Mechanisms of maternal rank 'inheritance' in the spotted hyaena, *Crocuta crocuta*

ANNE L. ENGH*, KATRINA ESCH*, LAURA SMALE† & KAY E. HOLEKAMP*

Departments of Zoology* and Psychology†, Michigan State University

Maternal rank 'inheritance', the process by which juveniles attain positions in the dominance hierarchy adjacent to those of their mothers, occurs in both cercopithecine primates and spotted hyaenas. Maternal rank is acquired in primates through defensive maternal interventions, coalitionary support and unprovoked aggression ('harassment') directed by adult females towards offspring of lower-ranking individuals. Genetic heritability of rank-related traits plays a negligible role in primate rank acquisition. Because the social lives of *Crocuta* and cercopithecine primates share many common features, we examined whether the same mechanisms might operate in both taxa to promote maternal rank 'inheritance'. We observed a large clan of free-living spotted hyaenas in Kenya to test predictions of four mechanistic hypotheses. Hyaena rank acquisition did not appear to be directly affected by genetic heritability. Unprovoked aggression from adult female hyaenas was not directed preferentially towards low-ranking cubs. However, high-ranking mothers intervened on behalf of their cubs more frequently and more effectively than low-ranking mothers. Maternal interventions and supportive coalitions appeared to reinforce aggression directed at 'appropriate' conspecific targets, whereas coalitionary aggression directed at cubs apparently functioned to extinguish their aggressive behaviour towards 'inappropriate' targets. Young hyaenas and primates thus appear to 'inherit' their mothers' ranks by strikingly similar mechanisms.

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A variety of different factors are known to affect dominance status in gregarious vertebrates including genetic influences (e.g. Craig et al. 1965; Moss et al. 1982; Kikkawa et al. 1986), body size (e.g. Clutton-Brock et al. 1982), age (e.g. Goodall 1986; Pusey & Packer 1997), tenure in the social group (e.g. Sugiyama 1976; Smale et al. 1997) and political machinations (de Waal 1982). In many cercopithecine primates, maternal rank is an extremely important determinant of offspring social rank. That is, during early ontogeny, the ranks of young primates come to be highly correlated with those of their mothers (*Macaca fuscata*: Kawai 1958; *M. mulatta*: Missakian 1972; *M. sylvanus*: Paul & Kuester 1987; *M. fascicularis*: de Waal 1977; *M. arctoides*: Estrada 1978; *M. nemestrina*: Bernstein 1969; *M. radiata*: Silk et al. 1981a, b; *Papio cynocephalus*: Hausfater 1975; *P. anubis*: Johnson 1987; *Cercopithecus aethiops*: Horrocks & Hunte 1983; *Theropithecus gelada*: Dunbar 1980). As in these myriad primate species, the social ranks of young spotted hyaenas are also strongly influenced by the ranks of their

Correspondence: K. E. Holekamp, Department of Zoology, Michigan State University, East Lansing, MI 48824-1115, U.S.A. (email: holekamp@pilot.msu.edu).

mothers (Frank 1986; Holekamp & Smale 1991, 1993; Smale et al. 1993; Jenks et al. 1995). The process by which youngsters assume positions in the dominance hierarchy adjacent to those of their mothers is called maternal rank 'inheritance' by primatologists (e.g. Harcourt & Stewart 1987). Although social rank is relational and is not literally inherited, we adopt this same terminology here. Furthermore, following Chapais (1992) we assume that maternal rank 'inheritance' includes processes of both rank acquisition and rank maintenance.

The social lives of spotted hyaenas are comparable in many respects to those of cercopithecine primates (Frank 1986; Holekamp & Smale 1993; Smale et al. 1993; Holekamp et al. 1999, in press). Like most primates, *Crocuta* are long-lived mammals that bear small litters requiring a long period of nutritional dependence on the mother. Like cercopithecine primates, *Crocuta* live in permanent social groups, the members of which cooperatively defend communal territories. Social groups in both taxa contain multiple adult males and multiple matrilines of adult female kin with offspring, including individuals from several overlapping generations. Males in both taxa typically disperse from their natal groups whereas females are usually philopatric (Cheney & Seyfarth 1983;

Henschel & Skinner 1987; Pusey & Packer 1987; Mills 1990; Smale et al. 1997). Adults of both taxa can be ranked in a linear dominance hierarchy based on outcomes of agonistic interactions, and priority of resource access varies with social rank (Tilson & Hamilton 1984; Andelman 1985; Frank 1986). In both *Crocuta* and various Old World primates, female reproductive success is strongly correlated with social rank (Altmann et al. 1988, 1996; Frank et al. 1995; Holekamp et al. 1996). In both taxa, members of the same matriline occupy adjacent rank positions in the group's hierarchy, and female dominance relations are extremely stable across a variety of contexts and over periods of many years. Juvenile hyaenas of both sexes acquire ranks immediately below those of their mothers (Holekamp & Smale 1991, 1993; Smale et al. 1993), and nonlittermate siblings assume relative ranks that are inversely related to age in a pattern of 'youngest ascendency' like that seen in many cercopithecine primates (e.g. Horrocks & Hunte 1983). In both primates and hyaenas, kin associate more closely than nonkin, and individuals direct affiliative behaviour towards kin more frequently than towards nonkin (Seyfarth 1980; Seyfarth & Cheney 1984; East et al. 1993; Holekamp et al. 1997). In both taxa, high-ranking animals are preferred over lower-ranking individuals as social companions (Seyfarth 1980, 1981; Holekamp et al. 1997). Furthermore, patterns of greeting behaviour in *Crocuta* follow primate patterns of social grooming (East et al. 1993), in which individuals prefer to direct affiliative behaviour towards high-ranking nonkin (Seyfarth & Cheney 1984). Finally, triadic and more complex interactions (e.g. coalitions) appear to play important roles in the acquisition and maintenance of social rank in *Crocuta* (Mills 1990; Zabel et al. 1992; Holekamp & Smale 1991, 1993; Smale et al. 1993; Jenks et al. 1995), as they do in many cercopithecine primates (Cheney 1977; Walters 1980; Datta 1983, 1986; Harcourt 1988, 1992; Pereira 1989; Chapais et al. 1991; Chapais 1992).

A number of studies have attempted to determine how young primates 'inherit' their mothers' ranks, and several possible mechanisms have been proposed. The simplest hypothesis suggests that genetic inheritance of rank-related behavioural tendencies or physical characteristics account for the 'inheritance' of maternal rank. Unprovoked aggression directed preferentially by adult females towards offspring of lower-ranking females has also been proposed as a mechanism of maternal rank 'inheritance' (Berman 1980; Horrocks & Hunte 1983). Another mechanism known to function importantly in primates involves defensive interventions by mothers on behalf of their offspring when the latter are engaged in disputes with conspecifics (Cheney 1977; Berman 1980; Horrocks & Hunte 1983; Netto & Van Hooff 1986). Finally, third-party support, or coalition formation, during aggressive interactions appears to play an important role in acquisition of maternal rank in primates (Cheney 1977; Walters 1980; Datta 1983; Bernstein & Ehardt 1985; Ehardt & Bernstein 1992).

'Inheritance' of maternal rank occurs in both wild and captive groups of spotted hyaenas, including groups that vary widely in size and composition (Holekamp & Smale 1993; Smale et al. 1993; Jenks et al. 1995). Free-living *Crocuta* cubs attain their ranks within their peer cohorts within the first 8 months of life (Holekamp & Smale 1993), and they attain their ranks relative to older clan members somewhat later (Smale et al. 1993). In light of the striking similarities between the social lives of spotted hyaenas and cercopithecine primates, we set out to determine whether young hyaenas 'inherit' maternal rank via the same processes as young monkeys. Working with one large group of free-living hyaenas in Kenya, we tested predictions of each of the four mechanistic hypotheses enumerated above.

METHODS

We monitored a single clan of spotted hyaenas from June 1988 to June 1999 in their 65 km^2 core home range in the Talek area of the Masai Mara National Reserve, Kenya. We made daily behavioural observations of the 67 offspring of 22 adult female clan members present in the clan between June 1988 and April 1991. Throughout this period, observers were present in the study area 23–31 days per month. Individual hyaenas were identified by their spot patterns and other unique characteristics, such as ear notches. Mother–offspring relationships were determined on the basis of nursing associations.

Behavioural observations took place near dawn (0600–0900 hours) and dusk (1630–1930 hours) when hyaenas were most active. Data were recorded throughout the clan's home range and during all activities. Behaviour was recorded during weekly 30-min focal animal surveys of individual cubs, and continuous critical incident ('all-occurrence' Altmann 1974) sampling of agonistic behaviour displayed by all Talek hyaenas. Aggressive behaviours included threat, bite, chase and approach in attack posture, whereas submissive behaviours included avoidance or withdrawal from interaction, submissive posture, headbob and carpal crawl (see Kruuk 1972 for definitions). We classified all aggressive behaviours by adult females towards cubs as 'provoked' if they occurred during nursing or feeding, or if they immediately followed pesky or aggressive behaviour by the targeted cub. We classified aggressive behaviours not meeting any of these criteria as 'unprovoked.' We defined coalitions as two or more hyaenas concurrently behaving aggressively towards a third. When coalitions formed, we recorded the identities of all aggressors, as well as the order in which they joined the interaction. The first aggressor involved in a coalition was called the initiator, any individuals joining the initiator were called supporters, and the recipient of the aggression was termed the victim.

We identified maternal interventions when an adult female interrupted an interaction between her cub and another individual. We classified interventions as either 'aggressive' or 'nonaggressive.' Aggressive interventions involved approach followed by threat, attack, or displacement behaviour by the mother towards the individual interacting with her cub. Nonaggressive interventions involved approach followed by distraction (e.g. initiation of a greeting ceremony) or blocking (e.g. the mother

Table 1. Relationships among the sample sets of hyaena cubs

	All cubs participating in coalitions*	Cubs surviving to 18 months of age†	Cubs surviving to 24 months of age‡
N	67	38	20
Female	30	15	7
Male	37	23	13
Mean female rank (SD)	11.27 (5.85)	10.47 (5.38)	8.71 (5.47)
Mean male rank (SD)	10.11 (6.22)	9.39 (5.94)	9.54 (6.79)
Number of subjects with ≥1 sibling	64	31	12
Number of littermate pairs	23	10	5

*See Figs 4, 5.
†See Figs 1, 2, 3.
‡See Fig. 6.

positioning herself between her cub and its opponent). Additionally, we classified the context of each intervention as either food-related or nonfood-related. A food-related intervention took place during a dispute over access to or possession of a food item. A maternal intervention was considered effective when the hyaena interacting with the cub in question desisted from interacting with that cub during or immediately after the intervention.

We determined the social rank of each clan member based on its position in a matrix of appeasement behaviours displayed during dyadic agonistic interactions (Martin & Bateson 1988). The 'winner' was the animal being appeased, while the 'loser' was the animal exhibiting appeasement behaviour. By convention, we assigned the most dominant animal in the hierarchy a rank of one. A juvenile's 'maternal rank' referred to its mother's position within the adult female hierarchy. Low-born individuals were those of lower maternal rank than the focal animal, while high-born animals had a higher maternal rank than the focal animal (e.g. Datta 1983). A cub was considered high-ranking if its mother's rank was 10 or higher and low-ranking if her rank was below 10. There was no significant sex bias within the sample set (Table 1; $\chi^2_2 = 0.75$, NS) and rank was unrelated to cub sex in all of the sample subgroups examined (Table 1; Student's t test: $t_{65} = 0.78$, $N = 67$, $P = 0.44$; $t_{36} = 0.57$, $N = 38$, $P = 0.58$; $t_{18} = -0.28$, $N = 20$, $P = 0.79$)

Ages of all juvenile hyaenas were known to within 1 week, as described previously (e.g. Holekamp et al. 1996). In all analyses below, hyaenas were called cubs until 18 months of age, subadults from 18 to 24 months, and adults over 24 months (Matthews 1939; Smale et al. 1993). Spotted hyaenas acquire their adult ranks by 18 months of age, and generally maintain these ranks as long as they remain in the natal clan (Smale et al. 1993). However, as in primates, rank acquisition occurs in stages in *Crocuta*: social rank relative to peers is acquired at 0–6 months of age, and this rank relative to peers becomes perfectly aligned with maternal rank by 6–8 months of age (Holekamp & Smale 1993). Cubs acquire their social ranks relative to adults between 8 and 18 months of age (Smale et al. 1993). Therefore, for analyses of behavioural

changes over time (below), we calculated separate rate values for each cub during each of the following age intervals: 0–6, 7–8, 9–18 and 19–24 months. Only individuals that survived at least 24 months ($N = 20$) were included in these longitudinal analyses. Siblings, offspring and parents were considered to be kin in the analyses below, and all other animals were considered to be nonkin.

Rate data were compared in most analyses. We calculated hourly rates of maternal intervention, aggressions received and coalition formation for each cub by dividing the total number of interventions, aggressions received, or coalitions involving that cub by the total number of hours during which the cub was observed. We calculated rates of female aggression by dividing the number of unprovoked aggressions directed by each adult female towards each cub by the number of hours during which each female–cub dyad was observed within 200 m of each other. We then calculated mean rates of aggression directed against high-born and low-born cubs for each adult female. Only cubs that survived for at least 18 months ($N = 38$) were considered in analyses of female aggression and maternal intervention.

We assessed directionality in coalitionary interactions for each cub by calculating the proportion of all coalitions that reinforced the adult hierarchy in which that cub participated. Thus, if a cub joined five coalitions, three of which were directed against low-born victims, then we assigned that cub a value of 0.60 for supporting coalitions. We then calculated 95% confidence intervals (CIs) for these proportions averaged over all cubs. When 95% CIs did not include the 0.50 predicted if cubs were equally likely to participate in coalitions directed at high- and low-born animals, then we considered the results to be significantly different from chance expectations. All cubs participating in at least one coalition were included in these analyses.

We calculated Spearman's correlation coefficients in all analyses using social rank as an independent variable and assessed the significance of each relationship via Kruskal–Wallis tests. In all cases in which data were not normally distributed, we used standard nonparametric tests, such as Wilcoxon and Freidman tests for analysis.

RESULTS AND DISCUSSION

Genetic Heritability

Although rank relationships among adult females were generally extremely stable throughout the 11-year study period, changes in rank relationships associated with a single clan fission event early in the study indicated that genetic heritability cannot account for 'inheritance' of maternal rank in spotted hyaenas. That is, when members of three low-ranking matrilines permanently emigrated from the Talek clan between November 1989 and June 1990, they were initially accompanied by two adult females (sisters) and their offspring from a middle-ranking matriline, as described previously (Holekamp et al. 1993). Although no members of the low-ranking matrilines ever returned to Talek, the two middle-ranking females returned after an absence of 1 year. As they attempted to rejoin the Talek clan, both of these females were the targets of severe attacks by all other adult females, including those which they had previously outranked (Holekamp et al. 1993). Both absentee females were ultimately able to rejoin the Talek clan in 1991, but their new ranks were at the bottom of the adult female hierarchy, where they have remained ever since. Offspring born to these females before clan fission fell in rank along with their mothers when they returned to Talek, and all of the subsequent offspring produced by these two females 'inherited' their mothers' new ranks, rather than their mothers' initial ranks in the clan's hierarchy. The fact that the ranks of these females and their offspring changed so dramatically during the study period strongly suggests that genetic heritabilty is unlikely to function as an important mechanism mediating rank acquisition in this species.

Unprovoked Aggression

If unprovoked female aggression contributes to maternal rank 'inheritance', then rates of unprovoked aggression directed by adult females towards offspring of lower-ranking females should be higher than rates at which they harass offspring of higher-ranking females. Furthermore, this hypothesis predicts that rates of unprovoked aggression received by cubs from adult females should be correlated with the cubs' maternal ranks. We observed no difference between the hourly rates of unprovoked aggression directed by adult females at low-born and high-born cubs (Wilcoxon signed-ranks test: $Z_2=0.601$, $P=0.548$). In addition, hourly rates at which cubs received unprovoked aggression from adult females were not correlated with cubs' maternal ranks ($r_S=0.14$; Kruskal–Wallis test: $H_{18}=16.16$ $P=0.51$; Fig. 1). Thus unprovoked female aggression does not appear to function importantly in acquisition of maternal rank in *Crocuta*.

Maternal Intervention

If maternal interventions function to promote maternal rank 'inheritance' in spotted hyaenas, then
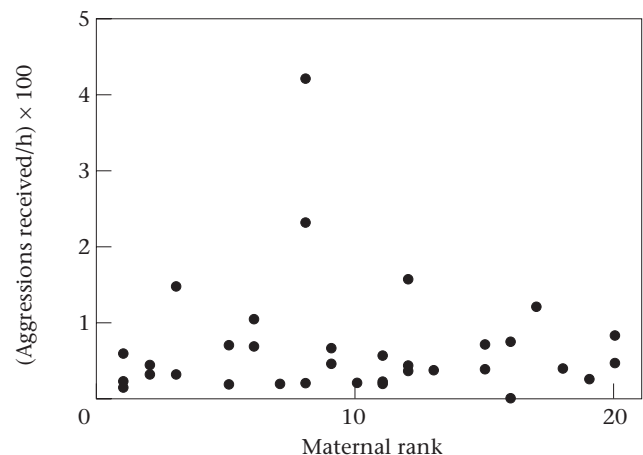

Figure 1. Hourly rates at which adult females directed unprovoked aggressive behaviours at cubs, ordered on the basis of the victim's maternal rank.
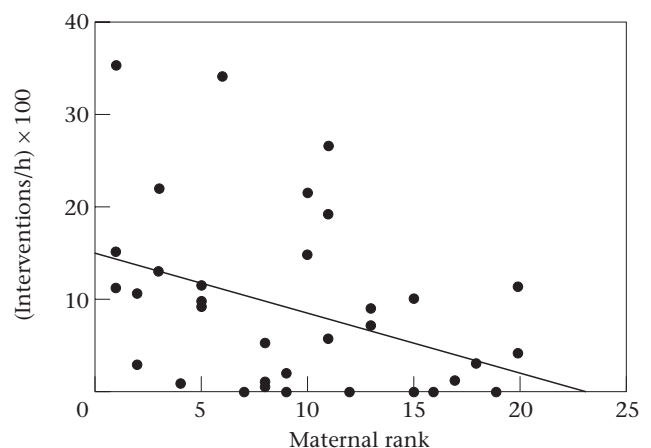

Figure 2. Hourly rates at which adult female hyaenas intervened on behalf of their offspring, ordered on the basis of their social rank.

intervention rates should be inversely correlated with maternal rank, and high-ranking females should intervene on behalf of their offspring more effectively than low-ranking females. The rates at which female hyaenas intervened on behalf of their cubs were indeed significantly correlated with maternal rank ($r_S= -0.41$; Kruskal–Wallis test: $H_{18}=31.08$, $P=0.03$; Fig. 2). Only 27 of 818 maternal interventions (3.3%) occurred in response to a direct aggressive attack. Most interventions occurred before the 'intruder' had a chance to behave aggressively towards the cub. For example, mothers frequently intervened against any individuals that approached their cubs while the cubs were feeding on small scraps. This supports Berman's (1980) suggestion that the mere presence of the mother may curb rates of aggression directed towards high-ranking cubs. Indeed, there was a strong but nonsignificant trend for high-ranking cubs to receive lower overall rates of aggression than low-ranking cubs ($r_S=0.64$; Kruskal–Wallis test: $H_{18}=24.27$, $P=0.15$). Thus low-ranking mothers had more opportunities to intervene on behalf of their cubs, yet they intervened at far lower hourly rates than high-ranking females.
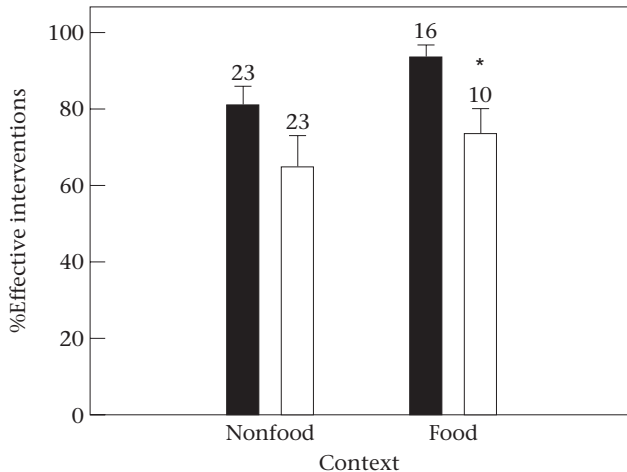
Figure 3. Mean+SE percentage of maternal interventions against high-born (□) and low-born (■) opponents that were effective in food and nonfood contexts. Sample sizes represent numbers of mother–cub pairs observed.

Figure 4. Mean+SE percentage of coalitions that reinforced the existing dominance hierarchy organized in terms of victim, initiator and supporter of the attack. Numbers of cubs are indicated above bars.

Intervention strategies of adult females did not depend on either the relative ranks of the contestants (Mann–Whitney $U=133.5$, $N_1=39$, $N_2=33$, $P=0.375$) or the context in which interventions occurred ($U=58.00$, $N_1=46$, $N_2=26$, $P=0.172$). Aggressive interventions were common regardless of whether or not the situation involved food. In food-related contexts, mothers often stood next to cubs with food and threatened any approaching animal. Overall, high-born females were found to be more effective when intervening on behalf of their offspring than low-born females ($U=829.5$, $N_1=39$, $N_2=33$, $P=0.03$). In particular, high-born females were more effective than low-born females in food-related contexts ($U=127.5$, $N_1=16$, $N_2=10$, $P=0.01$; Fig. 3), where there was an obvious benefit to winning. Thus, our data confirmed that high-ranking mothers intervened on behalf of their offspring both more frequently and more effectively than low-ranking mothers.

Coalitionary Support

Acquisition of maternal rank in *Crocuta* might be facilitated either by coalitionary support of young or coalitionary targeting of young. First, if a cub is supported by conspecifics when it attacks another animal, then this supportive behaviour may function in both militaristic and operant conditioning senses to reinforce the cub's behaviour towards that target animal. Second, if a cub engaged in a dispute with another animal is attacked by a coalition of conspecifics, then its aggressive behaviour towards the original target may be rapidly extinguished. This hypothesis predicts that, when hyaena A joins hyaena B in an aggressive interaction against hyaena C, hyaena A will join the individual that should win according to the 'rules' of maternal rank inheritance. This hypothesis also predicts that hourly rates of coalition formation in support of cubs, or rates of coalition formation against cubs, should vary with maternal rank. Besides receiving higher rates of coalitionary support, the
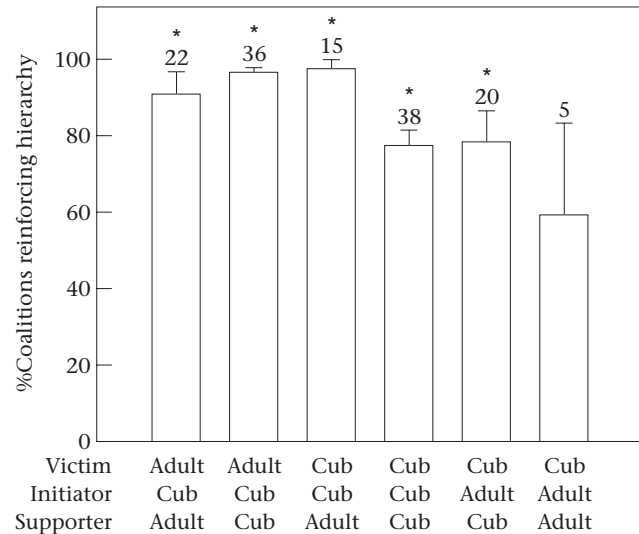
offspring of high-ranking females should have more allies, and higher-ranking allies, to support them than should the offspring of low-ranking females. In addition, youngsters may facilitate acquisition or maintenance of maternal rank by providing support in coalitions against low-born individuals. Such joining behaviour should permit cubs to reinforce their dominant status over that of target animals.

When adult hyaenas supported cubs in coalitions against other cubs or adults, they were more likely to do so against low-born than high-born opponents. This was true both for conflicts between cubs and their peers (95% CI=0.73–1.00; Fig. 4). and for conflicts between cubs and adults (95% CI=0.70–0.99; Fig. 4). Cubs also supported other cubs more frequently against low-born than high-born adults (95% CI=0.87–1.00) and cubs (95% CI=0.60–0.89). Adult aggression against cubs was rarely supported by others, and when this occurred, there was no tendency for the adult initiator of aggression to be higher-ranking than the cub's mother (cub supporter: 95% CI=0.46–0.89; adult supporter: 95% CI=0.15–0.95).

When supporters were divided into kin and nonkin categories, youngsters of high maternal rank were found to have significantly more kin providing support than youngsters of low maternal rank (Student's t test: t_{48}, $P=0.004$), but we found no significant difference in the number of nonkin providing support ($t_{55}=1.73$, $P=0.102$). Additionally, the ranks of supporters were correlated with the maternal ranks of the youngsters receiving support ($r_S=0.600$; Kruskal–Wallis test: $H_{16}=26.86$, $P=0.04$). Despite having more and higher-ranking allies, high-ranking cubs received coalitionary support at hourly rates that did not differ significantly from rates at which low-ranking youngsters received coalitionary support ($r_S=-0.06$; $H_{18}=22.74$, $P=0.20$). Thus, in comparison to cercopithecine primates, spotted hyaenas receive relatively little coalitionary support from nonrelatives during
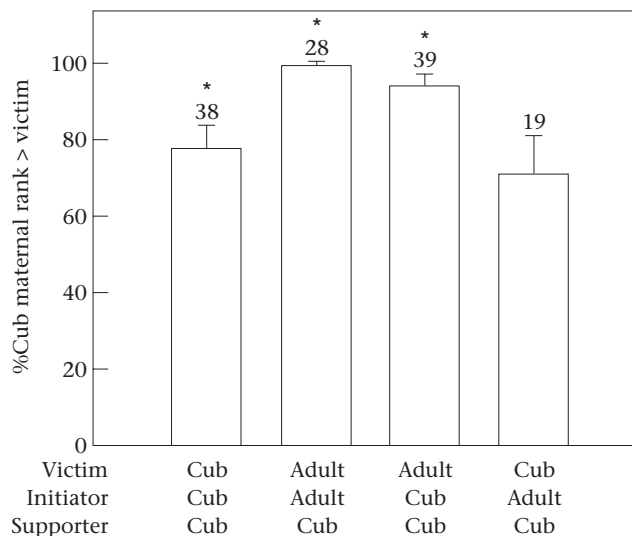
Figure 5. Mean+SE percentage of coalitions joined by cubs in which the joining cub was higher ranking than the victim of attack. Coalitions are grouped according to the age of the victim and initiator of the attack. Numbers of supporting cubs are indicated above bars.

Figure 6. Age-related changes during the first 2 years of life in the hourly rates +SEM at which a mother intervened on behalf of her own cub, a cub joined another hyaena attacking a third animal, a cub was the victim of coalitionary aggression, and a cub initiated an attack in which one or more conspecifics joined. Means for 20 cubs are represented by each data point.

rank acquisition. Hourly rates of coalitionary attacks directed against cubs were not significantly related to maternal rank (r_S=0.49; H_{18}=21.70, P=0.25), but in most cases in which a cub was the victim of coalitionary attack, the initiator of aggression was of higher maternal rank than the victim (Fig. 4).

When cubs joined coalitions against other animals, they tended to do so against low-born individuals (Fig. 5). Cubs joined coalitions with both adults (95% CI=0.86–1.00) and cubs (95% CI=0.81–0.99) against low-born adults much more commonly than against high-born adults. They also joined coalitions initiated by cubs against low-born cubs more frequently than against high-born cubs (95% CI=0.60–0.89). Although cubs also tended to join adults attacking low-born cubs more than high-born cubs, this tendency was not significant (95% CI=0.46–0.89).

Age-Related Trends

Spotted hyaena cubs attain their ranks within their peer cohorts within the first 8 months of life (Holekamp & Smale 1993) and attain their ranks relative to older clan members when they are 8–18 months of age (Smale et al. 1993). If some mechanisms are important for attainment of rank in relation to juvenile peers, but not for attainment of rank in relation to adults, then the rates of the behaviours associated with those mechanisms should drop after the cub has attained its rank in relation to its peers. Thus, behaviours that facilitate attainment of rank in relation to peers should occur at high rates during the first 8 months of life, behaviours that facilitate attainment of rank in relation to adults should occur frequently between 8 and 18 months of age, and behaviours functioning to maintain rank should be common after 18 months of age.
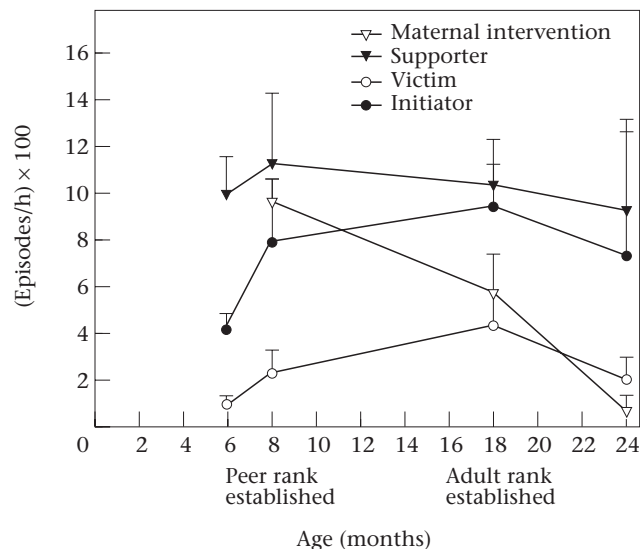
Hourly rates of maternal intervention on behalf of cubs dropped significantly between 8 and 18 months ($F_{1,18}$=5.92, P=0.015; Fig. 6) and again between 18 and 24 months ($F_{1,18}$=5.0, P=0.025). Thus maternal intervention appears to play a strong role in attainment of rank within the peer cohort and possibly also within the entire clan, but probably plays a relatively small role in rank maintenance. Hourly rates of third-party support dropped significantly between 18 and 24 months of age ($F_{1,18}$=5.56, P=0.018). This indicates that coalitionary support may figure prominently in rank attainment both within the peer cohort and in relation to the rest of the clan, but also that coalitionary support may be less critical for rank maintenance than for its establishment. Nevertheless, the high rates of coalitionary support given to youngsters older than 18 months of age, suggest that coalitions may function importantly at all stages of a hyaena's life. Hourly rates of coalition formation against cubs were relatively low, and did not vary significantly with age over the first 24 months of life ($F_{3,18}$=6.17, P=0.104). Hourly rates at which cubs joined coalitions also did not vary significantly between age intervals ($F_{3,18}$=2.85, P=0.415), but were relatively high throughout the first 2 years of life. Thus joining behaviour may function importantly in both acquisition and maintenance of maternal rank.

GENERAL DISCUSSION

During the process of socialization, rank relations of juvenile spotted hyaenas rapidly come to conform to their clan's existing social structure as expressed in the adult female hierarchy (Holekamp & Smale 1993; Smale et al. 1993; Jenks et al. 1995). Although youngsters are

initially equally likely to direct aggression towards high-born and low-born conspecifics, their behaviour rapidly changes such that they direct aggression exclusively at targets of lower maternal rank, and youngsters soon assume rank positions immediately below those of their mothers in the clan's dominance hierarchy (Holekamp & Smale 1993; Smale et al. 1993). In the present study we tested predictions of four hypotheses, each suggesting a different mechanism by which the process of maternal rank 'inheritance' might be mediated in this species. Furthermore, a fifth hypothesis that we were not able to address in the present study suggests that young hyaenas may 'inherit' their ranks by observing their mothers interact and thereby learning their relative ranks (Kawai 1965; Sade 1972; Gouzoules 1975; Altmann 1980; Walters 1980).

Various lines of indirect evidence from free-living hyaenas in our study population, and in those of other workers, fail to support the genetic heritabilty hypothesis. For example, the social rank of a juvenile hyaena changes when its mother rises or falls in the clan's dominance hierarchy (Holekamp & Smale 1993; Holekamp et al. 1993), suggesting that social rank is far too labile to be directly determined by behavioural or morphological traits that are strongly heritable. In addition to our own observations of rank reversals associated with Talek clan fission, observers watching hyaena populations elsewhere in Africa have observed revolutionary coalitions formed by members of low-born matrilines overthrowing the alpha matrilines in their respective study clans (Mills 1990; H. Hofer & M. L. East, personal communication). Thus, it seems no more likely that genetic heritability directly mediates acquisition of maternal rank in spotted hyaenas than it does in cercopithecine primates. This should perhaps be expected since, if genetic differences led directly to differences in social rank, then the genes associated with high rank would become fixed within only a few generations, and hence the genetic basis for differences in social rank would be quickly eliminated.

Although unprovoked female aggression ('harassment') may play a strong role in rank acquisition in some primates (Gouzoules 1975; Lee & Oliver 1979; Berman 1980; Silk et al. 1981b; Horrocks & Hunte 1983), it does not appear to influence rank 'inheritance' in hyaenas. Low-ranking juveniles in some monkey species receive more unprovoked aggression than high-ranking juveniles, and rates at which such aggressive acts are received by youngsters are inversely correlated with maternal rank (e.g. Horrocks & Hunte 1983). However, our data failed to reveal these trends during the process of rank acquisition in *Crocuta*. Adult female hyaenas did not direct unprovoked aggression more frequently towards low-born cubs than towards high-born cubs, and we found no relationship between the rates of unprovoked aggression received by cubs and their maternal ranks.

As occurs in many primates (e.g. Cheney 1977; Berman 1980; Walters 1980; Horrocks & Hunte 1983), interventions by mothers on behalf of their offspring appear to play a critical role in hyaena rank 'inheritance'. High-ranking female hyaenas intervened on behalf of their offspring more frequently, and more effectively, than

low-ranking females. When low-ranking females intervened, they tended to use physical blocking or distraction tactics, whereas high-ranking females used high levels of aggression against their cubs' opponents. In a study of maternal rank acquisition among captive *Crocuta*, Jenks et al. (1995) reported that only high-born females intervened on behalf of their cubs, whereas we often saw both low-born and high-born females intervene. We suspect this discrepancy can be explained by the fact that Jenks et al. (1995) scored only aggressive behaviours as interventions whereas we recorded both aggressive and non-aggressive interventions. In any case, Jenks et al. (1995) concluded as we did that maternal interventions were extremely important mechanisms of maternal rank acquisition. Most maternal interventions occurred in response to a potential threat, rather than in response to aggression directed towards cubs. This type of intervention is likely to be very important in a species such as the hyaena where the potential is high for cubs to sustain injury when engaged in altercations with larger, stronger adults. Low-ranking individuals that behave aggressively to high-born youngsters when the latter are present with their mothers risk severe retaliation for their actions. Subsequently, even when mothers are not present with their offspring, the threat of maternal intervention may influence the behaviour of other group members (Cheney 1977; Berman 1980), thereby promoting both acquisition and maintenance of maternal rank.

Finally, coalitionary support appears to play an important role in rank 'inheritance' in hyaenas. Although the rate at which cubs receive coalitionary support is not related to their maternal ranks, the vast majority of all support for cubs is given when cubs behave aggressively towards low-born opponents (Figs 4, 5). Conspecific support of cubs during their aggressive interactions with low-born individuals may positively reinforce both aggressive behaviour by the attacking cubs and appeasement behaviour by their victims. The bulk of coalitionary attacks on juveniles are formed against low-born individuals, and these attacks may serve to punish aggressive acts by cubs that are directed towards inappropriate (i.e. higher-ranking) targets. High-born cubs have more allies, and more powerful allies, than low-born cubs, and the threat of coalitionary aggression from these allies may represent a ubiquitous and powerful reminder of the status quo.

Our findings germane to coalition formation in wild hyaenas are similar to those obtained for captive prepubertal hyaenas by Zabel et al. (1992). Although hourly rates of coalition formation in the wild are roughly an order of magnitude lower than those observed in captivity, in both situations high-born hyaenas are more likely than low-born hyaenas to initiate and support attacks, and low-born animals are more likely to be targets of group attacks. Among both captive and wild hyaenas, coalitionary attacks appear to reinforce the existing dominance hierarchy. However, ontogenetic trends described in the present study (Fig. 6) indicate that coalition formation may play a far more important role in challenging the existing hierarchy, and thus in rank acquisition, than suggested by data on captive hyaenas.

Cubs may play an active role in the acquisition and maintenance of maternal rank by joining coalitions, particularly those directed against low-born individuals, since cubs preferentially join hyaenas attacking lower-born animals. By joining in aggression against low-born individuals, cubs can reinforce their own dominant status relative to the victim. Although maternal interventions may be critical for cubs to gain their peer ranks and align these with maternal ranks, coalitions may play a larger role for older cubs that are attaining, and later maintaining, their ranks in relation to hyaenas outside their peer group.

When *Crocuta* cubs are first brought to the communal den at approximately 1 month of age, they display appeasement behaviour to all other hyaenas they meet there, and adults generally only direct mild aggression towards very young cubs when their play interrupts adults' naps by the den. During the course of rank acquisition, cub submissive behaviour appears to be extinguished in interactions with some conspecifics, such that appeasement persists only towards a subset of conspecifics. Cubs begin initiating attacks on nonsibling conspecifics during their third month of life (Holekamp & Smale 1993), and enter a stage during which they direct both aggressive and appeasement behaviours simultaneously at larger-bodied hyaenas. Aggressive behaviour directed by cubs towards high-born conspecifics appears to be rapidly extinguished via punishing counterattack or coalitionary aggression, and perhaps also by relatively rare and ineffective maternal interventions. By contrast, cub attacks on low-born conspecifics are likely to be reinforced by effective protection from the mother, coalitionary support from other clan members, and perhaps also by immediate improved access to contested resources.

Our analysis of age-related trends observed during maternal rank inheritance suggests that the process of rank acquisition begins with defensive maternal interventions in which the cub does not participate. If play turns too rough or another hyaena gets nasty, cubs may solicit maternal aid with vocalizations (East & Hofer 1991; Holekamp et al. 1999), but mothers often intervene without any apparent cub solicitation of aid. Later in development, cubs start joining mothers when mothers intervene on their behalf. Later still, cubs begin initiating attacks on conspecifics, and often enjoy third-party support from their mothers or other allies when these attacks are directed at low-born animals. This sequence of events appears to lead to rank reversals, first with peers and then with older juveniles and adults. Low-born opponents first cease behaving aggressively towards high-born cubs, and later begin appeasing them. Once these rank reversals have occurred, cubs appear to maintain their ranks, not only by winning in dyadic encounters with low-born conspecifics (Holekamp & Smale 1993; Smale et al. 1993), but also by obtaining third-party support against low-born animals, and perhaps also by joining attacks on low-born animals.

It appears that the proximate mechanisms of maternal rank 'inheritance' in spotted hyaenas are strikingly similar to those found in cercopithecine primates. In both groups, maternal intervention in disputes plays a key role in rank attainment, with the mother asserting her dependent offspring's status just below her own. Coalitions also seem to play a strong role in rank 'inheritance' in both primates and hyaenas. In hyaenas, coalitionary support by kin and nonkin appears to reinforce aggression against appropriate' targets, whereas aggressive coalitions serve to punish 'inappropriately' directed aggressive behaviour by cubs. Additionally, cubs may join in coalitions against low-born individuals to reinforce their own status. Genetic heritability is not an adequate explanation for maternal rank 'inheritance' in either primates or hyaenas. The key mechanistic difference in rank 'inheritance' between these taxa is that low-ranking cercopithecine juveniles may experience a high degree of unprovoked aggression from high-born adult females (e.g. Horrocks & Hunte 1983), whereas low-ranking juvenile hyaenas do not receive such harassment. However, the frequency with which unprovoked aggression occurs among adult female hyaenas suggests that harassment might function in the maintenance of rank relationships in animals older than those examined here. In any case, the fact that the mechanisms of maternal rank 'inheritance' are so strikingly similar in *Crocuta* and cercopithecine primates suggests that rank acquisition in both taxa might be mediated by common cognitive processes.

Acknowledgments

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