purification through chromatography by using a modification (Fusani *et al.*, 2000) of the method described by Wingfield and Farner (1975) and thus eliminating the usual cross-reactions. Thus Goymann *et al.* (2001) provide a highly specific measure of these three androgens. The results show that free-ranging spotted hyena females follow the standard mammalian pattern, with testosterone concentrations in reproductively active males being an order of magnitude higher than in females (Table V), and androstenedione levels being similar in both sexes (Table VI). In summary, there is little evidence to support the idea that androgen levels in adult female spotted hyenas are abnormally high, or likely to cause hyperaggression or pathological problems during reproduction.

We have proposed an alternative idea that links prenatal androgen levels to facultative siblicide in spotted hyenas (East *et al.*, 1993; Hofer and East, 1995a; East and Hofer, 1997). We consider it probable that the elevated levels of androgens (androstenedione in females, testosterone in males) recorded during fetal development, at birth, and during the initial months of life (Glickman *et al.*, 1987; Frank *et al.*, 1991; Licht *et al.*, 1992) have been selected to produce neonates primed for high levels of sibling rivalry (East *et al.*, 1993). High concentrations of circulating androgens (especially testosterone and 5- α -dihydrotestosterone) in adult females during the final period of pregnancy are thought to be one source of testosterone circulating in the fetus (Matthews, 1939; Licht *et al.*, 1992). If this is the case, then we suggest that the elevation of androgens during the final period of pregnancy may have been selected to contribute to the production of neonates primed for sibling rivalry (East *et al.*, 1993).

It has been thought that high androgen levels in female fetuses and neonates were involved in the formation of the hypertrophied clitoris (Frank

et al., 1991). However, as antiandrogen treatment during fetal development has not produced females without a pseudo-penis, it is unlikely that androgen-dependent mechanisms are solely responsible, and androgen-independent mechanisms are likely to play an important role in the development of the enlarged clitoris (Drea *et al.*, 1998).

VIII. THE FITNESS CONSEQUENCES OF VIRILIZATION

When female spotted hyenas give birth, the hypertrophied clitoris ruptures on the caudal side, causing a large, bleeding wound that may be a source of infection. Many primiparous captive females produce stillbirths, whereas subsequent deliveries are easier (Glickman *et al.*, 1992; Frank *et al.*, 1995). In the Serengeti, the loss of a first litter at parturition implies a reduction in terms of lifetime reproductive success of at least 5% (East *et al.*, 1993). Thus, the maintenance of the hypertrophied clitoris entails a fitness cost for females. If so, direct selection pressure must have operated to maintain this large (1% of body weight, Matthews, 1939) erectile organ (East *et al.*, 1993).

A possible selective advantage for females that have the opening to their reproductive tract (urogenital meatus) displaced to a position forward of their hind legs at the tip of their hypertrophied clitoris is that males have considerable difficulty locating and penetrating the clitoris opening (Kruuk, 1972). Although the hypertrophied clitoris is not erect during mating, its presence and position prevent males from achieving intromission without the complete cooperation of the female (East *et al.*, 1993). We have proposed that this provides females with control over the mechanics of copulation and that male mating success might depend on close male–female relationships (East *et al.*, 1993). With strong female control over copulation, the importance of sexual selection for male fighting prowess is likely to be reduced. If males stand to gain little by fighting with each other, because females do not select mating partners on the basis of their fighting ability, then game theory predicts that fights between males should be rare and/or fighting intensity low (Maynard Smith, 1982). This idea is consistent with the observed low levels of aggression among competing males (Frank, 1986b; East and Hofer, 1991b, 2001).

The challenge hypothesis (Wingfield *et al.*, 1990) has successfully explained how different mating strategies may affect patterns of androgen secretion in several avian species, but the hypothesis has rarely been tested in mammalian species. The hypothesis predicts that if direct competition for females is low, as is the case among male spotted hyenas, then there should be no association between male social status and plasma androgen concentrations. Goymann (1999) found no association between plasma androgen levels and male social

status among Serengeti postdispersal males. Similarly, in some stable primate groups, where challenges are rare among group males, a lack of correlation between androgens and male social status has also been reported (Sapolsky, 1993).

The challenge hypothesis (Wingfield *et al.*, 1990) predicts a rise in male androgen levels during periods of mate guarding and courtship, and consistent with this prediction Goymann (1999) found that Serengeti males that excluded other males from approaching females had significantly higher androgen levels than males that were not defending females.

If a male spotted hyena is more likely to be selected as a mating partner if he has developed a relationship with a female, then males should actively foster relationships with females. The high investment by males in the courtship of specific females and the submission of males to females at food resources are consistent with the idea that males invest in fostering relationships with females (East and Hofer, 2001; see later). Thus, in contrast to the prevailing idea that females had to be virilized, large, and aggressive to dominate males, we suggest that the maintenance of the pseudo-penis imposed on males a need to cultivate relationships with females, and an important factor in this process was male submission (East and Hofer, 2001). The activation of these sex-reversed traits (decreased male aggression, female dominance) in adult spotted hyenas may be mediated by mechanisms other than elevated or decreased levels of peripheral androgens (Goymann, 1999).

IX. THE MALE-DOMINANCE HIERARCHY: QUEUING FOR SOCIAL STATUS

We propose that the female pseudo-penis has not only decreased selection for male aggression, but has also influenced the manner in which immigrant males acquire social status (Table I). Social status among immigrant male hyenas is not linked to physical characteristics such as measures of skeletal size or body mass, and males do not fight to acquire status (East and Hofer, 2001). Instead, the social status of immigrant males is correlated with duration of tenure, and thus males acquire social status by queuing (East and Hofer, 1991b, 2001). The queuing convention observed by immigrant males is relatively strict (cf. Kokko *et al.*, 1998) as successively arriving males wait their turn to rise in social status and rarely use aggressive contests to increase in status (East and Hofer, 2001).

Why do immigrant males observe queuing conventions and why do newcomers not attempt to jump the queue? We have shown that several factors are likely to contribute to the stability of the male social hierarchy (Table I). When males reach high social status they form coalitions with other queuing males more often than when they are mid- or low-ranking. High-ranking

males also form coalitions with females against lower ranking males, whereas mid- and low-ranking males do not form coalitions with females. Coalitions among high-ranking males and between high ranking males and the socially dominant females may contribute to the stability of the hierarchy among the males and deter queue jumping (East and Hofer, 2001). Furthermore, greeting ceremonies (see later) among immigrant males chiefly involve individuals of similar social status and may help confirm their relative status to both participants (East *et al.*, 1993).

X. MALE-FEMALE BEHAVIOR

Immigrant males of high social status invest considerable time in following (shadowing) particular females irrespective of whether or not the females are in estrus (East and Hofer, 2001). Shadowing behavior appears to be a tactic employed by immigrant males to foster relationships with particular clan females. Immigrant males also attempt to exclude possible competitors from the vicinity of females.

High-ranking males shadow and defend females more often than mid- and low-ranking males. High-ranking males also shadow a larger number of clan females and concentrate their shadowing effort mostly on high-ranking females (East and Hofer, 2001). High-ranking males probably prefer to associate with high-ranking females because they are more valuable mating partners, since cub growth rate, cub survival, and reproductive success of Serengeti females increase with social status (Hofer and East, 1993c, 1996; Golla *et al.*, 1999).

Relationships between immigrant males and clan females vary with male social status and tenure. Females are generally more tolerant of males with high social status and long tenure than males with shorter tenure and low social status (East and Hofer, 2001). Males with high social status and longer tenure display higher levels of friendly behavior toward females. Such females in turn are more tolerant of long-tenured males than more recent immigrant males (Table I). Thus there are status-related differences in the quality of relationships between males and females (East and Hofer, 2001). These findings are consistent with our idea that relationships between immigrant males and females are strengthened with increased male tenure (East and Hofer, 1991b; East *et al.*, 1993).

The reproductive success of a spotted hyena male may not be directly linked to his investment in building relationships with and defending females, but rather depend on female mate choice. The strength of male-female bonds may influence female mate choice, but other factors such as genetic quality may also be involved. In the Serengeti, where females commute and breed

throughout the year, female mate choice is likely to be restricted to those males that are present in the clan territory during her period of estrus (East and Hofer, 2001).

XI. NATAL POSTDISPERSAL MALES

It was thought that male spotted hyenas always disperse from their natal groups (Kruuk, 1972; Frank, 1986a,b; Mills, 1990). However, in the Serengeti sexually mature males do not always disperse. In contrast to immigrant males, natal males that do not disperse acquire top rank in the male social hierarchy soon after they begin to compete with immigrant males for access to females. Genetic analysis of paternity has demonstrated that these natal postdispersal males father cubs (M. L. East, H. Hofer, T. Burke, and K. Wilhelm, unpubl. data), so a lack of dispersal does not prevent successful reproduction. Holekamp and Smale (1998) have suggested that low levels of testosterone in natal males before they disperse may be due to persistent exposure to female kin, and that following dispersal and exposure to novel sexually receptive females in a new clan, male testosterone levels increase. However, the existence of reproductively active, postdispersal natal males in Serengeti clans suggests that testosterone levels in males may be more closely linked to male-male conflict over access to mates (Goymann, 1999). It is probable that natal postdispersal males gain immediate high rank in the immigrant male hierarchy due to the social dominance they acquired from their mother over all immigrant males during their development. Natal males are dominant to female clan members ranked below their mother, but when natal males start to compete with immigrant males for access to females they habitually submit to and are socially subordinate to the females they previously dominated (East and Hofer, 2001). This reversal of behavior is not due to increased aggressiveness from adult females, but rather because postdispersal males habitually submit when they begin to approach clan females as potential mates.

XII. CONFLICT RESOLUTION

Much has been written about conflict and aggression in hyena society but affiliative behavior, cooperation, and conflict resolution among clan members has received much less attention. There is certainly conflict among members of spotted hyena clans over access to resources, but there is also much cooperation. Coalitions are important for the maintenance of social status in both male and female dominance hierarchies (East *et al.*, 1993; Hofer

and East, 1996; East and Hofer, 2001). Clan members also cooperate in the acquisition and defense of carcasses against intra- and interspecific competition, defense of territory boundaries against neighboring groups, defense of young at the communal den against predators, group hunting and allo-suckling (Kruuk, 1972; Mills, 1985; East and Hofer, 1991b; Knight *et al.*, 1992; East *et al.*, 1993; Hofer and East, 1993c). Thus clan members need to strike a balance between conflicts that arise in competitive situations and the cooperative pursuit of shared interests against clan members, competitors from other clans, and interspecific predators and competitors (Hofer and East, 2000).

When members of a hyena clan meet, they often participate in a greeting ceremony in which two animals stand side by side, head to tail, with their hind legs lifted while they investigate each other's anal-genital area (Wickler, 1965). We have shown that greetings are ritualized ceremonies in which socially subordinate animals actively signal submission to more dominant group members (East *et al.*, 1993). The distribution of chosen greeting partners is consistent with the distribution predicted by optimality models of primate affiliative behavior that assume that individuals value social relationships as a resource (Table I, Seyfarth, 1977). Thus, hyena greeting ceremonies help to build relationships in a manner reminiscent of grooming in primates, and thus contribute to the stability of the social hierarchy (East *et al.*, 1993).

If female spotted hyenas value relationships with other females in their clan, in a similar manner to that seen in primates (Seyfarth, 1977), then a conflict that is behaviorally expressed as an aggressive encounter might damage that relationship (de Waal and van Roosmalen, 1979). If so, both opponents might be expected to actively repair the damage to the relationship by initiating neutral or friendly reunions after an aggressive encounter. We have shown that the behavior of females after an aggressive encounter differs from that before the encounter. Losers are more likely to initiate a friendly reunion than winners, and the probability of losers initiating a friendly reunion increases if after the initial conflict there is an escalated conflict with further aggression between opponents (Hofer and East, 2000).

In a fission–fusion society, individuals have the option to reduce conflict by simply avoiding possible sources of conflict. For example, in the Serengeti, subordinate females undertake long-distance foraging trips more often than dominants (see earlier) and by doing so reduce possible conflict with dominant females over food resources within the territory. We predict that simple avoidance of conflict may be a more common tactic in fission–fusion societies than in more close-knit societies and that active reconciliation may be a more prominent aspect of close-knit societies (Hofer and East, 2000).

XIII. CONCLUSION

Previously it has been assumed that the evolution of female dominance, the masculinization of female genitalia, and siblicide in spotted hyenas was driven by selection for elevated levels of androgens that increased female aggressiveness and body size. We argue that current knowledge of the ecology, behavior, and endocrinology of spotted hyenas does not support this view. Adult female spotted hyenas do not have abnormally elevated levels of androgens, and female aggression should not be seen as the only force that shapes hyena social life. Cooperative and affiliative behaviors that foster the maintenance of relationships are equally important in the functioning of hyena society.

To explain habitual submission by males to females we link female control over copulation with their enlarged clitoris or pseudo-penis. As males are unable to mate with uncooperative females they need to cultivate relationships with females. We suggest that habitual submission is an important part of this process. We propose that female control over mating has also reduced selection for male fighting prowess, as relationships with females are a non-transferable resource. This, we suggest, has led to the observed low levels of physical male-male conflict, to a lack of a correlation between social status and plasma androgen levels in immigrant males, and to the evolution of a male social queue.

There is little evidence to support the notion that elevated levels of androgens in both male and female neonates is a by-product of selection for androgenized, large, aggressive adult females. Data from free-ranging hyena populations also cast doubt on the idea that androgenized neonates commit "habitual" (obligate) siblicide in same-sexed twin litters. Sibling rivalry in spotted hyenas is linked to levels of maternal provisioning of milk, and facultative siblicide occurs when the milk supplied by mothers is insufficient to support twin litters.

XIV. SUMMARY

It has been proposed that the evolution of female dominance in spotted hyenas (*Crocuta crocuta*) was due to selection for increased levels of androgens leading to increased aggressiveness and body size as well as to the development of an enlarged penile clitoris. Siblicide in spotted hyena twin litters has also been viewed as a by-product of selection for androgenized, aggressive adult females. These ideas, however, do not fit current knowledge of the behavior, ecology, and endocrinology of this species. We outline an alternative route to female dominance that links female control

over mating (due to their enlarged clitoris) to the need for males to establish relationships with females before successful copulation is possible. This idea provides a likely explanation for habitual male submission to females, for low levels of aggression among competing males, for a lack of association between male social status and plasma androgen concentration, and for the investment by males in establishing relationships with females. Relationships with females improve with male tenure and are a nontransferable resource, and these are factors that are likely to have contributed to the evolution of a queue for social status among immigrant males. Free-ranging adult female spotted hyenas have perfectly ordinary, and thus not abnormally elevated, levels of androgens, and dominance in spotted hyena society is not related to body size. Hence, the assumed link between androgens, aggression, and body size does not exist. Aggression is not the only means of resolving conflicts among females, and there is substantial evidence that social relationships are a resource valued by females. As females that receive antiandrogen treatment during fetal development still develop an enlarged clitoris, androgen-dependent mechanisms are unlikely to be solely responsible for the development of this structure. Elevated levels of androgens in neonates of both sexes do not result in the "habitual" (obligate) death of a cub in same-sexed twin litters, and they are unlikely to result in contrasting behavior in adults (increased aggression in females, decreased aggression in males). Elevated levels of androgens in neonates are more likely linked to sibling rivalry and facultative siblicide when the milk provided by mothers falls below the level required to rear two cubs.

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