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The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas

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Abstract. In East Africa, spotted hyenas live in large clans in a highly structured society dominated by females. A clan is a fission-fusion society where members are often solitary or in small groups. Spotted hyenas have a ritualized greeting during which two individuals stand parallel and face in opposite directions. Both individuals usually lift their hind leg and sniff or lick the anogenital region of the other. The unique aspect of greetings between individuals is the prominent role of the erect 'penis' in animals of both sex. Female spotted hyenas have fused outer labiae and a 'pseudo-penis' formed by the clitoris which closely resembles the male penis and can be erected. During greetings subordinates signalled submission with gestures which were not necessarily reciprocated by the dominant participant. Asymmetries were most pronounced in greetings between adult females where the probability of asymmetries increased with the divergence in rank between partners. Greetings between adult females and males were uncommon and restricted to males above median rank, principally the alpha male. Models of primate affiliative behavior assume that benefits derived from social relationships with different individuals are not equal and that individuals are selected to maximize the benefits they receive from social relationships with others. The observed distribution of greetings between partners of different rank matched the predictions of these models. An examination of non-adaptive hypotheses on the evolution of the 'pseudo-penis' demonstrated that the conventional scenario linking (initial) virilization of female genitalia with selection for female dominance does not explain either the initial virilization, nor the evolution of the 'pseudo-penis' to its current form and use. We sketch a new scenario that links (1) initial virilization to the occurrence of neonatal siblicide amongst members of a twin litter, and (2) costs of maintenance, 'pseudo-penile' control over copulation and male submission. Our analysis confirms previous adaptive hypotheses on the function of the 'pseudo-penis' in greetings and suggests new hypotheses to account for hitherto unexplained features.

Key words: Hyena communication – Female-dominated – Penis submission

Introduction

In many social mammals, subordinate individuals actively submit to dominants during ritualized greetings that confirm asymmetries in relationships between greeting partners (Schenkel 1967; Mech 1970; Klingel 1972; de Waal 1982; Colmenares 1990). In the Serengeti, spotted hyenas live in a highly structured society in large, stable groups called clans (Hofer and East 1993a, b, c). Females are dominant over males and within clans there are separate female and male dominance hierarchies (Kruuk 1972; Frank 1986b; Mills 1990; East and Hofer 1991a). A clan is a fission-fusion society, where members are often solitary or occur in small groups (Kruuk 1972; Mills 1985). Individuals participate in greetings (Wickler 1964; also termed meeting ceremonies, Kruuk 1972; Mills 1990) most often when they initially encounter another clan member, but greetings also occur when individuals have been in each others' company for some time (Kruuk 1972; Mills 1990). If greetings in spotted hyenas are used to actively confirm asymmetries in social status between greeting partners, we predict that (1) subordinates should initiate greetings more often than dominants; (2) greeting gestures should reliably distinguish the relative rank of a greeting partner; (3) asymmetries in the display of greeting gestures should be most pronounced when greetings involve participants that differ widely in social status.

In primates, affiliative social interactions such as grooming are important in the formation and maintenance of social bonds (Fairbanks 1980; Silk et al. 1981; Mehlman and Chapais 1988). If social bonds have long-term implications for the individuals involved (Dunbar 1980; Seyfarth 1983; Seyfarth and Cheney 1984) and

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the benefits obtained from affiliative social interactions are not equal for all members of a group, individuals should preferentially seek affiliative interactions with those group members that can provide benefits (Cheney and Seyfarth 1990). This implies that there is an optimal set of group members with which each individual should try to interact (Seyfarth 1977, 1983). Here we describe the distribution of greetings between clan members visiting the communal den and assess this distribution in the light of predictions about the selection of grooming partners in primates with linear dominance hierarchies (Seyfarth 1977, 1983; Dunbar 1980; Cheney and Seyfarth 1990).

A unique aspect of greetings between spotted hyenas is the prominent role of the erect 'penis' in animals of both sex. Female spotted hyenas have a 'pseudo-penis' formed by the clitoris which closely resembles the male penis in form and size (Frank et al. 1990) and can be erected (Matthews 1939; Neaves et al. 1980; Frank et al. 1990). There is no vulva, the labiae are fused and the urogenital tract passes through the clitoris. Greetings typically involve two hyenas standing parallel, facing in opposite directions. The hind leg nearest the animal being greeted is usually raised while each animal sniffs or licks the erect 'penis' (Wickler 1964; Kruuk 1972; Mills 1990), and the anal scent gland (personal observation) of its partner. There has been a long-running debate about the evolution, ontogenetic development and function of the female 'pseudo-penis' of spotted hyenas, on both proximate and ultimate levels, but centered mainly around the role of the 'penis' in greeting ceremonies (see Wickler 1964, 1965a, b; Kruuk 1972; Racey and Skinner 1979; Gould 1981; Gould and Vrba 1982; Lindeque and Skinner 1982; Hamilton et al. 1986; Lindeque et al. 1986; van Jaarsveld and Skinner 1987; Sherman 1988; Frank et al. 1991). Hamilton et al. (1986) stated that the display of an erect 'penis' in spotted hyenas is correlated with low social status, but prior to the present study no quantitative data were available on the use of this signal by individuals of different sex and social status. As we will show, the use of an erect 'penis' as a signal of submission is unique to spotted hyenas. We will therefore consider the current information available on the development of the female 'pseudo-penis' and its use as a signal in greeting ceremonies. We will then suggest a new approach to this topic.

Methods

Study clans. Data were collected from two clans between June 1987 and April 1992. The majority of the data were collected during observation periods at communal dens. Individuals in both clans were recognized by their spot patterns, scars and other natural features such as ear 'notches'. All clan members were individually known (Hofer and East 1993a). Individuals were sexed using differences in body outline (Frank 1986a), reproductive status (lactation), examination of hair and histological samples (Wurster et al. 1970; Yost 1977) and, from the 3rd month of age onwards, the shape of the phallic glans (Frank et al. 1990). Females were philopatric and each clan contained several matrilines. Females were classified as adults when they reached 3 years of age (Hofer and East 1993a). Males were classified as adults when they reached 2 years of age, and most males dispersed from their natal clan after this age (Hofer and East 1993a). Some males remained with their natal clans for several months after they reached maturity. All reproductively active males within each clan were known or assumed to be immigrants. The two study clans held territories at the woodland/plains boundary in the Serengeti National Park. For details on the social and spatial behavior of clans in the Serengeti see Hofer and East (1993a, b, c). Both study clans were habituated to the presence of a vehicle at the den.

Data collection. Data used in this analysis were of two kinds. (1) From behavioral data recorded mainly at dusk (approximately 1700–2000 hours) and dawn (approximately 0600–0900 hours) at communal dens between June 1987 and March 1992, we extracted the identity of animals that participated in 3396 greetings. These data were used to describe the distribution of greetings between clan members of different sex, age and social status, and included greetings involving 50 adult females, 29 immigrant males, 23 subadults, and 100 cubs. (2) Detailed records of the behavior of individuals involved in 1530 greetings observed between April 1988 and April 1992; these records included: date; time; identity of participants; who initiated the greeting; how the greeting was initiated; which participant lifted its leg first, the position of the leg and tail of both partners; which participants had their 'penis' erect; for how long each partner lifted its leg; the behavior and vocalizations of both partners during the greeting; which partner terminated the greeting; how the greeting was terminated; the total time of the greeting measured from when both partners stood head to tail until they separated. This sample included 47 adult females, 35 adult males, 32 subadults and 55 cubs.

Data analysis. The social rank of adult clan members was based on an interaction matrix using aggressive actions (lunging, chasing, biting, pushing), and submissive reactions (retreat, cower, ears down, tail between legs) in dyadic interactions recorded *ad libitum* (see Frank 1986a; East and Hofer 1991a). This produced a linear hierarchy for both adult females and males. In one clan the hierarchy showed no rank reversals during the study, but death and immigration resulted in shifts in rank. In the second clan rank reversals occurred when the alpha matriline (alpha female plus her two reproductive daughters) were deposed by a coalition of four mid-ranking females. Participants in greetings were therefore assigned a rank appropriate for the day on which the greeting occurred. Holekamp and Smale (1991) have shown that spotted hyena cubs typically 'inherit' their social rank from their mother. For the purpose of comparing social dominance between cubs we assigned cubs the social rank of their mother. This index of a cub's social status was also used to consider the importance of a cub's social status during greetings with other clan members.

The number of potential greeting partners present at communal dens varied with prey availability within a clan territory, and the number of females with dependent cubs in the den (Hofer and East 1993c), and thus need to be corrected for den attendance. We carried out significance tests on the distribution of greeting frequencies by comparing the number of observation periods where at least one greeting between individuals of a given pair of categories occurred with the number of observation periods where at least one individual of both categories was present. One observation period is equivalent to 2–3 h of observation (East and Hofer 1991b). For assessing the distribution of greetings of immatures with adult females and immigrant males we calculated individual greeting rates per hour for each adult rank. We scored time at the den by following the procedures outlined in East and Hofer (1991b).

For significance tests concerning greeting gestures, data were summarized per individual (Machlis et al. 1985). In tests where we related social status to greeting gestures that could be expressed separately by both greeting partners we proceeded as follows. For greetings between individuals of the same category and if sample sizes were sufficient, we matched the response of each individual when it was dominant with its response when it was subordinate and tested for differences in response due to social status with a Wilcoxon signed-rank test. A score was the number of greetings when, for instance, an individual as the subordinate partner lifted its leg divided by the number of greetings the individual participated in as a subordinate partner. As these tests exclude top- and bottom-ranking individuals the results are conservative. When sample size was insufficient for such comparisons we compared the scores summarized per individual of dominants with those of subordinates using a Mann-Whitney *U*-test. In mixed-category greetings, differences in the use of gestures between categories was also tested with a *U*-test. Unlike greeting gestures that were displayed by each greeting partner, scoring of who initiated and who terminated a greeting was common to both participants. In assessing the relationship of social status to initiation and termination in mixed-category greetings we therefore used Wilcoxon signed-rank tests to compare the score of the subordinate and dominant category summarized for each individual that belonged to the subordinate category. If an individual was involved in less than three greetings within a particular test group, it was excluded from the analysis.

Statistical and graphical analyses were performed on a personal computer using SYSTAT 5.0 (Wilkinson 1990). All probabilities were two-tailed. Regression residuals were tested for normality using the Lilliefors test as implemented in SYSTAT (using corrected *P*-values, see Wilkinson 1990). For all models examined, residuals were normally distributed. Nonlinear models were preferred if their fit was substantially better than linear models.

Table 1. Frequencies of greetings between different age and sex categories

Greeting partners		Frequency	Percentage
ADULTS	SAME SEX		
Female	female	618	18.7
Male	male	169	5.1
ADULTS	MIXED SEX		
Female	*natal male*	69	2.1
Female	*alpha male*	24	0.7
Female	*immigrant male other than alpha*	14	0.4
Female	male (total)	107	3.2
ADULTS	IMMATURES		
Female	immature	1299	39.4
Male	immature	467	14.1
IMMATURES	IMMATURES		
Immature	Immature	641	19.4
Total		3301	100.0

Immature includes subadults and cubs

Results

The mean duration of a greeting ceremony between two hyenas was 19.9±19.7 s ($\bar{X}\pm$S.D., $n=1259$). Amongst greetings between adults, those between females at 24.3±20.6 s ($n=230$) lasted significantly longer than greetings between males at 14.2±12.8 s ($n=97$) or between males and females at 16.2±14.6 s ($n=43$; Kruskal-Wallis test $H=32.74$, $df=2$, $P<0.0001$, and *a posteriori* multiple comparisons, Conover 1980, p. 231). Table 1 displays the frequency of greetings between different age/sex categories at the communal den. Amongst adults, 69% of all greetings were between females, 19% between males and only 12% were between adults of different sex. Greetings between females and natal males (prior to their dispersal) made up 64% of mixed-sex greetings between adults. When correcting for den attendance, (1) adult females greeted natal males significantly more frequently than immigrant males ($G_1=23.35$, $P<0.0001$), (2) greetings between immigrant males and adult females occurred significantly less often than either immigrant male/immigrant male ($G_1=19.78$, $P<0.0001$) or female/female greetings ($G_1=89.18$, $P<0.00001$). The majority (63%) of greetings between immigrant males and females involved the alpha male. With one exception, all other immigrant males that greeted adult females were above median rank, and thus immigrant males above median rank greeted adult females more frequently than males below median rank after correcting for den attendance ($G_1=20.60$, $P<0.0001$). The majority of immigrant males were never observed to greet an adult female.

In contrast to greetings between adults, a large proportion (51%) of greetings between immatures involved individuals of the opposite sex. Immatures of both sex greeted both adult females and immigrant males. There was no significant relationship between the frequency of greetings between immatures and adult females and adult female rank (Fig. 1 a). In contrast, there was a rapid decline in the frequency of immature greetings with immigrant male rank. Immatures rarely greeted low-ranking adult males but frequently greeted the alpha male (Fig. 1 b).

Initiation

We identified the individual that initated a greeting by two criteria. (1) The individual that directly approached an animal which it then greeted. By this criterion, adult females initiated greetings more often when they were the subordinate participant than when they were the dominant participant. Younger participants also initiated more often than older participants (Table 2). (2) Kruuk (1972) defined the initiator as the animal that lifted its hind leg first. Applying this criterion, individual adult females initiated greetings more often when they were the subordinate participant than when they were

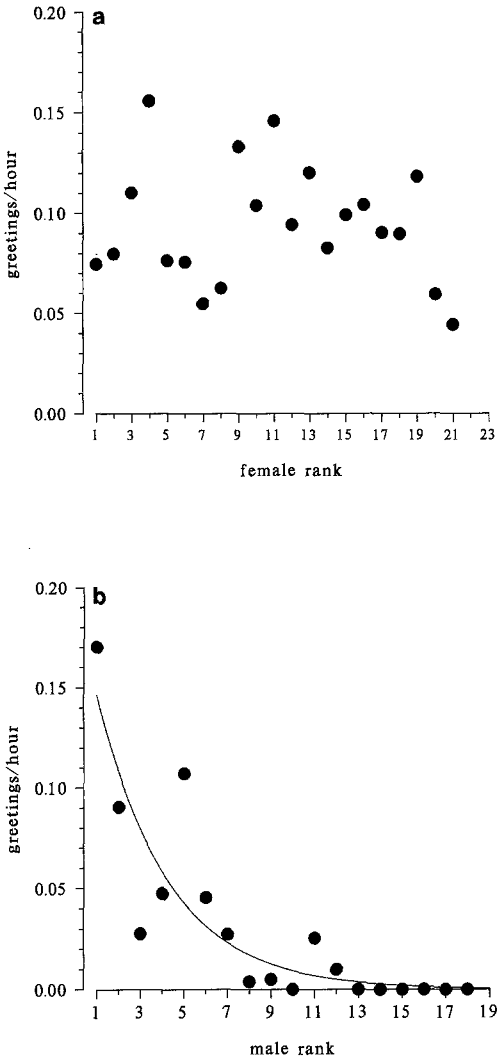

Fig. 1 a, b. The rank of adults greeted by immatures (i.e. cubs and subadults). **a** Adult females (Spearman's $\rho=0.04$, NS); **b** immigrant males ($Y=0.199\times \mathrm{EXP}(-0.306\,X)$, $t_{\mathrm{slope}}=4.127$, $df=16$, $P<0.001$, $r^2=0.77$)

dominant. In greetings between immigrant males and adult females, males lifted their legs first in all greetings except one. In greetings between individuals from different age categories, younger individuals initiated by lifting their leg first more often than the older participant.

In 18% of greetings between adult females and 6% of greetings between adult males a dominant animal appeared to force a subordinate to greet by pushing at the side or beneath the hind leg of the subordinate, or by standing over the subordinate while it was lying or nursing cubs (difference $G_1=11.32$, $P<0.001$). The frequency of forced initiation was independent of the difference in rank between female participants (considering females with a difference of 1–4, 5–8, and 9–14 rank positions: $G_2=3.23$, NS).

Following intrasexual agonistic encounters between adults, the 'loser' occasionally greeted the 'winner' of the encounter. The initiation of greetings as a form of reconciliation or appeasement accounted for 8% of greetings between adult females and 9% between adult males.

Greeting gestures

Greetings involved ritualized gestures, but the display of gestures was not necessarily symmetrical in both greeting partners. Three body parts were involved in the most prominent gestures displayed during a greeting: the hind leg (lifted or not lifted); the 'penis' (erect or not erect) and the tail. There were four possible tail positions: (1) relaxed, i.e. hanging down and covering the sub-caudal scent-gland (see Kruuk 1972, Fig. 58c); not considered a special gesture below; (2) tail held between the hind legs and curled along the belly (see Kruuk 1972; Fig. 58d), covering the sub-caudal scent gland [this is a submissive signal used by subordinates in agonistic interactions (unpublished data)]; (3) tail root held horizontally away from the body, thereby exposing the

Table 2. Relative rank and likelihood of initiation of a greeting

Greeting partners		Initiation by approach Wilcoxon signed-rank test			Initiation by lift leg first Wilcoxon signed-rank test		
		z	*P*	*n*	*z*	*P*	*n*
Adult female	adult female	3.102	<0.002	17	3.172	<0.0002	18
Immigrant male	immigrant male	1.153	NS	6	2.201	<0.03	6
Subadult	adult female	−2.359	<0.02	13	−2.399	<0.02	12
Subadult	immigrant male	[a]		0	[a]		0
Cub	adult female	−2.007	<0.05	37	−5.022	<0.00001	38
Cub	immigrant male	−3.759	<0.002	21	−2.053	<0.04	14
Cub	subadult	1.746	NS	10	[a]		6
Cub	cub	0.586	NS	8	[a]		5

An individual was scored as initiator if it (1) approached its greeting partner, (2) was the individual to lift its hind leg first. Significant results indicate that the subordinate/younger of two greeting partners was significantly more likely to initiate the greeting than the dominant/older partner. Sample sizes are the number of individuals with sufficient data for each test

[a] Sample sizes too small for tests to be meaningful

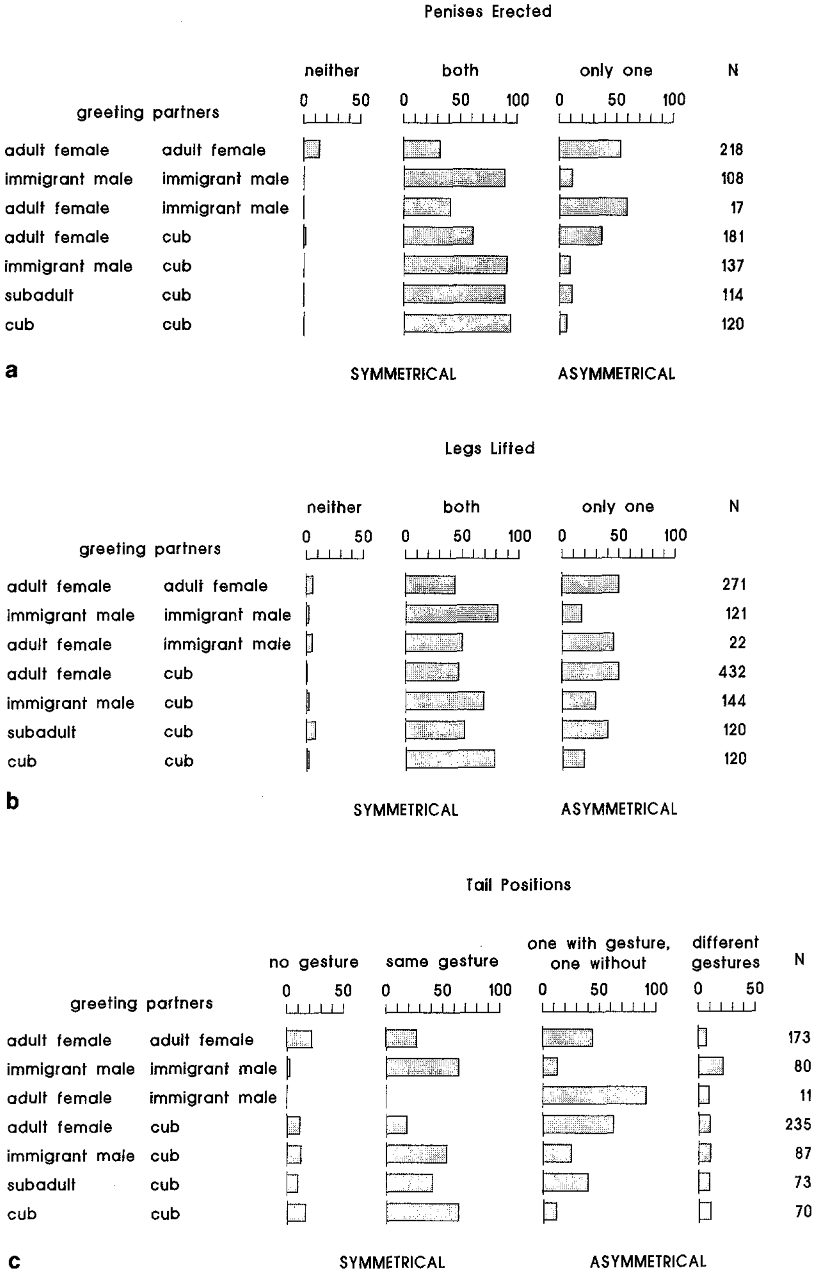

Fig. 2a–c. The proportion of greetings where (1) either both or none of the partners displayed a particular greeting gesture (symmetrical greeting), (2) one partner displayed a particular greeting gesture while the other one did not, and in the case of tail position, the two partners displayed different kinds of gestures (asymmetrical greeting). Gestures are **a** erection of 'penis', **b** lifting of the hind leg, **c** various tail positions

sub-caudal scent-gland (see Mills 1990, Fig. 5.4); (4) tail held vertically upwards (see Kruuk 1972, Fig. 58a, b) exposing the sub-caudal scent-gland. A tail in this position typically is a signal of aggression but it has also been attributed to extreme "social attraction" (Kruuk 1972).

Figure 2 shows the proportion of greetings where (1) either both or neither of the participants displayed a particular greeting gesture (symmetrical greeting), (2) one participant displayed a particular gesture while the other one did not, or in the case of tail position, the two partners displayed different kinds of gestures (asymmetrical greeting). The asymmetric display of an erect 'penis' was common in greetings involving adult females (Fig. 2a). Greetings not involving adult females were typically symmetrical with both partners displaying an erect 'penis'. Symmetrical greetings where neither participant erected a 'penis' were most frequent between adult females. Considering the lifting of a hind leg (Fig. 2b), asymmetrical greetings during which only one participant lifted a hind leg were most common in greetings involving adult females. Greetings involving other age/sex categories were typically symmetrical with both participants lifting a leg. Instances where both participants failed to lift their legs were rare. In contrast to the two previous gestures there was a large proportion of greetings between adult females where neither participant used tail position as a gesture. Overall, tail position was less commonly used as a gesture than the position of the 'penis' or leg (Fig. 2c). For leg, 'penis' and tail position, greetings between adult females and immigrant males were asymmetrical in the majority of cases, while greetings between immigrant males and between cubs were rarely asymmetrical (Fig. 2a–c).

Table 3. The use of two greeting gestures ('penile erection' and lifting of hind leg) by partners of different social status, sex and age

Greeting partners		'Penis' erect Wilcoxon signed-rank test			Leg lifted Wilcoxon signed-rank test		
		z	P	n	z	P	n
Adult female	adult female	2.722	<0.01	17	2.417	<0.02	18

		Mann-Whitney U-test				Mann-Whitney U-test			
		U	P	n_1	n_2	U	P	n_1	n_2
Immigrant male	immigrant male	44	<0.02	14	12	41	NS	10	12
Adult female	immigrant male	[a]		3	5	[a]		3	5
Subadult	adult female	29.5	<0.001	15	14	72	<0.003	17	20
Subadult	immigrant male	[a]		1	1	[a]		1	1
Cub	adult female	66	<0.00001	50	30	138	<0.00001	51	33
Cub	immigrant male	111	<0.001	30	14	143	NS	30	14
Cub	subadult	135.5	NS	20	16	108	<0.03	20	17
Cub	cub	35	<0.03	10	12	27	NS	6	15

Significant results indicate that the subordinate or younger of two greeting partners was significantly more likely to use the gesture than the dominant/older partner. Sample sizes are the number of individuals with sufficient data for each test

[a] Sample sizes too small for tests to be meaningful

If exposing the scent-gland during a greeting serves to emphasize an individual's clan membership or more specifically its identity (see Discussion), then we would expect categories of individuals that meet less frequently to expose their scent-gland more often than categories of individuals that encounter each other frequently. We would then predict (see Discussion) that adult females, in particular nursing females, that are present at the communal den more frequently than adult males (Hofer and East 1993c) to expose their scent-gland less frequently than adult males. This was the case ($G_1 = 50.21$, $P < 0.00001$).

Dominance and greeting gestures

Do subordinates differ from dominants in their use of particular gestures? Individual adult females were more likely to erect their 'penis' and lift their legs when they were the subordinate participant than when they were the dominant participant (Table 3). In greetings between immigrant males, subordinates were more likely than dominants to erect their 'penis', but social status did not influence leg lifting. During greetings between cubs, subordinates were more likely than dominants to erect their 'penis', but cub rank did not influence leg lifting (Table 3). During greetings between different age classes, the younger individual was more likely than the older participant to erect its 'penis' or lift its leg, except for leg lifting during greetings between cubs and immigrant males.

As the rank of adult females declined, the proportion of greetings in which they erected their 'penis' (Spearman's $\rho = 0.619$, $df = 19$ ranks, $P < 0.01$) or lifted their legs to cubs ($\rho = 0.609$, $df = 19$, $P < 0.01$) increased. Also, the proportion of 'penile' erections by adult females when greeting cubs grew as the difference in rank between the adult female and that of the cub, i.e. originally the rank of the cub's mother, increased ($\rho = 0.486$, $df = 18$, $P < 0.05$). There was no such correlation with leg lifting.

During greetings between adult females, each female was more likely to provide access to its caudal scent-gland when it was the subordinate participant than when it was dominant. This was true for tails held horizontally from the body (Wilcoxon signed-rank test, $z = 2.24$, $P < 0.01$, $n = 23$) and for tails held vertically up ($z = 2.07$, $P < 0.05$, $n = 18$). As the rank difference between greeting females increased the proportion of subordinates that held their tail up also increased ($\rho = 0.679$, $df = 11$, $P < 0.05$). Low-ranking females less often had their tails relaxed or their caudal scent-gland covered than high-ranking females ($\rho = 0.636$, $df = 15$, $P < 0.02$). As rank difference between adult female greeting partners increased so did the proportion of subordinate participants that held their tails between their legs ($\rho = 0.699$, $df = 10$, $P < 0.05$). Thus low-ranking females preferentially use two extreme tail positions ('tail between legs' and 'tail held vertically up') when greeting high-ranking females.

During greetings between immigrant males, the subordinate participant was less likely than the dominant to have its tail relaxed (Mann-Whitney U-test, $U = 284$, $n_1 = 18$, $n_2 = 21$, $P < 0.001$). The same was true of subordinate cubs when greeting dominant cubs ($U = 36$, $n_1 = 6$, $n_2 = 7$, $P < 0.02$). Cubs also used 'tails between legs' as a submissive gesture when greeting adult females. Cubs of low-ranking females were more likely to use this gesture than cubs of higher ranking mothers ($\rho = 0.467$, $df = 19$, $P < 0.05$). In addition, as the status of a cub's mother

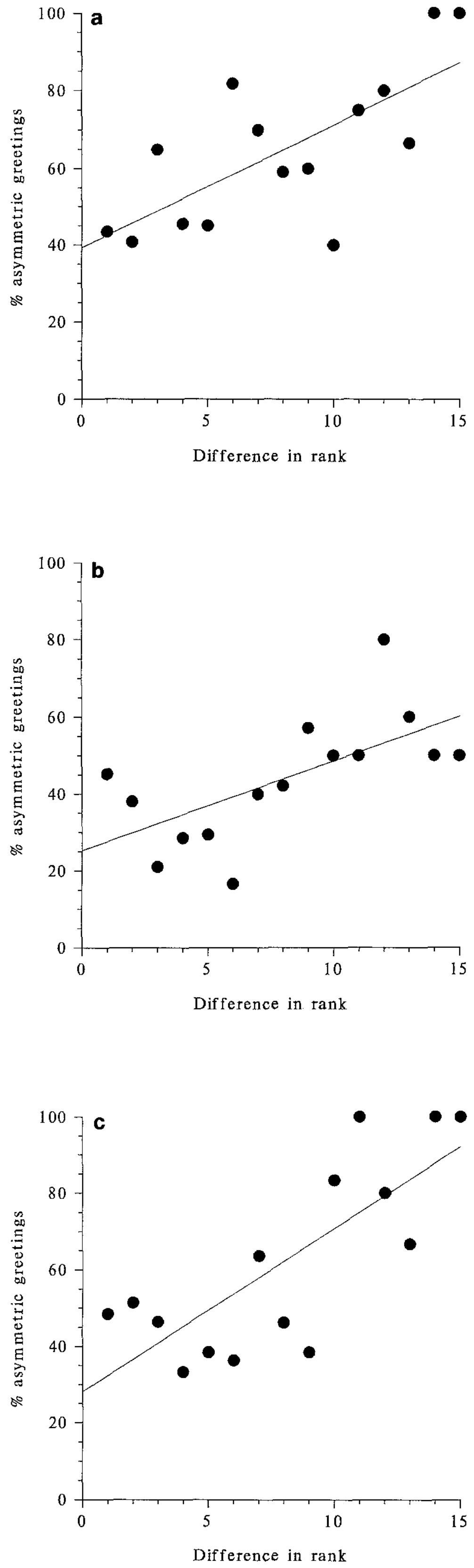

Fig. 3a–c. Percentage of greetings between adult females that were asymmetric in gesture in relation to the difference in the rank of greeting partners: **a** erection of 'penis', $Y=39.25+3.195\,X$, $F_{1,13}=13.52$, $P<0.003$, $r^2=0.51$; **b** tail position, $Y=25.29+2.324\,X$, $F_{1,13}=9.20$, $P<0.01$, $r^2=0.42$; **c** leg position, $Y=28.09+4.262\,X$, $F_{1,13}=19.30$, $P<0.001$, $r^2=0.60$

declined the proportion of greetings in which cubs held their tails horizontally from the body increased when greeting adult females ($\rho=0.639$, $df=15$, $P<0.02$).

Amongst adult females, there was a positive linear association between the proportion of asymmetrical gestures and the degree of divergence in rank (Fig. 3). We found no such significant associations in greetings between adult males and greetings between cubs. We assessed asymmetry in the duration of leg lifting in relation to rank by scoring a difference in duration of leg lifting with a (1) negative sign if the dominant lifted its leg longer, (2) positive sign if the subordinate lifted its leg longer. Subordinates lifted their legs for a significantly longer time than dominants in greetings between adult females ($U=0$, $n_1=6$, $n_2=6$, $P=0.003$) and immigrant males ($U=0$, $n_1=6$, $n_2=10$, $P=0.001$). Among adult females, there was also a positive association between the difference in the duration each leg was lifted and the difference in rank that approached significance ($\rho=0.508$, $df=14$ means of time differences, one for each rank difference, $P=0.075$). This was not the case for adult males ($\rho=0.500$, $df=9$, NS).

Termination

Most greetings were terminated by one animal walking, running or jumping away from its partner (Table 4). Sometimes one greeting partner lunged at or bit the other, or termination occurred because individuals other than the greeting partners became involved. In these cases a greeting participant was threatened or chased by an individual not involved in the greeting or a greeting participant chased a third individual. The relative frequency of different types of behavior terminating greetings varied between different age/sex categories (Table 4). The highest frequency of aggressive terminations occurred at the end of greetings between adult females, and greetings between adult females were most frequently interrupted by interference from an individual not involved in the greeting.

In greetings between immigrant males, subordinates were more likely to terminate greetings than dominants (Table 5). This was not the case for greetings between adult females, or between cubs. In greetings between age categories, younger partners terminated greetings more frequently than dominants except for greetings between cubs and males (Table 5).

Greetings within matrilines

In this analysis, only offspring born or nursed during the period of the study were considered members of a particular maternal lineage. Of the total number of greetings ($n=225$) involving alpha females, 39% were with individuals known to be direct descendants of these alpha females. This contrasts with all other females whose greetings involved an offspring only in 5% of all cases ($n=514$). Thus, the offspring of alpha females greeted their mothers more frequently than offspring of

Table 4. Percentage of occurrence of behaviors used by different age/sex categories to terminate a greeting

Category		Behaviors involving greeting partners only		Behaviors involving individuals other than greeting partners		n
		Turning, walking, running, jumping away from partner	Lunge or bite partner	Threatened or chased away by individual not involved in greeting	Chases uninvolved individual	
Adult female	adult female	77.5%	12.9%	7.6%	2.0%	249
Immigrant male	immigrant male	95.2%	1.8%	2.8%	0.9%	106
Adult female	immigrant male	90.0%	5.0%	5.0%	0.0%	20
Adult	subadult	86.2%	10.9%	0.0%	2.9%	138
Adult female	cub	89.8%	6.8%	2.9%	0.5%	383
Immigrant male	cub	91.7%	4.1%	4.1%	0.0%	145
Subadult	cub	92.1%	4.9%	2.0%	1.0%	101
Cub	cub	87.9%	7.1%	5.1%	0.0%	99

Table 5. Relative rank and likelihood of termination of a greeting

Greeting partners		Wilcoxon signed-rank test		
		z	P	n
Adult female	adult female	1.018	NS	17
Immigrant male	immigrant male	2.665	<0.01	9
Cub	cub	1.742	NS	13
Subadult	adult female	2.229	<0.03	23
Subadult	immigrant male	2.666	<0.01	9
Cub	adult female	5.816	<0.000001	44
Cub	immigrant male	2.200	NS	23
Cub	subadult	2.263	<0.03	12

Significant results indicate that the subordinate/younger of two greeting partners was significantly more likely to terminate the greeting than the dominant/older partner

lower-ranking females greeted theirs ($G_1=75.85$, $P<0.0001$).

Rank of greeting partners

In order to assess the distribution of greetings of a focal group of adults with adjacent ranks, in relation to the rank of their partners, we used focal groups that included three adjoining rank positions. This had the advantage that the number of unique rank combinations of greetings within the focal group was equal to the number of unique combinations of greetings formed by that focal group with individuals of any of the other rank positions. For instance in the case of high-ranking adult females the group of focal ranks was defined as ranks 1 to 3. This provided for three unique rank combinations within the focal group (between individuals ranked 1 and 2, 1 and 3, and 2 and 3). Similarly, the number of specific rank combinations of that focal group with each rank for positions 4, 5, ... n would be three (e.g. with rank 4 the unique combinations would be 1 and 4, 2 and 4 and 3 and 4).,

Figure 4 illustrates how the frequency of greetings of a focal group of adults was distributed in relation to the rank of their partners. High-ranking females (rank 1–3, $n=304$) greeted mostly other high-ranking females (Fig. 4a) and greeted lower-ranking females progressively less frequently as the divergence in rank between greeting partners increased (Spearman's $\rho=0.89$, $df=17$, $P<0.001$; here and in subsequent tests greetings within the focal category were excluded). Similarly, mid-ranking females (rank 7–9, $n=182$) also greeted each other most frequently (Fig. 4b). The relative frequency of greetings of mid-ranking females with higher ranking females tended to increase with target rank ($\rho=0.81$, $df=6$, $P=0.065$). In contrast the relative frequency of greetings of mid-ranking females with lower ranking females declined with target rank ($p=0.90$, $df=11$, $P<0.001$). No trend was apparent ($\rho=0.27$ NS, $df=14$ higher target ranks) in the distribution of greetings of low-ranking females (rank 15–17, $n=86$). In contrast to the two other focal groups, low-ranking females rarely greeted other females within the focal group (Fig. 4c).

Similar to females, high-ranking males (rank 1–3, $n=64$) preferred to greet other high-ranking males (Fig. 4d). There was a sharp drop in the relative frequency of greetings of high-ranking males with a decline in target rank ($\rho=0.93$, $df=12$, $P<0.001$). In contrast to mid-ranking females, mid-ranking males (rank 7–9, $n=58$) greeted other males in their category very rarely (Fig. 4e) and were mostly involved in greetings with males in rank

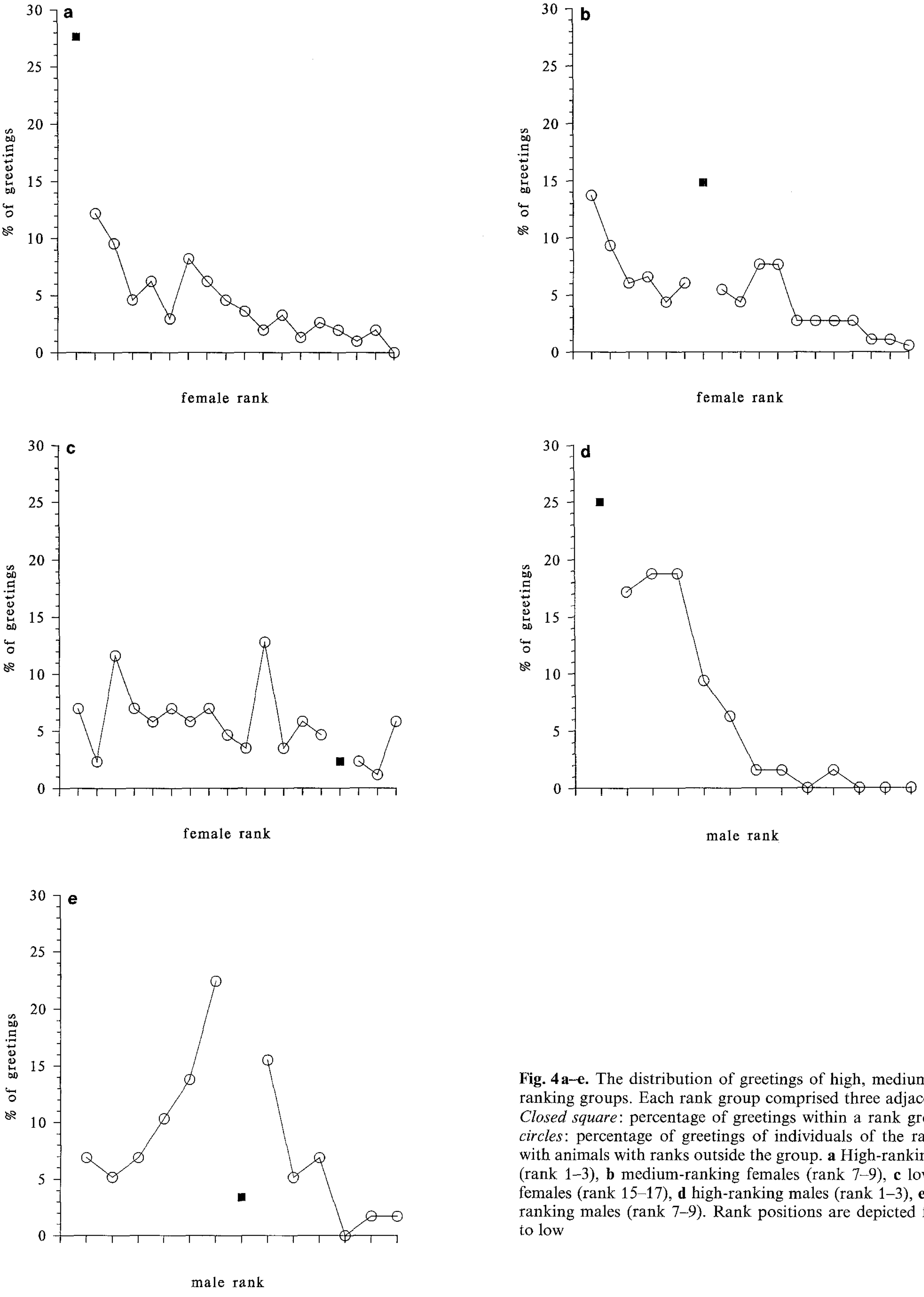

Fig. 4a–e. The distribution of greetings of high, medium and low ranking groups. Each rank group comprised three adjacent ranks. *Closed square*: percentage of greetings within a rank group; *open circles*: percentage of greetings of individuals of the rank group with animals with ranks outside the group. **a** High-ranking females (rank 1–3), **b** medium-ranking females (rank 7–9), **c** low-ranking females (rank 15–17), **d** high-ranking males (rank 1–3), **e** medium-ranking males (rank 7–9). Rank positions are depicted from high to low

categories immediately above and below their own. In particular, the relative frequency of greetings with higher ranking males declined with an increase in target rank ($\rho = 0.90$, $df = 6$, $P < 0.02$). There was a trend that the relative frequency of greetings declined with target rank in greetings with lower ranking males but this was not significant ($\rho = 0.75$, $df = 6$, NS). Low-ranking males were not considered as a focal group due to small sample sizes (we observed a total of 12 greetings by them).

Discussion

Many forms of greetings have been described from social mammals (yellow-bellied marmot, *Marmota flaviventris*: Armitage 1962; Sciuridae: Steiner 1975; African elephant, *Loxodonta africana*: Douglas-Hamilton 1972; zebra, *Equus burchelli*: Klingel 1972; wolf, *Canis lupus*: Mech 1970; wild dog, *Lycaon pictus*: Kühne 1965a, b; domestic dog, *Canis familiaris*: Schenkel 1967; striped hyena, *Hyaena hyaena*: Fox 1971a; brown hyena, *Parahyaena brunnea*: Mills 1990; felids: Leyhausen 1960; primates: Wickler 1965a, b, 1967; Kummer 1968; Nishida 1970; de Waal 1982; Colmenares 1990). In some species greetings permit subordinates to actively submit to dominants; this is also the case in spotted hyenas where greetings are a ritualized, active form of submission that confirm asymmetries in status between greeting partners. Greeting gestures may be derived from juvenile behavior (wolf: Mech 1970; elephant: Douglas-Hamilton 1972; brown hyena: Mills 1990), or reproductive behavior, i.e. presentation by subordinates of both sex and mounting by dominants of both sex (primates: Wickler 1966, 1967; Sugiyama 1971; Jolly 1972; Stammbach 1978; Colmenares 1990). In zebras subordinate males use gestures similar to those diplayed by females in oestrus when greeting dominant stallions (Klingel 1972). Fox (1971b) suggested that in Canidae inguinal and genital presentation is derived from early mother/cub interactions, and the same may be true for anal protrusion in the striped hyena (Fox 1971a). Thus submissive greeting gestures are often derived from behavioral traits typical of subordinate members of social groups, such as juveniles or females in male-dominated societies. Compatible with this line of thinking is the result of this study that in the female-dominated society of spotted hyenas a typically male trait, the erect 'penis', is used as a signal of submission during greetings. In all other mammalian species that use penile displays during interactions, males are dominant to females, and the erect 'penis' is used as a display of dominance (Ploog and MacLean 1963; Wickler 1967; Anthoney 1968; Jolly 1972; Weigel 1979). Even among platyrrhine species (*Ateles* spp., *Alouatta* spp.) in which females have an enlarged clitoris, the enlarged clitoris is used by females to display dominance (Ploog 1967).

We propose that by lifting their tails during greetings, spotted hyenas expose their sub-caudal scent gland to advertise by olfactory cues their identity and/or clan membership. Subordinates expose their scent glands more commonly than dominants during greetings. During social interactions, striped hyenas also lift their tails and portrude slit-like scent glands on either side of the anus, a behavior most frequently displayed by subordinates (Fox 1971a). Brown hyenas can distinguish scent-marks of their own group from those of neighbours (Mills et al. 1980) and Mills (1990) has suggested that spotted hyenas may be able to distinguish the scent-marks of clan members. Even if clan members that meet frequently can identify each other by means other than odor, individuals that encounter each other less often may minimize the chance of aggression that could arise from mistaken identity by permitting the inspection of their scent to confirm their identity and clan membership. This may explain why greeting partners that meet infrequently lift their tails and expose their scent-gland more often than partners that regularly meet. We also predict that individuals that had been absent from the den should scent-mark at a higher rate on their return than during periods of frequent den attendance. This hypothesis awaits testing.

Benefits, asymmetries and submission

Here we consider the costs and benefits of greetings and the distribution of greetings amongst clan members. We use models of primate grooming to predict the optimal distribution of greeting partners and compare the predictions with our results.

Greetings may entail costs. Two gestures, the lifting of the hind leg and the erection of the 'penis', expose a vulnerable part of the body to close contact with the jaws of the greeting partner. We have occasionally observed cubs to bite the underside or erect 'penis' of another cub or a subadult during a greeting. Thus there is clearly a potential for injury.

Greetings may also provide benefits. Benefits to adult females include: (1) A mechanism whereby females resolve conflicts in a way that minimises the chance of potentially damaging physical conflicts. Clan cohesion depends on the resolution of conflicts between members. The potential for conflict among female clan members is high, as competition for access to food resources is intense (Kruuk 1972). Typically the alpha female and her matriline dominate large carcasses (Frank 1986b). (2) Affiliative behavior may reduce social stress. Stress can have detrimental effects on the immune system (Sapolsky 1982; Kiecolt-Glaser and Glaser 1991; Munck and Guyre 1991; Alberts et al. 1992) and heart rate (Eisermann 1992). Nursing females attending their offspring at the communal den suffer considerable harassment from dominant females (unpublished data). It is possible that relationships cultivated by subordinate females with dominants reduce the harassment and stress they and their cubs suffer. (3) Affiliative behavior may permit the acquisition and/or maintenance of high rank through the formation of strongly bonded coalitions of females. High rank is important because top-ranking females have shorter interbirth intervals (Frank 1986b), produce cubs at a higher rate, and their cubs grow faster and survive better than those of subordinate females (unpublished data). Coalitions between females play a vital role in the maintenance of rank in captive hyenas (Frank et al. 1989), while in our study population, coalitions of females were able to depose alpha matrilines when they held the numeric advantage. In primates with linear dominance hierarchies, affiliative behavior is thought to help establish and maintain bonds between group members (Seyfarth 1977; Dunbar 1980; Fairbanks 1980; Silk et al. 1981; Cheney and Seyfarth 1990), and coalitions can be important in the maintenance of rank (Datta 1983; Chapais 1988).

It appears that affiliative behavior in female spotted hyenas may be as beneficial as, or even more beneficial than in most primate societies. Our results indicated that females actively signal acceptance of their current relative social status to their greeting partner, and subordinates initiated greetings and displayed greeting gestures more often than dominants. The increase in the proportion of greetings that are asymmetric with the divergence in rank between females indicates that greeting partners were aware of each other's relative rank. This point was also demonstrated by the positive correlation of the relative frequency with which different greeting gestures were used by subordinates with the rank difference between greeting partners. If a subordinate failed to greet a dominant it was sometimes forced into a greeting, suggesting that dominants may view a lack of active submission (i.e. failure to greet) as a challenge.

The benefits of affiliative behavior in males are less obvious than in females, as males are at the bottom of the feeding hierarchy, mate choice is probably controlled by females (East and Hofer 1991 b) and the dominance hierarchy is mainly the result of a queueing system (East and Hofer 1991 b). If male reproductive success is a function of a non-transferable resource, e.g., a special relationship with females (East and Hofer 1991 b, and see below), then acquisition of rank by physical combat between males is unlikely to increase paternity. This may explain why levels of aggression between male clan members are low (Frank 1986 b; East and Hofer 1991 b), why asymmetries in the gestures displayed during greetings between males are less common than in greetings between females, and why, in contrast to females, the number of forced greetings was low. It seems that emphasis of dominance by high-ranking males is less important in immigrant males than females.

Mills (1990) noted that immigrant males never greeted adult females. In this study we found that although immigrant males regularly visited the communal den, with one exception they made no attempt to greet adult females unless they were above median rank. Given the separation of female and male dominance hierarchies and the general intolerance of females to the close proximity of males, the low frequency of greetings between adult females and immigrant males, and particularly the lack of greetings between females and immigrant males below median rank, may be a consequence of males avoiding situations in which they may be injured. Why, then, do males participate in potentially dangerous greetings with females at all? We suggest mixed-sex greetings involving top-ranking males, in particular the alpha male, help to promote their relationships with females, and thus increase mating opportunities. Greeting females may also help top-ranking males to maintain their social position within the male hierarchy by advertising their special relationship with females to subordinate males.

As greetings probably assist immatures to integrate into the social structure of the clan, it is not surprising that rates of greeting of adult females and immatures do not vary with the rank of the adult female. The systematic variation in the proportion of 'penile' displays of adult females when greeting cubs emphasizes the influence of the rank of a cub's mother on the socialization of the cub and is one mechanism that permits the enforcement of 'rank inheritance'. If social and nutritional benefits acquired by offspring of alpha females are larger than those provided by lower-ranking mothers, we would expect offspring of alpha females to greet their mothers more often than other cubs greet theirs. This was confirmed by the results. Greetings between immatures and immigrant males involved chiefly males above the median rank and primarily top-ranking males. Top-ranking immigrant males are generally tolerated by females and permitted closer to immatures than subordinate immigrant males. Thus high-ranking males have more opportunities to associate with and be greeted by immatures. These greetings may help high-ranking males develop associations with immature females that will eventually become potential reproductive partners.

In greetings between cubs, both partners typically displayed all gestures, thus asymmetries in greetings between cubs were rare. Cub rank had no influence on the initiation and termination of greetings between cubs. This is compatible with the propositions that (1) dominance relationships between cubs may be poorly defined, (2) the ability to display rank during greetings may be poorly developed in cubs, and/or (3) the need for cubs to display rank may be small. Currently we do not know whether one or several of these factors apply. Asymmetries were more common during greetings between subadults and cubs than between cubs, indicating that in subadults the need and/or competence to display dominance is greater than in cubs.

Competition and partner choice

Models of primate affiliative behavior assume that the benefits derived from social relationships with different individuals are not equal, and that individuals are selected to maximize the benefits they receive from social relationships with others. Affiliative behavior with high-ranking individuals (Seyfarth 1977) or close kin (Dunbar 1980) are thought to provide the highest benefits and therefore high-ranking individuals are preferred grooming partners and are the target of most grooming attempts. Consequently, individuals compete for access to high-ranking individuals, and as a result females with adjacent rank are frequent grooming partners, while low-ranking individuals suffer from competition for access to higher-ranking individuals (Seyfarth 1977, 1983; Seyfarth and Cheney 1984; Cheney and Seyfarth 1990).

Our results on the distribution of greetings amongst adults confirm these predictions, with one interesting exception. As predicted, top-ranking females greeted females less frequently as the rank of their partner declined. Also as predicted, mid-ranking females greeted other mid-ranking females most frequently but, in contrast to vervet monkeys, *Cercopithecus aethiops* (Cheney and Seyfarth 1990) increased their proportion of greetings with the target rank of higher-ranking partners. In contrast to many primate troops, a spotted hyena clan is a fission/fusion society where individuals are often absent from the social centre of the clan, the communal den, for several days (Hofer and East 1993c). Because competitors are often not present, competition for access to high-ranking females may be reduced, thus allowing easier access for mid-ranking females to top-ranking females than in primate societies. Low-ranking females rarely greeted top-ranking females which indicates that they were competitively excluded.

The distribution of greetings amongst males matched the pattern observed in female primates (Cheney and Seyfarth 1990). As in spotted hyena females, high-ranking males mostly greeted other high-ranking males but the decline in greetings with rank was more dramatic than in females. This was because (1) subordinate males visited the den less frequently than high-ranking males (East and Hofer 1991b), and (2) access to top-ranking males was limited for lower-ranking males because top-ranking males spent much of their time in close vicinity to the den (unpublished data). In stark contrast to female primates, lower-ranking males were not excluded from greeting top-ranking males by members of the same sex but by the close proximity of the top-ranking males to females, the dominant sex. Thus, greetings often required top-ranking males to leave the immediate den area and approach lower-ranking males. This top-ranking males did, and for this reason the initiations by approach amongst males were not influenced by rank, in contrast to initiations by lifting the hind leg first. Mid-ranking males may also direct the majority of their greetings to males adjacent in rank because these males may be more important to them in the queueing system than the current top-ranking males.

In societies based on matrilines in which rank is 'inherited' (Holekamp and Smale 1991), the distribution of affiliative behavior is thought to be dominated by kin relationships (Gelada baboons, *Theropithecus gelada*, Dunbar 1980) or the result of a mixed strategy where a large amount of grooming occurs between kin and the remainder is directed at high-ranking individuals (bonnet macaques, *Macaca radiata*, Silk et al. 1981). If attraction among kin was the prime factor affecting the distribution of greetings, then the proportion of greetings with kin should be similar in all matrilines, regardless of their rank. Alternatively, if both relatedness and rank are important we predicted that the proportion of greetings between members of high-ranking matrilines should be higher than that amongst low-ranking matrilines. In spotted hyenas the latter is clearly the case as offspring of alpha females greeted their mothers more frequently than offspring of all other mothers.

The evolution of virilization of female genitalia

Penile displays accompany mating behavior in several mammals (bottle-nosed dolphin, *Tursiops truncatus*: Brown and Norris 1956; Ugandan kob, *Kobus kob*: Buechner and Schloeth 1965; bonobos, *Pan paniscus*: de Waal 1988; Kano 1992; wildebeest, *Connochaetes taurinus*: Estes 1991), while in some primates they are signals of dominance (Ploog and MacLean 1963; Wickler 1967; Jolly 1972; Weigel 1979). Spotted hyenas are unique amongst mammals in using an erect 'penis' as a gesture of submission. On an ultimate level (Sherman 1988), the evolutionary origins of the 'pseudo-penis' have been attributed to non-adaptive processes and adaptive selection pressures. The non-adaptive hypotheses (Fig. 5) state that female virilization was (1) an incidental by-product of selection for elevated prenatal androgen levels leading to large size and social dominance of females over males (Gould 1981; Gould and Vrba 1982); (2) a consequence of a punctuated genetic translocation (van Jaarsveld and Skinner 1987). The adaptive hypotheses attribute the evolution of the 'pseudo-penis' (1) directly to selective advantages of a conspicuous structure that focuses the attention of greeting partners and keeps partners together over a longer period, thereby facilitating the re-establishment of social bonds (Wickler 1965b; Kruuk 1972); (2) indirectly to a two-stage process where (i) initial virilization of female genitalia evolved as a by-product of selection for larger body size and aggressiveness to obtain a competitive feeding advantage, (ii) a penile signal was incorporated into greetings, favoring selection for the enlargement and erectile nature of the 'pseudo-penis' (Hamilton et al. 1986).

Although the evolutionary history of the female 'pseudo-penis' is unknown, and current function does not imply historical origin (Gould and Lewontin 1979), two questions are pertinent: (1) Is the current non-adaptive hypothesis sufficient to account for the present day ocurrence and structure of the 'pseudo-penis'? (2) Do females with a 'pseudo-penis' incur a cost due to its presence? The non-adaptive argument is that we do not require an adaptive explanation if we can identify a mechanism that creates that trait as an incidental by-product of selection operating on a different trait. All current non-adaptive scenarios state that masculinization of the female external genitalia was driven by selection for female dominance via selection for neonatal androgenization leading to large, aggressive, adult females (Fig. 5). Is this so?

Masculinization and female dominance. Masculinization of female external genitalia is rare in mammalian species and where it occurs it is not associated with female dominance in any species other then the spotted hyena (e.g., European moles *Talpa europaea*: Matthews 1935; platyrrhine monkeys: Ploog 1967; Oppenheimer 1977). In mammalian species, female dominance is also uncom-

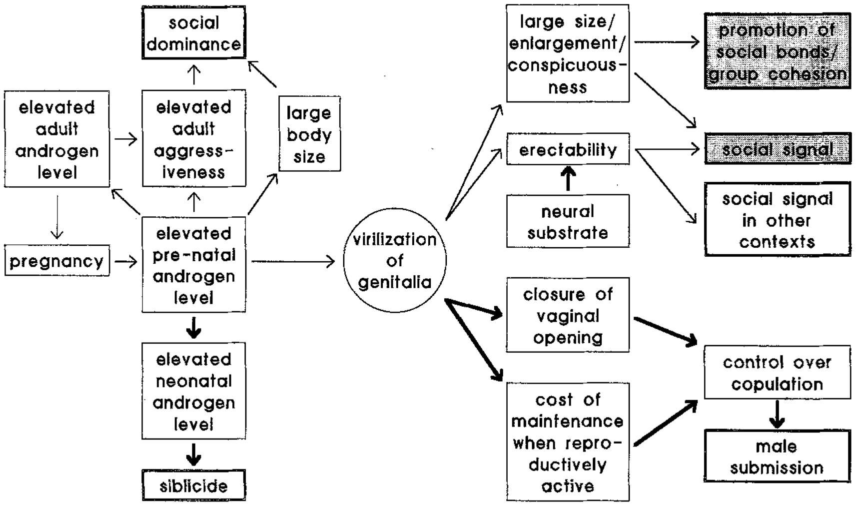

Fig. 5. Schematic overview of hypothesized traits and their links involved in the evolution of the 'pseudo-penis' in female spotted hyenas. Key traits on which selection pressures were hypothesized to operate are surrounded by *double-lined boxes.* Key traits in non-adaptive scenarios are depicted on the *left* (siblicide and social dominance) while those postulated in adaptive scenarios are listed on the *right.* The series of traits to the *right of the central circle* all refer to current features of the female 'pseudo-penis'. *Shaded boxes* refer to functions in a greeting. *Thick arrows* indicate traits and links first proposed by Hofer and East (1992) and this study

mon, but does occur in a wide variety of species (Ralls 1976; Hrdy 1981) and is typical in Lemuriformes (Jolly 1984; Richard 1987; Kappeler 1990; Young et al. 1990). However, masculinization of female external genitalia has not been recorded in any female-dominated species except for the spotted hyena. Female dominance in 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; unpublished data) and body size in males and females is not related to social rank in our Serengeti population or in captive animals (Frank et al. 1989). In several primate species (*Saimiri, Cebus, Cercopithecus talapoin, Macaca mulatta, Erythrocebus patas*) coalitions of females can successfully challenge dominance of larger males (Hall 1967; Kaplan and Zucker 1980; Harvey et al. 1987; Robinson et al. 1987; Smuts 1987), while in spotted hyenas coalitions are important in the maintenance of female rank (see above), and may have been important in the development of female dominance (Frank et al. 1989).

Androgens. Adult female spotted hyenas do not have significantly higher levels of androgens than adult males (Racey and Skinner 1979; Frank et al. 1985; Lindeque et al. 1986; van Jaarsveld and Skinner 1991; Glickman et al. 1992b). Androgen levels in female spotted hyenas are not elevated in relation to androgen levels in female brown or striped hyenas (van Jaarsveld and Skinner 1987). The striking aspect of the hormonal profile of adult spotted hyenas are the low androgen levels of adult males compared with males of other hyena species (van Jaarsveld and Skinner 1987, 1991).

In summary, neither comparative evidence nor current knowledge of spotted hyena behavior and endocrinology support the non-adaptive scenario that links selection for social dominance with elevated pre-natal androgen levels via body size or aggressiveness. There is, however, an alternative hypothesis that links pre-natal androgen levels to *siblicide* (Hofer and East 1992). Spotted hyenas are unique amongst mammals in that there is frequent fatal neonatal aggression between members of a twin litter (Frank et al. 1991). Siblicide is associated with extremely high neonatal aggression and high androstenedione levels at birth and during ontogeny (Frank et al. 1991; Licht et al. 1992). Frank et al. (1991) proposed that siblicide is "another phenomenon that may have originated as a by-product of selection for female androgenization". In contrast, we suggested that the exceptionally large (Gittleman and Oftedal 1987) investment in lactation and long nursing period in spotted hyenas (East et al. 1989; Hofer and East 1993c) favors strong selection for high neonatal aggression leading to siblicide (Hofer and East 1992, Fig. 5). Following this line of argument, the elevated levels of androgens (androstenedione in females, testosterone in males) recorded during foetal 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 for to produce neonates primed for severe agonistic encounters with fully erupted teeth and open eyes. High concentrations of circulating androgens (especially testosterone and dihydrotestosterone) in adult females during the final period of pregrancy 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 agonistic encounters.

Costs and benefits of maintaining the pseudo-penis

We now turn to our second question and ask: If our non-adaptive scenario for the *initial* virilization of female genitalia is correct, are there anatomical components of the 'pseudo-penis' and/or behavioral features of its use that are inexplicable unless we postulate selective pressures that operated directly on the 'pseudo-penis'?

Hamilton et al. (1986) pointed out that (1) large functionless organs are usually selected against, and the 'pseudo-penis' is a large organ, as it makes up circa 1% of adult body mass (Neaves et al. 1980); (2) experimentally induced virilization of female genitalia in a variety of species did not produce a penile structure equivalent to that of the male. There are no reports that parturition is impeded in female primates with virilized genitalia while female moles have a *separate* vaginal opening at the base of their 'pseudo-penis' (Matthews 1935; Niethammer 1990). In contrast, when female spotted hyenas give birth, the 'pseudo-penis' ruptures on the caudal side, causing a large wound (several centimeters) that may be a source of infection. Unusually many primiparous captive females produce stillbirths while subsequent deliveries are easier (Glickman et al. 1992a). Losing a first litter at parturition implies a loss in terms of lifetime reproductive success of at least 5% (unpublished data). These points suggest that maintenance of the 'pseudo-penis' in spotted hyenas entails a cost and that direct selection pressures operated to maintain the pseudo-penis *in its current form.*

The fusion of outer labiae. We propose a 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. The structure and position of the 'pseudo-penis' dictates that males have considerable difficulty locating and penetrating the clitoris opening (Kruuk 1972). Although the 'pseudo-penis' is not erect during mating, its presence and position prevent males from achieving intromission without the complete cooperation of the female, i.e., forced copulations are impossible. Females thus gain control over the mechanics of copulation and male mating success becomes dependent on the relationships they develop with females. Thus, the importance of sexual selection for male fighting prowess is minimal because an amicable relationship with a female is a non-transferable resource. As males achieve little by fighting with each other, game theory predicts that fights should be rare and/or fighting intensity low (Maynard Smith 1982; Harper 1991). This hypothesis explains (1) why aggression amongst contemporary males is low (Frank 1986b; East and Hofer 1991b), (2) why males expend extensive effort on courting females (East and Hofer 1991b), (3) their unusually low androgen levels, (4) why asymmetries in gestures in greetings between males are less common that in greetings between females, and (5) why the number of forced greetings between immigrant males was low. In short, maintenance of the 'pseudo-penis' facilitated the evolution of male submission by providing females with control over mating in a species where males do not contribute to parental care (Fig. 5).

The ability to erect the 'pseudo-penis'. There are no reports that females of species other than spotted hyenas with masculinized genitalia can fully erect the enlarged clitoris. This is probably a consequence of sexual dimorphism found in Onuf's nucleus, the area in the sacral spinal chord responsible for erecting the 'penis' which is well-developed in males but not in females in all species studied so far (Breedlove and Arnold 1980; Forger and Breedlove 1986). We predict that in spotted hyenas, Onuf's nucleus is monomorphic in structure. If this is the case, then the ability to erect the 'pseudo-penis' might be another trait that is not explained by the non-adaptive scenario (Fig. 5).

Behavioral aspects. Our previous discussion referred to a number of benefits associated with greetings but did not specify the contribution of the 'penis'. The adaptive hypotheses on the role of the 'penis' in greeting ceremonies specifically claim that the presence of the 'penis' augment the benefits gained from a greeting. The hypotheses of Wickler (1964, 1965b), Kruuk (1972) and Hamilton et al. (1986) predict that (1) categories of adults that meet infrequently should display an erect 'penis' relatively more frequently than categories of adults that meet frequently; (2) greetings should last longer and be more likely to be asymmetric with respect to 'penis' erection in adult females than in other categories where the benefits of greetings appear to be relatively smaller; (3) the erect 'penis' provides information not available through other greeting gestures. In line with these predictions (1) greetings between immigrant males who meet infrequently included a substantially higher proportion of cases with both individuals erecting their 'penis' than greetings between adult females who meet more frequently; (2) greetings between adult females lasted significantly longer and comprised a higher proportion of asymmetric greetings with respect to 'penis' erection than greetings between males. Our results show that during greetings there are gestures besides the erect 'penis' that are available to signal submission. However, the erect 'penis' is the only gesture that reliably signals absolute rank as well as relative rank difference in greetings between adult females and cubs. This emphasizes the influence of the rank of a cub's mother on the socialization of the cub because it permits cubs to assess the social status they obtain from their mother in relation to that of an adult female greeting partner. Thus, it provides a mechanism that permits the enforcement of 'rank inheritance' (cf. Holekamp and Smale 1991).

Previously, discussions of the importance of the erect 'penis' in social situations has been restricted to greetings, with the exception of Hamilton et al. (1986). However, an erect 'penis' is used as a submissive signal in a wide variety of social situations (unpublished data). A detailed study of the use of the erect 'penis' in all social contexts may uncover additional points for consideration (Fig. 5).

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References

Alberts SC, Sapolsky RM, Altmann J (1992) Behavioural, endocrine and immunological correlates of immigration by an aggressive male into a natural primate group. Horm Behav 26:167–178

Armitage KB (1962) Social behavior of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Anim Behav 10:319–331

Anthoney TR (1968) The ontogeny of greeting, grooming, and sexual motor patterns in captive baboons (superspecies *Papio cynocephalus*). Behaviour 31:358–372

Breedlove SM, Arnold AP (1980) Hormone accumulation in a sexually dimorphic motor nucleus of the rat spinal cord. Science 210:564–566

Brown DH, Norris KS (1956) Observations of captive and wild cetaceans. J Mammal 37:311–326

Buechner HK, Schloeth R (1965) Ceremonial mating behaviour in Ugandan kob (*Adenota kob thomasi*, Neumann). Z Tierpsychol 22:209–225

Chapais B (1988) Rank maintenance in female Japanese macaques: Experimental evidence for social dependency. Behaviour 104:41–59

Cheney DL, Seyfarth RM (1990) How monkeys see the world. University of Chicago Press, Chicago

Colmenares F (1990) Greeting behaviour in male baboons, I: Communication, reciprocity and symmetry. Behaviour 113:81–114

Conover WJ (1980) Practical non-parametric statistics. 2nd ed, John Wiley, Chichester

Datta SB (1983) Relative power and the maintenance of dominance. In: Hinde RA (ed) Primate social relationships: an integrated approach. Blackwell Scientific, Oxford, pp 103–112

Douglas-Hamilton I (1972) On the ecology and behaviour of the African elephant: the elephants of Lake Manyara. DPhil thesis, Oxford University

Dunbar RIM (1980) Determinants and evolutionary consequences of dominance among female gelada baboons. Behav Ecol Sociobiol 7:253–265

East ML, Hofer H (1991a) Loud calling in a female-dominated mammalian society: I. Structure and composition of whooping bouts of spotted hyaenas, (*Crocuta crocuta*). Anim Behav 42:637–649

East ML, Hofer H (1991b) Loud calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyaenas, (*Crocuta crocuta*). Anim Behav 42:651–669

East ML, Hofer H, Türk A (1989) Funcitons of birth dens in spotted hyaenas (*Crocuta crocuta*). J Zool Lond 219:690–697

Eisermann K (1992) Long-term heart rate response to social stress in wild European rabbits: predominant effect of rank position. Physiol Behav 52:33–36

Estes RD (1991) The behavior guide to African mammals. University of California Press, Berkeley

Fairbanks LA (1980) Relationships among adult females in captive vervet monkeys: Testing a model of rank related attractiveness. Anim Behav 28:853–859

Forger NG, Breedlove SM (1986) Sexual dimorphism in human and canine spinal cord: role of early androgen. Proc Natl Acad Sci USA 83:7527–7531

Fox MW (1971a) Ontogeny of a social display in *Hyaena hyaena*: anal protrusion. J Mammal 52:467–469

Fox MW (1971b) Socio-infantile and socio-sexual signals in canids: a comparative and ontogenetic study. Z Tierpsychol 28:185–210

Frank LG (1986a) Social organisation of the spotted hyaena (*Crocuta crocuta*). I. Demography. Anim Behav 35:1500–1509

Frank LG (1986b) Social organisation of the spotted hyaena (*Crocuta crocuta*). II. Dominance and reproduction. Anim Behav 34:1510–1527

Frank LG, Davidson JM, Smith ER (1985) Androgen levels in the spotted hyaena *Crocuta crocuta*: the influence of social factors. J Zool London A206:525–531

Frank LG, Glickman SE, Zabel CJ (1989) Ontogeny of female dominance in the spotted hyaena: perspectives from nature and captivity. Symp Zool Soc London 61:127–146

Frank LG, Glickman SE, Powch I (1990) Sexual dimorphism in the spotted hyaena (*Crocouta crocuta*). J Zool London 221:308–313

Frank LG, Glickman SE, Licht P (1991) Fatal sibling aggression, precocial development and androgens in neonatal spotted hyaenas. Science 252:702–704

Gittleman JL, Oftedal OT (1987) Comparative growth and lactation energetics in carnivores. Symp Zool Soc London 57:41–77

Glickman SE, Frank LG, Davidson JM, Smith ER, Siiteri PK (1987) Androstenedione may organize or activate sex-reversed traits in female spotted hyaena. Proc Natl Acad Sci USA 84:3444–3447

Glickman SE, Frank LG, Licht P, Yalcinkaya T, Siiteri PK, Davidson J (1992a) Sexual differentiation of the female spotted hyaena. Ann N Y Acad Sci 662:135–159

Glickman SE, Frank LG, Pavgi S, Licht P (1992b) Hormonal correlates of 'masculinization' in female spotted hyaenas (*Crocuta crocuta*). 1. Infancy to sexual maturity. J Reprod Fert 95:451–462

Gould SJ (1981) Hyena myths and realities. Nat Hist 90:16–24

Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist program. Proc R Soc London B205:581–598

Gould SJ, Vrba ES (1982) Exaptation – a missing term in the science of form. Paleobiology 8:4–15

Hall KRL (1967) Social interactions of the adult male and adult females of a patas monkey group. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 261–280

Hamilton WJ III, Tilson RL, Frank LG (1986) Sexual monomorphism in spotted hyaenas, *Crocuta crocuta*. Ethology 71:63–73

Harper DGC (1991) Communication. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford, pp 374–397

Harvey PH, Martin RD, Clutton-Brock TH (1987) Life histories in comparative perspectives. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 181–196

Hofer H, East ML (1992) Siblicide of spotted hyaenas is a consequence of allocation of maternal effort and a cause of skewed litter sex ratios. Abstracts. The Fourth International Behavioural Ecology Congress, Princeton University, Princeton 1992, p 119

Hofer H, East ML (1993a) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. Anim Behav 46:547–557

Hofer H, East ML (1993b) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuters' space use. Anim Behav 46:559–574

Hofer H, East ML (1993c) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. Anim Behav 46:575–589

Holekamp KE, Smale L (1991) Dominance acquisition during mammalian social development: The "inheritance" of maternal rank. Am Zool 31:306–317

Hrdy SB (1981) The woman that never evolved. Harvard University Press, Cambridge

Jaarsveld AS van, Skinner JD (1987) Spotted hyaena monomorphism: an adaptive 'phallusy'? S Afr J Sci 83:612–615

Jaarsveld AS van, Skinner JD (1991) Plasma androgens in spotted hyaenas (*Crocuta crocuta*): influence of social and reproductive development. J Reprod Fert 93:195–201

Jolly A (1972) The evolution of primate behaviour. Macmillan, New York

Jolly A (1984) The puzzle of female feeding priority. In: Small M (ed) Female primates: studies by women primatologists. Alan R. Liss, New York

Kano T (1992) The last ape. Pygmy chimpanzee behavior and ecology. Stanford Unviersity Press, Stanford

Kaplan JR, Zucker E (1980) Social organization of a group of free-ranging Patas monkeys. Folia Primatol 34:196–213

Kappeler PM (1990) Female dominance in *Lemur catta*: more than just female feeding priority? Folia Primatol 55:92–103

Kiecolt-Glaser JK, Glaser R (1991) Stress and immune function in humans. In: Ader R, Felten DL, Cohen N (eds) Psychoneuroimmunology, 2nd edn. Academic Press, New York, pp 849–867

Klingel H (1972) Social behaviour of African Equidae. Zool Afr 7:175–185

Kruuk H (1972) The spotted hyaena. University of Chicago Press, Chicago

Kühme W (1965a) Communal food distribution and division of labour in African hunting dogs. Nature 205:443–444

Kühme W (1956b) Freilandstudien zur Soziologie des Hyänenhundes (*Lycaon pictus lupinus* Thomas 1902). Z Tierpsychol 22:495–541

Kummer H (1968) Social organisation of hamadryas baboons; a field study (Bibl Primatol 6). Karger, Basel

Leyhausen P (1960) Verhaltensstudien an Katzen. Z Tierpsychol Beih 2:1–120

Licht P, Frank LG, Pavgi S, Yalcinkaya TM, Siiteri PK, Glickman SE (1992) Hormonal correlates of 'masculinization' in female spotted hyaenas (*Crocuta crocuta*) 2. Maternal and fetal steroids. J Reprod Fert 95:463–474

Lindeque M, Skinner JD (1982) Fetal androgens and sexual mimicry in spotted hyaena (*Crocuta crocuta*). J Reprod Fert 65:405–410

Lindeque M, Skinner JD, Millar RP (1986) Adrenal and gonadal contribution to circulating androgens in spotted hyaenas (*Crocuta crocuta*) as revealed by LHRH, hCG and ACTH stimulation. J Reprod Fert 78:211–217

Machlis L, Dodd PW, Fentress JC (1985) The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z Tierpsychol 69:201–214

Matthews LH (1935) The oestrous cycle and intersexuality in the female mole *Talpa europaea* Linn. Proc Zool Soc Lond 106:347–383

Matthews LH (1939) Reproduction in the spotted hyaena (*Crocuta crocuta*, Erxleben). Philos Trans R Soc Lond B230:1–78

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Mech LD (1970) The wolf. University of Minnesota Press, Minneapolis

Mehlman PT, Chapais B (1988) Differential effects of kinship, dominance, and the mating season on female allogrooming in a captive group of *Macaca fuscata*. Primates 29:195–217

Mills MGL (1985) Related spotted hyaenas forage together but do not cooperate in rearing young. Nature 316:61–62

Mills MGL (1990) Kalahari hyaenas. The comparative behavioural ecology of two species. Unwin Hyman, London

Mills MGL, Gorman ML, Mills MEJ (1980) The scent-marking behaviour of the brown hyaena *Hyaena brunnea*. S Afr J Zool 15:240–248

Munck A, Guyre PM (1991) Glucocorticoids and immune function. In: Ader R, Felten DL, Cohen N (eds) Psychoneuroimmunology, 2nd edn. Academic Press, New York, pp 447–474

Neaves WB, Griffin JE, Wilson JD (1980) Sexual dimorphism of the phallus in spotted hyaena (*Crocuta crocuta*). J Reprod Fert 59:509–513

Niethammer J (1990) *Talpa europaea* Linnaeus, 1758 – Maulwurf. In: Niethammer J, Krapp F (eds) Handbuch der Säugetiere Europas 3/I: Insektenfresser, Primaten. Aula, Wiesbaden, pp 99–133

Nishida T (1970) Social behaviour and relationships among wild chimpanzees of the Mahale Mountains. Primates 11:47–87

Oppenheimer JR (1977) Communication in New World monkeys. In: Sebeok TA (ed) How animals communicate. Indiana University Press, Bloomington, pp 851–889

Ploog DW (1967) The behaviour of squirrel monkeys (*Saimiri sciureus*) as revealed by sociometry, bioacoustics, and brain stimulation. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 149–184

Ploog DW, MacLean PD (1963) Display of penile erection in squirrel monkeys (*Saimiri sciureus*). Anim Behav 11:32–39

Racey PA, Skinner JD (1979) Endocrine aspects of sexual mimicry in spotted hyaenas (*Crocuta crocuta*). J Zool London 187:315–326

Ralls K (1976) Mammals in which females are larger than males. Q Rev Biol 51:245–276

Richard AF (1987) Malagasy prosimians: female dominance. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 25–33

Robinson JG, Wright PC, Kinzey WG (1987) Monogamous cebids and their relatives: intergroup calls and spacing. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 44–53

Rowell TH (1974) The concept of social dominance. Behav Biol 11:131–154

Sapolsky RM (1982) The endocrine stress-response and social status in the wild baboon. Horm Behav 15:279–292

Schenkel R (1967) Submission: its features and functions in the wolf and dog. Am Zool 7:319–330

Seyfarth RM (1977) A model of social grooming among adult female monkeys. J Theor Biol 65:671–698

Seyfarth RM (1983) Grooming and social competition in primates. In: Hinde RA (ed) Primate social relationships: an integrated approach. Blackwell Scientific Press, London, pp 182–190

Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308:541–543

Sherman PW (1988) The levels of analysis. Anim Behav 36:616–618

Silk JB, Samuels A, Rodman P (1981) The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques *Macaca radiata*. Behaviour 78:111–177

Smuts BB (1987) Gender, aggression, and influence. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 400–412

Stammbach E (1978) On social differentiation in groups of captive female hamadryas baboons. Behaviour 67:322–338

Steiner AL (1975) 'Greeting' behaviour in some Sciuridae from ontogenetic, evolutionary and socio-behavioural perspective. Nat Can 120:737–751

Sugiyama K (1971) Characteristics of the social life of bonnet macaques (*Macaca radiata*). Primates 12:247–266

Waal FBM de (1982) Chimpanzee politics. Jonathan Cape, London

Waal FBM de (1988) The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. Behaviour 106:183–251

Weigel RM (1979) The facial expression of the brown capuchin monkey (*Cebus apella*). Behaviour 68:250–276

Wickler W (1964) Vom Gruppenleben einiger Säugetiere Afrikas. Mitt Max-Planck-Ges 56:296–309

Wickler W (1965a) Die äußeren Genitalien als soziale Signale bei einigen Primaten. Naturwissenschaften 52:269–270

Wickler W (1965b) Die Evolution von Mustern der Zeichnung und des Verhaltens. Naturwissenschaften 52:335–341

Wickler W (1966) Ursprung und biologische Deutung des Genitalpräsentierens männlicher Primaten. Z Tierpsychol 23:422–437

Wickler W (1967) Socio-sexual signals and their intra-specific imitation among primates. In: Morris D (ed) Primate ethology. Weidenfeld & Nicholson, London, pp 69–147

Wilkinson L (1990) SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois

Wurster DH, Benirschke K, Gray WC (1970) Determination of sex in the spotted hyaena *Crocuta crocuta*. Int Zoo Yrbk 10:143–144

Yost R (1977) Cytological sex determination in the spotted hyaena *Crocuta crocuta*. Int Zoo Yrbk 17:212–213

Young AL, Richard AF, Aiello LC (1990) Female dominance and maternal investment in strepsirrhine primates. Am Nat 135:473–488