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Coalition formation in a colony of prepubertal spotted hyenas

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INTRODUCTION

Alliances have been reported among free-ranging social carnivores, but not transitory coalitions. Alliances and their function have been described for lions, *Panthera leo* (Bertram 1975; Bygott *et al.* 1979; Packer and Pusey 1982), cheetahs, *Acinonyx jubatus* (Caro and Collins 1987), and coatis, *Nasura narica* (Russell 1983). Coalitions have been observed among captive wolves, *Canis lupus* (Fentress- *et al.* 1986; Jenks 1988; Zimen 1976), and they are an important element of social behaviour in captive spotted hyenas (*Crocuta crocuta*). Although there do not appear to be any published field studies of coalitions among social carnivores, Mech (1970, p.78) has observed group attacks among wild wolves that apparently involved coalition formation. In this chapter, we report on coalitions that formed in a colony of prepubertal spotted hyenas. Although these results were obtained under artificial circumstances, the existence of coalitions among spotted hyenas is supported by numerous field observations (Frank, personal observation). Kruuk (1972) described the `parallel walk', when two hyenas threaten a third by approaching in attack posture, walking shoulder to shoulder almost touching one another. A target hyena can be a member of the same clan, or an intruding animal. This description fits our definition of a coalition as an aggressive interaction during which two or more hyenas join to threaten or attack a third animal.

Advantages of forming alliances among carnivores usually relate directly to reproductive benefits, as when groups of males are able to outcompete single males for females or their territories. Benefits gained from forming coalitions may relate directly to reproductive success (for example, in wolf packs where only a single female breeds). Alternatively, coalition formation may directly affect dominance status and indirectly modulate reproductive success by allowing dominant animals to control access to resources (in spotted hyenas, for example).

Felids: lions and cheetahs

Male lions form alliances of 2-6 members in the Serengeti. They may be composed of siblings or related similar-aged cohort males which disperse together from their natal pride; or of unrelated males which join together subsequent to dispersal (Packer and Pusey 1982). Males which form alliances have a competitive advantage over single males in obtaining and maintaining possession of prides of females (Bertram 1975; Bygott *et al.* 1979; Packer and Pusey 1982). Male alliance partners are not ensured equal access to estrous females in a pride, but each male usually obtains some matings.

Lions are the only feud in which females are social. Most females remain in their natal pride for life, retaining close associations with 1-17 female relatives. Females occasionally leave their pride to avoid having their cubs killed by new males during pride takeovers. Females will support one another in aggressive interactions against males in efforts to prevent infanticide by immigrating males, and they may be wounded or even killed in these fights. Cooperatively defending cubs may be an important aspect of communal rearing among female lions (Packer and Pusey 1983).

Male cheetahs which form alliances (usually littermates) are more likely than single males to become territorial, and thereby gain access to solitary females within these territories (Caro and Collins 1987). Length of male tenure on territories is correlated with alliance size, and single territorial males are soon replaced by alliances of 2-4 males.

There is a higher incidence of single male cheetahs than single male lions in the Serengeti (41 per cent vs. 13 per cent). Caro and Collins (1987) suggest that this might reflect costs of sharing matings: some single cheetahs are able to defend a territory and mate, while single lions are highly unlikely to maintain possession of a pride, making mate sharing unavoidable among lions.

Wolves

Coalitions have been observed among captive wolves (Fentress *et al*. 1986; Jenks 1988), when individuals join ongoing dyadic aggressive encounters. In one colony of 10-12 wolves, including multiple males and females whose membership fluctuated from year to year, an average of 5.64 wolves participated in attacks (Fentress *et al.* 1986). The size of attacking groups ranged between 2-11 animals. In another wolf colony consisting of 8-10 animals, the number of aggressors ranged between 2-5 (Jenks 1988).

Other small carnivores

Coatis are a highly social species within the Procyonidae. Females and young live in bands, while adult males are solitary. Males are excluded from bands except during the mating season, apparently because they will opportunistic-ally prey upon juveniles (Russell 1981). Pairs of females within bands preferentially groom each other, and also support one another during infer-quent aggression that occurs (Russell 1983). Bands split when groups exceed 3-5 females, with fission occurring along previously established lines of affil-iation. Russell (1983) concluded that `. . . individuals choose to invest in new relationships to a degree dependent upon their apparent potential for devel-oping advantageous equitable relationships . . : , with kinship playing a secondary role to reciprocal support.

There are a number of social species among viverrids (Rood 1986), including the well-studied dwarf mongoose *(Helogale parvula).* Mongooses apparently associate in groups as a predator defence mechanism, allowing them to forage diurnally. The social system of the dwarf mongoose is similar to that of wolves: there are separate male and female dominance hierarchies, and only the alpha animals of each sex usually breed successfully. Other group members, including unrelated animals, may participate in the care of young in both dwarf (Rasa 1983; Rood 1978) and banded mongooses (*Mungos mungo,* Rood 1974). Dwarf mongooses may have preferred partners for grooming and resting (Rasa 1977). Male dwarf mongooses sometimes emigrate with other males and become breeders by taking over another pack (Rood 1990). There have been no observations that breeding females may be replaced by groups of intruding females, as occurs in males. Males in one solitary species, the slender mongoose (*Herpestes sanguineus*), can share home ranges and occasionally associate together (Rood and Waser 1978). Adult male slender mongooses have been seen denning, playing, travelling, and feeding amicably together (Rood 1989).

Among mustelids, the European badger *(Meles meles)* forms matrilineal groups which den in communal burrow systems ('setts') and share a common range (Kruuk 1989). However, mutually supportive relationships have not been described.

SPOTTED HYENAS

Female masculinization and social organization

Spotted hyenas cooperatively hunt ungulates, and feed competitively in large groups after a kill is made (Kruuk 1972). Juveniles are dependent on maternal. support for access to prey (Tilson and Hamilton 1984), and this access is correlated with maternal rank (Frank 1986). Adult females and their dependent offspring are dominant to males in nearly all social situations. Females are heavier and more aggressive than males (Frank *et al*. 1989), and they display a unique syndrome of anatomical masculinization: they possess no `normal' external female genitalia, but rather have a greatly hypertrophied clitoris that is fully erectile and nearly indistinguishable from the male penis (Matthews 1939). The vaginal labia are fused into a pseudoscrotum. The urogenital canal through which both mating and birth occur, traverses the length of the clitoris. This syndrome of `masculinization' is associated with elevated levels of androgens in female spotted hyenas (Frank *et al*. 1985; Glickman *et al*.1987; Lindeque and Skinner 1982; Racey and Skinner 1979).

The social system of spotted hyenas resembles that of many Old World primates (Frank 1986; Henschel and Skinner 1987; Mills 1985): females remain in their natal group (`clan') for life while males disperse to join other clans as adults. Maturing females acquire their mother's rank, resulting in stable dominance relations among matrilines over generations. Associations among related females are closer in higher-ranking matrilines (Frank 1986), presumably reflecting greater benefits that young females may accrue from the support of a high-ranking mother. Sons of high-ranking. females are dominant to females which rank lower than their mother, and they remain in a clan longer before dispersing than do lower-ranking sons. Again, this may reflect advantages of maternal support in the highly competitive feeding situation of hyenas. After dispersing to new clans, high-ranking males have better prospects of mating than do subordinates.

The Berkeley study

Observations of coalitions among captive spotted hyenas occurred during the course of a long-term study of behavioural and hormonal development, focused upon the unique sexual differentiation of this species. We have been particularly interested in the development of sex differences in aggressive behaviour and dominance. However, because of the extremely tight association between maternal rank and the status/behaviour of offspring, any differences between males and females during early life could easily be obscured. This, in turn, would have interfered with our attempts to understand the proximal mechanisms of sexual differentiation. We therefore chose to study these animals in peer. groups, without maternal influence.

The hormonal focus of our research required that a subset of hyenas have their ovaries or testes removed. Although one would not normally expect juvenile gonadectomy to influence sexually dimorphic behaviour during the juvenile or subadult period (see for example, LeBoeuf 1970; Musky 1955), the endocrine situation in hyenas is rather unusual. Female spotted hyenas have high circulating levels of the androgen androstenedione throughout the juvenile/prepubertal periods. (Glickman *et al*. 1987; Lindeque *et al*.1986).

Removal of the ovaries results in a marked decline in this hormone (Glickman *et al.* 1987). Since androstenedione has been found to facilitate aggressive behavior under certain circumstances in other species (Erpino and Chappelle 1971; Tsutsui and Ishii 1981), removing ovarian secretions through gonadectomy might reduce aggressiveness of female hyenas, including their participation in coalitions.

Coalitions, and possibly matrilineal alliances, may be an important factor in the near absolute dominance of female spotted hyenas over males in nature (Frank *et al.*1989). In this chapter we report frequency of occurrence and duration of coalition attacks, and size of the groups involved in attacks. We analyse effects of age, sex, and gonadal secretion on coalitions; i.e., which hyenas initiate coalition attacks, join to support the initiator, and are targets of attacks. The relationship between dominance status and coalitions will be examined to determine if attacks are more likely to be initiated by dominant animals, and if subordinate animals are more likely to be targets.

Animals joining coalitions can either challenge or reinforce a dominance hierarchy. By supporting coalition attacks against lower-ranking animals, the existing hierarchy is reinforced.. Alternatively, by joining coalitions against higher-ranking opponents, the. dominance rank of a targeted animal may be challenged. Among primates, individuals are less likely to initiate or join in supporting aggression when they rank below a target (Bernstein and Ehardt 1985; Cheney 1977; Datta 1983; Ehardt and Bernstein this volume, pp: 86-8; Kaplan 1978; Walters 1980), presumably due to risks of retaliation (but see de Waal this volume, pp. 238-9). We present data for hyenas on frequency of initiating and joining coalitions against dominant animals, to determine whether their participation in coalition attacks reinforced or challenged the dominance hierarchy.

Finally, we suggest that coalitions in hyenas and other social mammals may reflect a more general tendency to exhibit socially facilitated behaviour, i.e. `to do what other group members are doing'. Social facilitation of behaviour is found among many animal groups (Zajonc 1965), and may be particularly important among social carnivores. Social facilitation could serve to synchronize activities of individuals, within a group (see for example, Lockwood 1976), which may make cooperative group hunters more effective.

Subjects

Two cohorts of 10 infants each were collected under permit in Narok District, Kenya in December 1984/January 1985 and November/December 1985. Infants were between 1 week and 2 months of age at the time of collection. When cohort I was collected, we were unable to sex the infants by visual inspection, and it consisted of seven females and. three males. In addition to the biased: sex ratio, there was -a weight bias; two of the males showed slow growth and have remained unusually small as adults (Frank *et al*. 1989). The second cohort consisted of five females and five males.

Although there was daily contact with human caretakers, the hyenas lived in peer groups from the time of collection. Each cohort was housed in separate indoor-outdoor enclosures measuring 12 x 30 m at Berkeley, California.

Two females in cohort I and two females and two males in cohort II were bilaterally gonadectomized at 4-6 months of age. Mid-ranking animals, as determined by regular feeding competition tests (Frank *et al*. 1989), were selected for gonadectomy.

Behavioural sampling

Spontaneous behaviour of the older cohort was observed from September 1985 through August 1986 for this study. After September 1986 this cohort was divided into two separate groups, because of increasingly severe consequences of aggression. The younger cohort was sampled from March 1986 through August 1987, at which time it was subdivided for the same reason. Because of the nocturnal behaviour of the hyenas, observations were recorded between 1800 and 2200 hours using artificial light.

To assess the effects of age, data were subdivided into an early subadult age period (approximately 11.5-18 months of age; based on 62 h of observation for cohort I and 66 h for cohort II) and a late subadult age period (approximately 18-21.5 months of age; based on 19 h of observation for cohort I and 48 h for cohort II). The older age.period coincided with the first indications of pubertly according to radioimmunoassay of various gonadal hormones (unpublished data).. Male spotted hyenas are considered to be reproductively mature at approximately 2 years of age and females at 3 years (Kruuk 1972).

Critical incident sampling (Altmann 1974) of all occurrences of significant social behaviours (Martin and Bateson 1986) within each cohort was used. All instances of aggression, submission, affiliation, and specified social activities involving two or more animals were recorded at 30-s intervals in. an actor-behaviour-recipient format. By definition, coalitions involved two or more hyenas (as actors) threatening/attacking a target (the recipient). Aggressive behaviours included threatening postures (a forward `approach' movement with the ears and mane erect), one animal displacing another, bites and chasing/lunging attacks. Submissive behaviours included avoiding a threatening or attacking animal and appeasement postures, such as crawling on the carpals, with the head down or under and/or shaking the head from side to side, and an open mouth. Affiliative/prosocial behaviour were allogrooming, the meeting ceremony, and play.

Dominance ranks referred to in this study were determined from dyadic interactions during sampling of spontaneous social activities, when one member of a pair exhibited submissive behaviour. For each pair of animals, the hyena that received submissive displays during more 30-s. intervals was the dominant animal for that dyad. This measure of dominance is highly correlated with ranks based on dyadic aggressive interactions, and with ranks determined from competitive interactions during group feeding at a cluster of meaty neck bones. In each cohort, the 10 hyenas were ranked according to the total wins and losses in dyadic interactions. A rank of 1 was attributed to the alpha hyena and 10 to the lowest-ranked animal in each cohort.

COALITIONS AMONG CAPTIVE SPOTTED HYENAS

Coalitions: frequency and rates of recruitment

Coalitions occurred when two or more hyenas joined in threatening or attacking a third hyena. Typically, this began with a dyadic encounter. One of the combatants was then joined by one or more allies. Frequencies of coalition attacks within the two cohorts are presented in Table 5.1. On average, attacks occurred 2-3 times per hour. The duration of attacks averaged about 1.5 to 2.5 30-s intervals. Mean sizes of coalitions that were involved ranged between 2:5 and 3.7 hyenas between the age periods we sampled. However, on some occasions all nine animals joined in attacking, a single recipient. Almost half of the attacks were performed by two hyenas, with the occurrence of larger coalitions decreasing with their size (Fig: 5.1).

Table 5:1. Characteristics of coalition attacks in two cohorts of spotted hyenas during two age periods. Frequency, duration, and size of attacking coalitions. All values are means ± standard deviation. *N* is the total number of attacks.

Age	Early subadult	Late subadult
Cohort **I**	***N* = 180**	***N* = 51**
Attacks/h	2.9	2.7
Duration of attack*	2.6 ± 3.0	2.3 ± 1.6
Coalition size	3.2 ± 1.5	3.7 ± 1.7
Time to maximum coalition size*	1.7 ± 1.6	1.5 ± 0.8
Cohort II	***N* =**165	***N* =** 104
Attacks/h	2.5	2.1
Duration of attack*	1.6 ± 1.2	1.3 ± 0.8
Coalition size	3.0 ± 1.3	2.5 ± 0.8
Time to maximum coalition size*	1.3 ± 0.9	1.1 ± 0.3

*** Values for time-are number of 30-s intervals.**

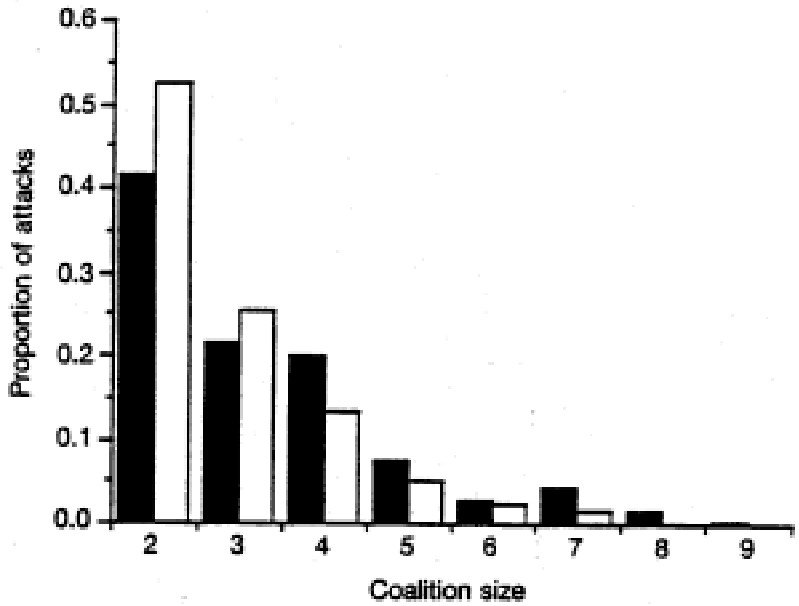


Fig. 5.1. Proportion of coalition attacks that occurred according to number of aggressors that were involved. Cohort I (solid bars), N = 230 attacks; cohort II (open bars), N = 269 attacks.

Attacking groups formed very quickly, and maximum coalition size tended to occur within one to two 30-s intervals.

Effects of age, sex, and. gonadectomy on. coalition attacks

Hyenas which participated in coalition attacks were characterized in one of three ways: (1) according to the animal which initiated an attack; (2) to the animals which joined or 'supported' the attack; and (3) to the animal which was selected as the recipient or `target' of the attack. Rates that individual hyenas initiated, supported, or were targeted in attacks are presented separately by cohort in Figs. 5.2(a-c), according to the sex and ages of the animals. Individual three-way unbalanced factorial analyses of variance were computed for each dependent variable, with sex, age, and cohort as the three independent variables. The three analyses revealed only one significant effect: an interaction between cohorts and age in rates of supporting coalitions (F = 5.01; d.f. = 1,16; p < 0.05). This was presumably due to a decline in supporting coalition attacks with age in cohort II in contrast with a slight increase with age in cohort I. Thus, within the confines of this study, with its relatively small sample sizes, neither sex, age, or cohort influenced rates that hyenas initiated, supported, or received coalition attacks.

Effects of gonadectomy were tested by combining data from both cohorts. Individual three-way unbalanced factorial analyses of variance were computed for each dependent variable, with sex, age, and gonadectomy as the three independent variables. We found no significant effects of gonadectomy on rates of initiating, supporting, or receiving coalition attacks.

Absolute dominance rank and frequency of coalition attacks

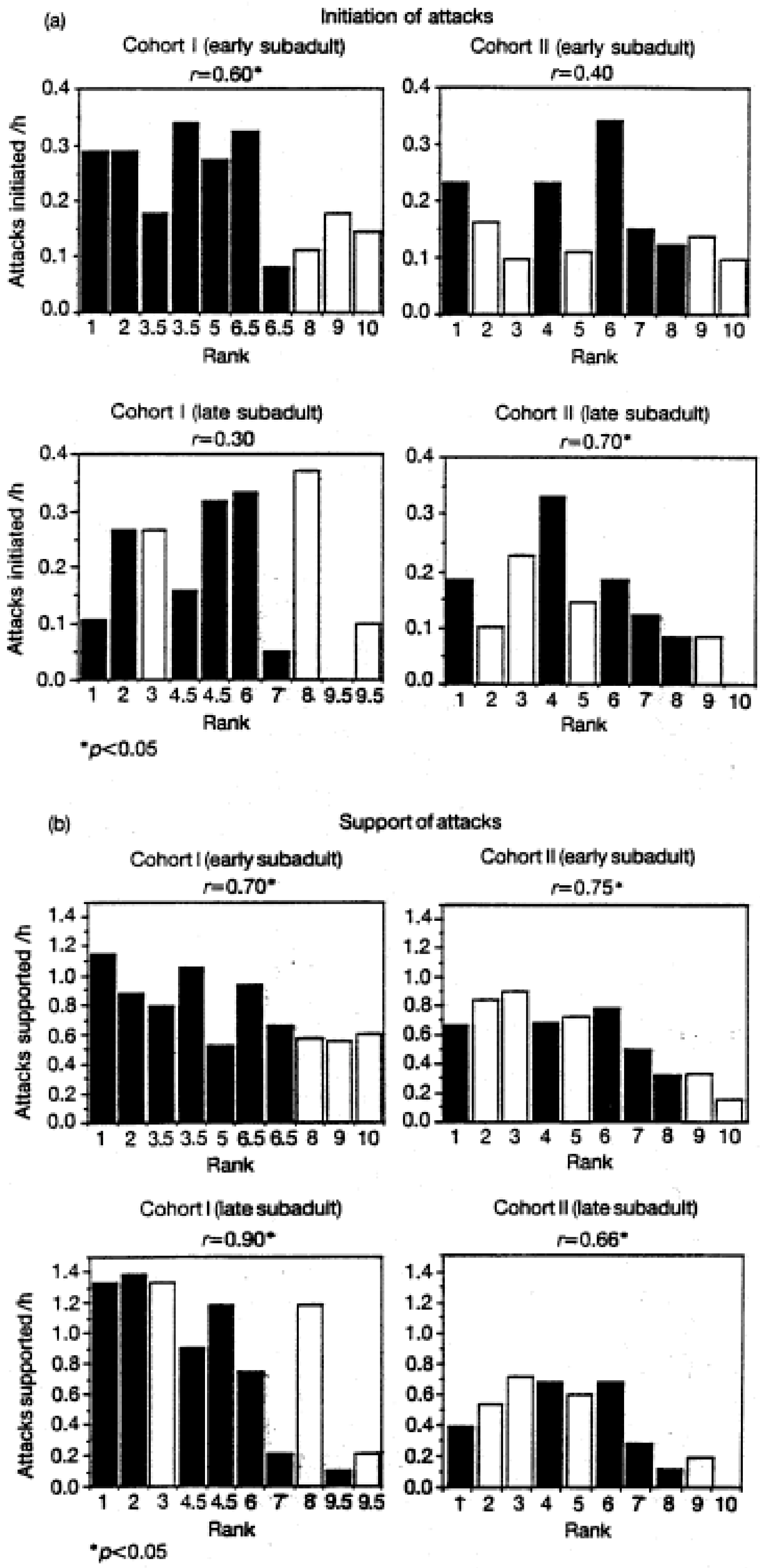
Correlations between dominance rank and rates of initiating, supporting, or being targeted during coalition attacks are presented by cohort and age period in Figs. 5.2(a-c). There was a tendency for dominant animals to initiate attacks more frequently than subordinates, although statistical significance was achieved in only two of four correlations. In contrast, supporting coalition attacks was significantly correlated with rank in a more robust manner. Dominant animals supported attacks more frequently than subordinates in both cohorts during both age periods. Subordinate hyenas tended to be targeted during group aggression more frequently than dominants. There were significant correlations between low dominance rank and being targeted during three of four cohort-age intervals, with particularly consistent effects in cohort II.

We have found no consistent sex differences in dominance rank among the captive hyenas. Females do not dominate males, despite having higher aggression rates and weights (Frank *et al*.1989). One exception to this lack of female dominance occurred in cohort I during the early subadult period. The three males in cohort I (which were the lightest in weight) ranked below all seven females at this age. Difference in mean rank was significant ($F = 12.99$; d.f. -1,8; $p < 0.01$). Although there were no sex differences in dominance rank during the remaining age periods, we calculated semi-partial correlations, controlling for sex differences, between dominance rank and frequency of receiving attacks (Table 5.2). Even with sex differences removed statistically, negative correlations between dominance rank and frequency of receiving attacks were still significant during both age periods in both cohorts.

Table 5.2. Semi-partial correlations between dominance rank and rates of receiving coalition attacks, with sex of spotted hyenas controlled.

	Early subadult	Late subadult
Cohort I	-0.70*	-0:67*
Cohort II	-0.85**	-0.73**

*** p < 0.05; ** p < 0.01.**


(a)
Initiation of attacks
Cohort I (early subadult)
r=0.60*
Cohort II (early subadult)
r=0.40
Attacks initiated /h
0.0
0.1
0.2
0.3
0.4
1 2 3.5 3.5 5 6.5 6.5 8 9 10
1 2 3 4 5 6 7 8 9 10
Rank
Cohort I (late subadult)
r=0.30
Cohort II (late subadult)
r=0.70*
1 2 3 4.5 4.5 6 7 8 9.5 9.5
*p<0.05
(b)
Support of attacks
Cohort I (early subadult)
r=0.70*
Cohort II (early subadult)
r=0.75*
Attacks supported /h
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Rank
Cohort I (late subadult)
r=0.90*
Cohort II (late subadult)
r=0.66*
*p<0.05

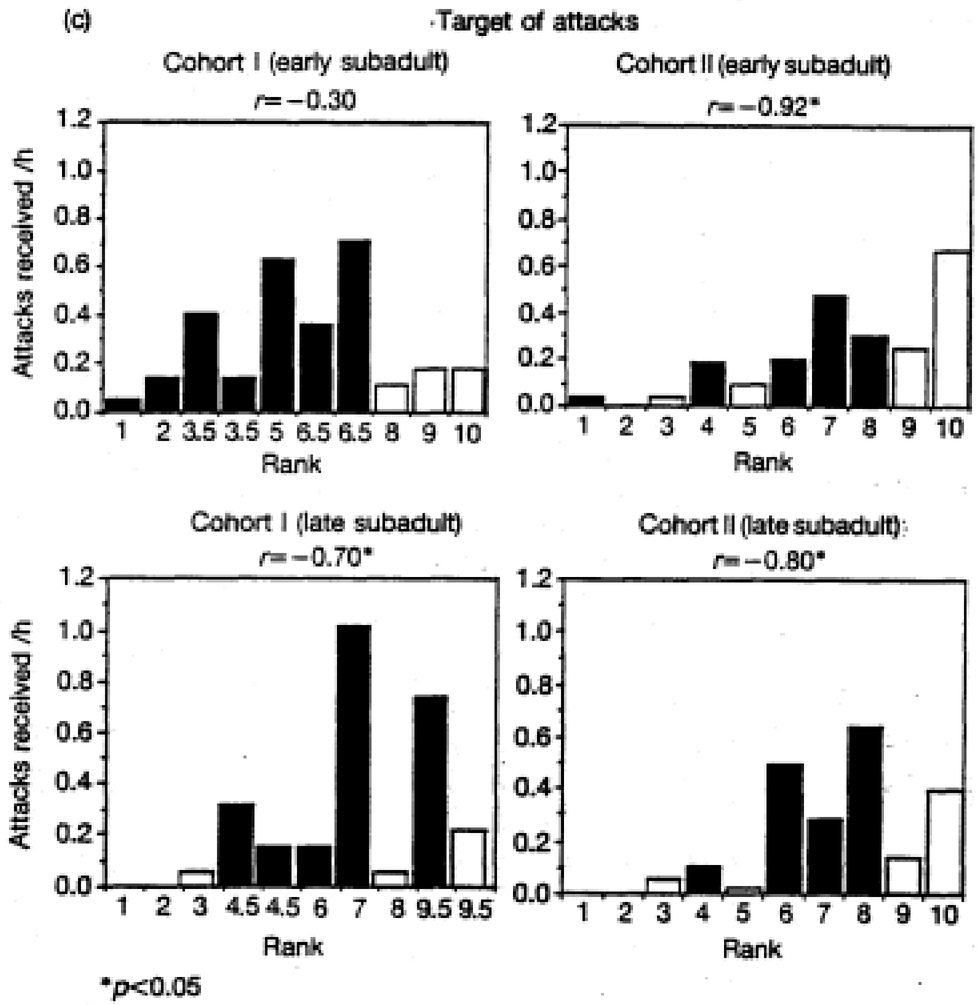


Fig. 5.2- Relationship between dominance rank and rates of initiating (a), supporting (b), and receiving (c) coalition attacks among prepubertal spotted hyenas. Rates were calculated from the number of 30-s intervals that each behavior occurred per hour of observation. Data are presented for each individual in both cohorts during two age periods. Spearman rank correlations (*r*) are provided between rank and rate of participation in attacks. Solid bars represent females and. open bars males.

It should be emphasized that this report deals only with prepubertal animals. In the wild, all resident adult males which immigrate into a clan are subordinate to females and juveniles, suggesting that events related to male dispersal and immigration may be important in the development of female dominance (Frank *et a1*.1989). Furthermore, rank changes occurred among. the captive females after they produced their first litters, and observations of maternal defensive aggression and coalition attacks by mothers on behalf of offspring suggest such behaviour may be important in the eventual dominance of females. Maternal. aggression is apparently related to the process of maternal rank acquisition by juveniles in wild hyenas, and this process is currently under study.

Relative dominance rank between participants of coalition attacks

Many primates are less likely to initiate or join in supporting aggression when they rank below a target, due to risks of retaliation. To estimate frequencies of initiating or supporting attacks against dominant animals, data need to be corrected for the number of *potential* dominant opponents available. In cohort I, for example, the three males which occupied the bottom ranks of the dominance hierarchy in the early subadult period had fewer opportunities to attack subordinates than did the seven females which occupied the higher ranks. That is, the lowest-ranked male could attack no subordinate hyenas since he was at the bottom of the hierarchy; the next higher male could attack only one subordinate hyena, etc. Females in this cohort had increasingly more opportunities to attack subordinates.

In order to deal with this problem, we first eliminated data from hyenas occupying the top and bottom ranks since neither of these animals had an opportunity to choose between dominant and subordinate targets-the hyena in the first rank could initiate or join attacks only against subordinates, while the hyena in the last rank could do so only against dominant opponents. For the remaining eight hyenas in each cohort, we estimated the number of attacks against subordinates that would be expected purely on the basis of chance. The second ranking animal, for example; has one dominant target and eight subordinate targets. If only chance factors were operating in initiating or joining attacks against other hyenas, one would expect 1/9 of the total attacks participated in by this particular, animal to be against dominant targets and 8/9 of the attacks to be against subordinate targets. Expected frequencies of attack were obtained by multiplying the appropriate chance ratio by the total number of attacks for each of the eight animals in both cohorts. Observed frequencies corrected for chance were calculated by subtracting expected frequencies from frequencies actually observed. Finally, we converted these corrected frequencies into rates (frequency/h) in order to compensate for different numbers of observation hours that were available for the two cohorts and different age periods.

When corrections for opportunities were calculated, no significant differences between male and female hyenas were found. Corrected data combined over sex are presented in Table 5.3, showing differences between observed and expected rates of initiating and joining attacks. Means in Table 5.3 are all positive, indicating a consistent tendency for hyenas to initiate and join attacks against subordinates. (A negative difference would indicate a tendency to attack dominants.) All of the means for cohort II are significantly different from zero, while only one mean for cohort I is significantly different from zero. Thus, hyenas in cohort I were equally as likely to initiate and support coalition attacks against animals that outranked themselves, as against lower-ranking animals during the early subadult age period.

Table 5.3. Differences between observed and expected rates of initiating and joining attacks (per hour) against subordinate hyenas. This analysis is corrected for the relative number of dominant and subordinate opponents. Each mean is based on eight subjects. All values are positive, indicating consistent tendencies to initiate and join attacks against subordinates.

		Initiating attacks		Joining attacks	
		Early subaduit	Late subadult	Early subadult	Late subadult
Cohort I	Mean	0.012	0.073	0.041	0.233*
	S.D.	0.044	0.099	0.093	0.140
Cohort II	Mean	0.080*	0.067*	0.260*	0.168*
	S.D.	0.055	0.032	0.105	0.118

*** *p* < 0.01; values are significantly different from zero.**

Behaviours preceding attacks against dominant animals.

Subordinate hyenas which initiated attacks against dominant animals were most frequently involved in asocial activity with a third hyena just prior to the attack. In cohorts I and II, respectively, 71 per cent and 52 per cent of these interactions began after a subordinate attacker had been involved in non-aggressive, prosocial behaviour (such as play, or sniffing each other, N =35 and 25 attacks in cohorts I and II; respectively). In all of these cases, the third hyena joined in the aggression and supported the lower-ranked initiator in the attack. In addition, on a few occasions a subordinate target successfully redirected a group attack against an initiator (in 17 per cent and 32 per cent of the attacks, in cohorts I and II, respectively). In these cases, hyenas which had joined the initial attack then supported that target in reversing the interaction and attacking the previous initiator.

Consequences of attacking dominant. hyenas

Forming coalitions with other animals and attacking hyenas that were higher ranking than themselves may have been a mechanism: for the three subordinate males in cohort I to rise in dominance rank. These three males all rose in rank: two by the conclusion of this study period, and one at a later date. During the late subadult age; one of these males rose from position 9 in the hierarchy up to position 3, while another rose from position 10 to 8.

DISCUSSION

Coalitions among social carnivores: spotted hyenas and wolves

Coalitions of 2-9 hyenas simultaneously attacking a target hyena were relatively common in both cohorts of prepubertal hyenas. Such coalitions have also been observed in nature (Frank unpublished data). Coalition threats/attacks observed in the present study are identical in appearance to those depicted by Kruuk (1972: Plates 38-40). Groups of resident hyenas gain advantages when they confront individual immigrants (Henschel and Skinner 1987).

Rates of coalition attacks appeared to be lower in wolf colonies compared to the hyena colony. During 435 h of observation, Fentress *et al*. (1986) observed 26 wolf attacks (0.06 attacks/h); rates of attack in the hyena colony were over 30 times higher. However, there were significant differences in group composition between the hyena and wolf colonies. The wolf colonies were more natural breeding groups, of mixed age and sex, while the hyena colony was composed entirely of immature animals during this study. This is particularly relevant since coalition attacks among wolves often involve mating competition. Nevertheless, there are similarities in coalitions between hyenas and wolves: in both species, transitory aggressive coalitions emerge during which both males and females threaten/attack a target animal. Animals participating in these coalitions shift from one attack to the next.

Effects of sex, age, and gonadectomy

Neither sex or age influenced rates that immature hyenas initiated, joined, or were targeted in coalition attacks. In contrast, female cercopithecine primates usually aid more frequently than males (Cheney 1977; Ehardt and Bernstein this volume pp. 85-8; Kaplan 1977; Kurland 1977; Massey 1977). It has been suggested that female aiding may help maintain the established social order of groups where they form the stable core (Bernstein and Ehardt 1985; Chapais this volume pp. 49-50). However, it seems likely that rearing immature hyenas in the absence of mothers may have obscured any sex differences that involve long-established matrilines. In nature, matrilines of females which live in the same area throughout their lives play a major role in defending territorial borders during disputes with other clans (Kruuk 1972). These same groups of females are also likely to confront individual intruders, including immigrating males. Until more coalition data are available from hyena clans in the field and from colony animals that include matrilines, it would be premature to draw any conclusions regarding differential behaviour of female and male hyenas compared to primates.

The function of coalition attacks may differ across species with different mating systems, and this may influence sex differences in coalition participation. For example, a single dominant female often monopolizes reproduclion among wolf packs (Rabb *et a1.*1967; Zimen 1976). Associated with this pattern, females initiated 92 per cent of coalition attacks and were targeted in 96 per cent of attacks in one colony (Fentress *et a1.*1986). In contrast, all female hyenas within a clan can breed, so they may not engage in aggression to suppress reproductive behaviour of other females. However, daughters of high-ranking females may have higher reproductive success (Frank, Holekamp, and Smale unpublished data), and both male and female offspring of high-ranking hyena females have competitive advantages during feeding (Frank 1986). Thus, participation in group attacks by both male and female hyenas might optimize their competitive effectiveness within a group.

Gonadectomy of juvenile hyenas produced a marked reduction in plasma levels of androstenedione and testosterone (Glickman *et al.*1987). However, there were no apparent effects of gonadectomy on initiating, supporting, or being the target of coalition attacks. This is consistent with data from dyadic aggressive interactions. Juvenile gonadectomy had no significant effects on individual levels of aggression or dominance rank during the subsequent subadult period (Frank *et al.* 1989). If there are activational effects of gonadal hormones during this time, they are not sufficiently robust to overcome the relatively small sample sizes in this study and enduring effects of social learning that may occur prior to gonadectomy. After puberty, there will be an even greater discrepancy between hormonal profiles of intact and gonadectomized subjects. It is possible that there will be effects of gonadectomy on aggressive interactions and coalitions during the postpubertal period.

Dominance rank and rules of coalition formation

In considering the relationship between dominance and participation in coalitions, it is necessary to distinguish between absolute dominance rank within a group and relative dominance rank between two individuals. Absolute dominance rank correlates with absolute frequencies of participation in coalition attacks. Dominant animals tended to initiate and support attacks more frequently than subordinates, and subordinate hyenas tended to be targeted during attacks more frequently than dominants. Similarly, among wolves, coalitions usually involved a group of dominant animals attacking a subordinate (Zimen 1976). Thus, coalition attacks among both spotted hyenas and wolves tend to reinforce the existing dominance hierarchy.

In order to understand the functional consequences of coalitions for individuals within a group, it is necessary to examine the relative dominance ranks of initiators and supporters in relation to the rank of targets. Individuals that join coalitions may benefit from closer association with dominants (Cheney 1977; Seyfarth 1977, 1980). If an animal that joins an interaction is subordinate to a targeted animal, it gains safety from the coalition in challenging its dominance, although with risks of retaliation. If an animal that joins an interaction is dominant to a targeted animal, it has safety from the coalition in reinforcing its own dyadic dominance over the target (Waiters 1980; Datta 1983). Both tactics occurred among the captive hyenas.

All of the hyenas in cohort II, regardless of dominance rank, joined attacks when they were dominant to targeted animals during both age periods. Thus, coalitions in that cohort contributed to reinforcing the existing hierarchy, not challenging it. A similar situation existed during the late subadult period in cohort I. Hierarchy-reinforcing behaviours appear to be the rule among wolves as well. Dominant animals frequently participated in coalition attacks against subordinates in one wolf colony (Jenks 1988), and the dominant female in another colony participated in 82 per cent of attacks (Fentress *et al*. 1986).

Hyenas, wolves, and primates: aiding-at-risk

Cercopithecine primates (Bernstein and Ehardt 1985; Cheney 1977; Datta 1983; Kaplan 1978; Waiters 1980), hyenas, and wolves are less likely to aid another individual when they rank below an opponent: Initiating or supporting attacks against dominant animals (‘aiding-at-risk’;-Bernstein and Ehardt 1985), occurred infrequently in the hyena colony. However, it did occur among hyenas in cohort I during the early subadult period: three low-ranking hyenas joined and initiated attacks against animals that outranked them. Even after data were appropriately corrected for the number of potential subordinate opponents available, hyenas in cohort I were equally likely to initiate and join attacks against dominants as against subordinates at this age. Hyenas in this cohort apparently gained safety from coalitions in challenging the dominance of targeted hyenas. Low-ranking hyenas in cohort I, which were all males during the early subadult period, seemed to use high female aggression and the readiness of females to attack other females to their own advantage for support in coalitions. Subordinates attacking or joining attacks against dominants may be infrequent but very important. Although these low-ranking males risked counterattack by targeting dominant hyenas, it appeared they were able to rise in the hierarchy by forming coalitions with other animals. These three males rose in rank during the late subadult period (Frank *et al.*1989). After they rose in rank, they contributed to reinforcing the hierarchy by joining coalitions against subordinate animals more frequently than they challenged the dominance of higher-ranked animals. Thus, during the late subadult period, animals in cohorts I and II behaved similarly.

Wolves have also been observed challenging the rank of dominant animals by joining coalitions. A subordinate male in one colony initiated a successful coalition attack against his dominant father, and was supported by a number of animals which were aiding-at-risk (Jenks 1988). The dominant father subsequently fell in rank.

Primates will aid-at-risk while supporting offspring and other kin (Chapais 1983). Captive spotted hyena coalitions appeared to differ from those among primates in the relative frequency of aiding-at-risk: our hyenas usually supported dominant aggressors, rather than subordinate targets. However, this might have been due to the composition of the group, which consisted entirely of immatures without adults present, particularly mothers which might come to the defence of their offspring. Since these data were compiled, there have been a number of births in the hyena colony, and mothers and infants have been observed while they were being introduced into the main group. There was one dramatic occurrence of a female aiding-at-risk when a higher-ranking female attacked one of her offspring. The low-ranking mother subsequently attacked the dominant female which was biting and carrying her infant. The dominant female released her grip on the infant and turned her attack to the subordinate mother. Such maternal aiding-at-risk has also been observed in a colony of hyenas maintained at the Amsterdam Zoo (Kranendonk *et a1*.1983). As in most mammals, maternal defence of young takes precedence over hierarchical considerations. .

Social facilitation and coalition formation

'Mob' behaviour and redirection in hyenas

An important aspect of hyena coalition behaviour is redirected aggression. When this occurs, an initial target of aggression attacks a lower-ranking third party, diverting the attention of the original attackers onto a `scapegoat' (see deWaal this volume, pp. 240-1, and Ehardt and Bernstein this volume, pp. 90-2, for similar behaviour in primates). Because hyenas have a strong tendency to join attacks, this is often a successful tactic. At kills in the wild, it is common to see a chain of aggression: hyena A chases B; B chases C, C chases D, and D chases vultures. Among the captive hyenas, an initial victim often redirected aggression to a lower-ranking target:. However, as noted above, there were a number of cases in which the attack was- redirected against the initial aggressor. We have not yet analysed the phenomena of redirected aggression quantitatively. But it appeared as if supporting hyenas had strong tendencies to join an attack against whichever animal was losing, as long as they were higher ranking than the target. This is more suggestive of mob behaviour or social facilitation (Zajonc 1965) than of cognitively based assessments of relative rank or cost/benefit analyses of the political outcome of aggression. It appears to be similar to antipredator mobbing in this- and other species. One must be cautious about inferring complex, cognitive processes when simpler explanations will suffice.

Hyenas have a very strong tendency to 'do what other hyenas are doing.'

(Woodmansee *et al*. 1991). The tendency of hyenas to join attacks against other hyenas could result from focusing on the stimuli provided by a subordinate hyena, rather than any active cognitive process of ‘joining’ a dominant attacking hyena(s). A general tendency to do what other group members are doing could then serve to maintain or improve the position of individuals within a social group.

Synchrony in social carnivores

Socially facilitated behaviour, or synchrony, was a prominent feature of activities in the hyena colony. One or more animals would often join an individual that was engaged in solitary activities, e.g. scent-marking, defecating, or intently surveying its surroundings. Social facilitation also occurred when individuals joined a group of hyenas that was engaged in social interactions; as when a third hyena approached and joined a pair that was playing, or engaged in the meeting ceremony (Kruuk 1972). ('The meeting ceremony is an affiliative behaviour in this species, during which either sex may have an erection that other animals) will investigate.) Behaviours such as vigorous play, manipulating objects, shadowing a hyena (i.e: following at very close distances), group aggression, and even the meeting ceremony commonly recruited groups of three or more animals into the activity.

Synchronous activities have been reported in other social carnivores as well. For example, wolves engage in communal greeting,. howling, and play prior to a hunt (Fox 1971; Mech 1970). Similarly, African wild dogs *(Lycaon pietas*) engage in group activities including scratching, yawning, communal greeting, and play prior to hunting (Estes and Goddard 1967; Kuhme 1965; Malcolm 1979). These group behaviours may reinforce mutual dependence and friendliness (Kuhme 1965), and may be characteristic: of cohesive groups (Lockwood 1976). Synchronization of elimination has been noted in several carnivores, including spotted hyenas (Kruuk 1972; Woodmansee *et al*. 1991), African wild dogs (Kuhme 1965), and lions (Rudnai 1973). Among cooperative group hunters, it may be important that many group activities are coordinated. When social carnivores travel quickly, asynchronous animals might become separated from a group, and reduced cohesiveness could result in less effective hunting (Lockwood 1976).

Coalitions and alliances among social carnivores: future research

There are many gaps in our knowledge of coalitions and alliances among social carnivores. It is not clear whether an absence of data represents an absence of these behaviours among social carnivores, or rather a failure to report them. For example, there have been no studies of long-term alliances among spotted hyenas or wolves. However, anecdotal observations indicate that they do occur. Aggression among wild hyenas is more frequent between matrilines than within matrilines (Frank 1986), suggesting kin-related alliances may be occurring: In the Berkeley-study, two captive female spotted hyenas which supported one another during aggressive interactions were the top-ranking animals in cohort I during the early subadult period. When this cohort was split into two subgroups of five animals at a later age, these two females were separated. Each of them subsequently dropped in rank to become nearly the lowest-ranked animals within their group. It appeared that when they were deprived of reciprocal support, they were unable to maintain their position of dominance. Similarly, two captive female wolves which supported one another in aggressive interactions more frequently than other pairs subsequently rose in rank (Jenks 1988).

Among free-ranging animals, there have been some significant studies of alliances, but no quantitative reports of transitory coalitions. It is our impression that interesting patterns of alliance and coalition formation would emerge if these behaviours were studied among wolves and hyenas in nature. This might extend to other social carnivores as well. Better comparisonsbetween primates and carnivores await further studies on the latter group focused upon questions of reciprocity, relatedness, and the consequences of coalitions and alliances for reproductive success.

SUMMARY

Kin alliances and their function have been described in a few species of social carnivores, but there have been no quantitative field studies of coalitions. In this chapter we report on coalitions that formed in a colony of captive spotted hyenas. (*Crocuta crocuta*) during their first 2 years of life. Spotted hyenas resemble cercopithecine primate groups in social organization, living in matrilineal `clans' of up to 100 individuals. They hunt cooperatively, feed competitively, and den communally. Females are unique among mammals in being anatomically and behaviourally masculinized; they are more aggressive than males and dominant over them. In the wild, matrilineal associations of females are an important element of social organization, and probably a factor in the maintenance of individual females' rank and dominance over males.

In order to study sexual differentiation and anatomy, a captive colony was established. Research emphasis was on dominance relations and agonistic behavior among prepubertal hyenas in the absence of adults. Coalition attacks were a major feature of social interactions.

1. The mean number of hyenas involved in coalition attacks was about three, but as many as nine of ten animals were sometimes involved.

2. Neither sex, gonadectomy, age, or cohort influenced rates that hyenas initiated, supported, or received coalition attacks. Male and female hyenas were equally likely to engage in group attacks, unlike most primates. However, the lack of maternal influence on the juvenile hyenas, which is a powerful determinant of rank in the wild, may have significantly affected both the form and frequency of coalitions in this colony.

3. Captive females were not dominant over males during this age period.

4. Dominant animals were more likely than subordinates to both initiate and support attacks, and subordinates were more likely to be targets of group attacks.

5. Due to the tendency to join attacks against lower-ranking animals, coalition attacks among hyenas and wolves usually serve to reinforce existing dominance relations, as is sometimes the case among primates.

6. Attacking dominants ('aiding-at-risk') occurred infrequently. However, by forming coalitions with other animals and challenging the rank of dominants, hyenas may subsequently rise in rank.

7. In assessing the likelihood of attacking dominants or subordinates, it is necessary to adjust data for each individual according to the number of higher- and lower-ranking animals in a hierarchy.

8: The 'mob' nature of attacks, and the general tendency of hyenas to 'do what other hyenas are doing', suggest that group attacks may reflect a strong tendency to join any attack against lower ranking individuals. A general tendency to synchronise behaviour might be particularly significant to social predators, which must coordinate their actions in hunting, and in defence of both kills and territorial boundaries.

ACKNOWLEDGMENTS

We thank the Department of Wildlife Conservation and Management of the Government of the Republic of Kenya for permission to collect and export the hyenas- which form the basis of our colony. This research is supported by grant MN3 9917 from the National Institute of Mental Health.

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Coalitions and alliances in humans and.. other animals

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OXFORD NEW YORK TOKYO
OXFORD UNIVERSITY PRESS
1992