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Social Facilitation, Affiliation, and Dominance in the Social Life of Spotted Hyenas

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Spotted hyenas *(Crocuta crocuta)* are social carnivores, living in multifemale, multimale "clans."[1,2] With female philopatry and male dispersal, separate female and male dominance hierarchies, and female matrilines that constitute the fundamental social core of the clan, the social organization of spotted hyenas approximates that of many common old world monkeys in the broad outline of their sociality.[3,4] Membership in the clan enables hyenas to hunt prey as large as zebra and is essential to defense of kills against lions and of hunting territories against other groups of hyenas.

Spotted hyenas also display some rather unique characteristics. Adult females and their juvenile, or subadult, offspring dominate adult immigrant males in virtually all social interactions.[4-6] In addition, hyenas often spend their days alone at solitary dens, typically reassembling in the late afternoon and socializing at the communal den before forming smaller hunting parties. For many hyenas there is a daily transition from a solitary existence to the intense, highly differentiated social interactions of life within the clan.[1]

All social carnivores display a delicate balance between cooperation and competition. In spotted hyenas, competition may simply be evinced by speed-of-eating at a kill. That is, with a group of hyenas feeding at a dead wildebeest and reducing it to a small pile of horns and hooves in less than 30 minutes, the individual that can eat most rapidly will have an advantage over colleagues that eat more slowly. Overt aggression and the formation of dominance hierarchies also play a role in access to resources, and dominance rank is directly related to ultimate reproductive success[7]

The present paper focuses on the integration of cooperation and competition, and correlated behavioral mechanisms of aggression, dominance, and affiliation, within the social life of the spotted hyena. Towards that end, we focus on three themes that have emerged from our studies of these animals: (1) the emergence of individually differentiated systems underlying cooperation and competition from a more general tendency of hyenas to do-what-other-hyenas-are-doing; (2) the role of "meeting

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ceremonies" in mediating daily transitions between solitary and social existence; and (3) the fact that the most aggressive, dominant animals in our social groups are also, commonly, the most affiliative animals, displaying high levels of prosocial behavior in a variety of contexts. In regard to the last theme, Wingfield and his collaborators provided compelling evidence that in certain social systems, high levels of aggression are incompatible with successful mating and reproduction[8] That could be operative in hyenas as well, with consistent selection against excessive, undifferentiated aggression. However, there is another side to this issue. As long as aggression, dominance, and affiliation remain appropriately differentiated, they are not incompatible components of individual sociality.

THE BERKELEY HYENA PROJECT

The data cited in this report were drawn from a decade-long study of the morphology and behavior of spotted hyenas in captivity. Our research has focused on the physiological substrates of sexual differentiation and a set of questions raised by the unusual genital masculinization of this species. Female spotted hyenas have no external vagina, as the labia of the external vagina have fused to form a pseudoscrotum. The clitoris is hypertrophied, approximating the size and contour of the male penis, and female hyenas display erections similar to those of the male.[9-11] This clitoris is traversed by a central urogenital canal through which the female spotted hyena urinates, copulates, and gives birth.[10,12] Our investigations have provided a route through which an inactive androgen generated by the maternal ovary (androstenedione) is transformed by the placenta into testosterone and transmitted to developing fetuses of both sexes.[13,14] This maternally derived testosterone could provide at least a partial explanation of the genital masculinization observed in female hyenas. It might also contribute to the neonatal aggression observed in hyenas of both sexes[15] and the persistent aggressiveness of female spotted hyenas. Ongoing studies involving the administration of anti-androgens to pregnant femaIe hyenas, however, suggest that placental T is just one contributory factor, and other nontraditional mechanisms may be involved. [16,17]

Our studies were initiated with two groups of hyenas collected in Kenya as infants and reared in peer groups. In terms of behavior, a striking feature of our investigations was the emergence of the natural characteristics of hyena sociality in our peer-reared animals despite the absence of the many potentially critical aspects of the natural situation, including sustained maternal influence, the need to hunt for food, or danger from predation by lions. These included the gradual development of female dominance[18,19] and the ultimate appearance of female matrilineal organization, with a separate female dominance hierarchy, cubs acquiring their mother's rank, and dominance of all cubs and adult females over adult males.[20] In addition, as will be detailed, many of the specific behavioral mechanisms displayed by hyenas in nature not only have been observed in captivity, but also have followed the same rules of social expression as those found in nature. This has given us confidence that novel phenomena observed in our captive animals also occur in nature, but the frequency of expression is almost surely different in the natural situation.

SOCIAL FACILITATION OF BEHAVIOR

"In many behavior patterns a clear attraction is apparent between individuals which seems to exist regardless of sex or family tie. This is most obvious when one watches communal activities like zebra hunting, fighting between clans, pasting, social defecating, and so on. But with some activities, I had the impression that they were performed with the sole function of 'doing something together,'. . . "[1,p241].

For the dedicated spotted hyena watcher, one of the most striking characteristics of the spotted hyena is the tendency of individual animals to do what other hyenas are doing, that is, to exhibit social facilitation of behavior[21] In his work with wolves, Lockwood[22] made a similar set of observations and suggested that behavioral synchrony was required in social hunting groups on the move. It is a characteristic that pervades virtually every aspect of daily life. For example, within our colony, such social facilitation was observed to increase the probability of ingestive behavior, scent marking, meeting ceremonies, olfactory investigation, and play as well as promote the development of coalitions that serve to reinforce the existing dominance hierarchy.

Ingestive Behavior. In the natural setting, the cooperative hunting of spotted hyenas is followed by intensely competitive feeding. Even in our captive animals, for which food is provided on a daily basis and efforts are made to insure that the lowest ranking animal gets its share, the presence of a feeding hyena stimulates others to eat. The powerful faciiitatory effects of observing other hyenas eat could be used to overcome an experimentally induced food aversion[23] In this investigation, an aversion was established by pairing a novel food with lithium chloride in individual hyenas that were members of small social groups. The aversion was clear and inhibited eating as long as these individuals were tested in solitary fashion. However, when exposed to the food in concert with other group members that had not been conditioned, the conditioned animals could not resist joining their colleagues, even as the conditioned animals sometimes illustrated their ambivalence by approach-withdrawal or taking small, dainty bites instead of their preferred gulps of food. It was also possible to demonstrate social facilitation of spontaneous drinking at a spout in straightforward fashion. When two groups of hyenas ($n's = 5$ and 7) were released into a yard, individuals that watched a comrade drink were much more likely to drink in the minutes immediately following such drinking. The probability of a second animal drinking declined rapidly in the minutes that followed drinking by the first animal. Observation further indicated that social drinking was provoked by visual observation of the act on the part of the second animal (FIG. 1).

Scent-Marking. Hyenas scent-mark within their territories by communal defecating' as well as by marking stalks of grass and other objects with "paste" extruded from their anal scent glands.[24] Although we have seen hyenas defecate or strain to defecate when another hyena is defecating, we do not have good numbers in hand to document this aspect of social facilitation. However, Woodmansee and her collaborators[25] were able to quantify the social facilitation of pasting among animals in our colony. The probability of pasting was markedly increased by the prior pasting of another hyena, with the second animal apparently responding to both the visual stimulus of another hyena marking and the olfactory stimulus provided by the soapy odor of paste.

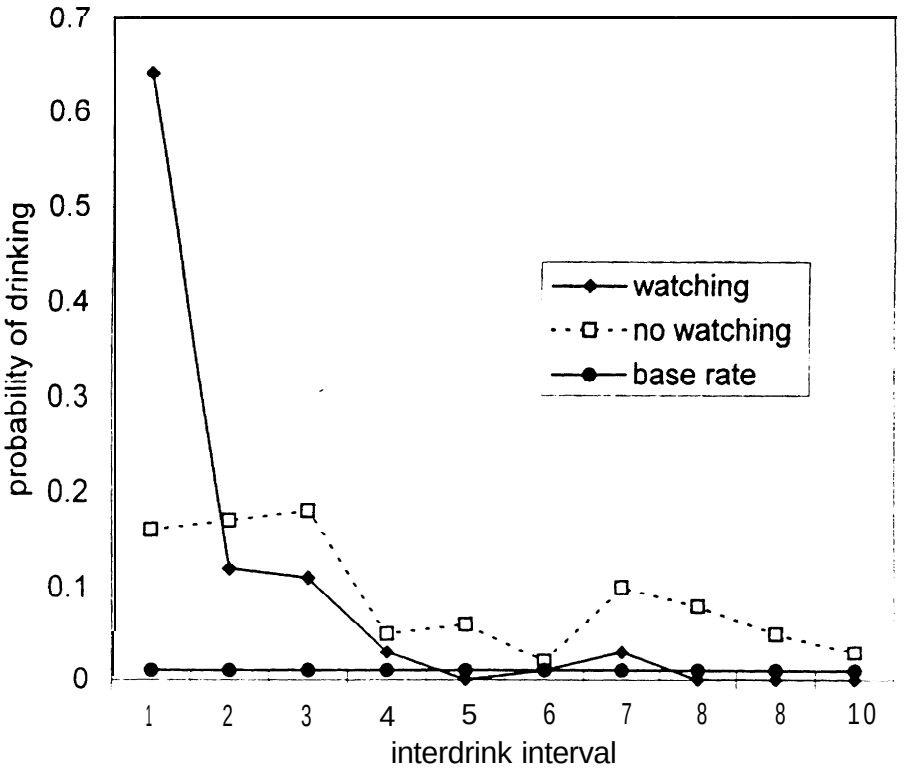

FIGURE 1. Probability of drinking as a function of time elapsed since another hyena drank. Inter-drink intervals (IDIs) represent successive 30-second intervals: ID 1 is comprised of drinking that occurred 0-30 seconds after another hyena drank; ID 2 is comprised of drinking that occurred 3l-60 seconds after another hyena drank, etc. Data are presented separately for instances in which hyenas had watched another hyena drink in the preceding 5 minutes and cases in which such observation had not taken place. The base rate is the expected probability if drinking had been distributed randomly in time.

Olfactory stimuli frequently provide the focus for socially facilitated group behavior patterns. "The reaction of any hyenas . . . to the sight and sound of another one regurgitating is to run up, sniff the results of this action, and then immediately roll in it, shoulder first, then with the whole back."[1,p.244] We also observed this within our colony and recorded several occasions on which groups of five to eight juvenile hyenas were simultaneously engaged in excited sniffing, with tails elevated, before rolling in the regurgitated product of one of their cohort (FIG. *2).* Less dramatic olfactory stimuli often result in "social sniffing." As described by Kruuk,[1,p.241] this typically involves a group of hyenas walking ". . . together at a brisk pace, fairly close, several with their tails up. Suddenly, one would stop, sniffing the ground in a place apparently randomly chosen-immediately all the others came rushing up, all starting to sniff the same place or immediately next to it." Mills[2] supports Kruuk's general description, although he suggests the possibility of an identifiable olfactory stimulus.

Coalitions. The preceding cases involve typical prosocial behavior patterns commonly enacted by groups of hyenas. However, affiliation and social facilitation also operate in the service of aggression and dominance. Kruuk,[1,p.225] and places [38&39] first

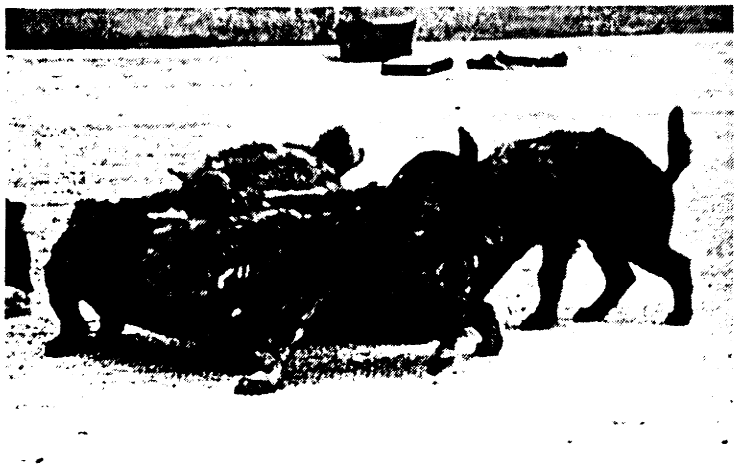

FIGURE 2. An excited group of juvenile spotted hyenas (note the erect tails). One hyena, in the center of the group. has just regurgitated some appropriately odoriferous material and the animals on the periphery were taking turns "roiling" in the substrate.

FIGURE 3. The hyena meeting ceremony. It is reasonably common, in the Berkeley colony, for a third hyena to approach and join two hyenas engaged in a meeting ceremony.

described the parallel walk in which two hyenas, walking shoulder to shoulder, threaten a third hyena by approaching the target animal in an attack posture. Mills[2] later described the formation of both transient and permanent coalitions in which groups of animals coordinate threats or attacks on individual hyenas. Such coalitions probably form more frequently in the captive situation because the entire group is in continuous proximity. However, the "rules" of coalition formation are presumably similar to those observed in nature. Within our colony, dyadic aggressive encounters were commonly joined by other hyenas according to a simple rule: join the side of the dominant animal as long as you are also dominant to the animal being threatened

or attacked[26] It is a rule that reinforces the existing dominance hierarchy and reduces social mobility in the group. Hyenas did occasionally aid at risk, that is, join a subordinate animal in attacking a higher ranking animal, but that was a relatively infrequent event. We also observed several small males enlist the aid of a high-ranking female in threatening/attacking a large female who, in a simple dyadic encounter, would have been expected to totally dominate the males. However, these latter cases are memorable precisely because they are exceptions. In general, one or more hyenas are drawn to an ongoing dyadic encounter, and the species-typical tendency to do what other hyenas are doing is activated. But at this point, social history enters as a variable and the animal has to remember her/his relationship to the combatants and adjust behavior accordingly. If our observing hyena is lower in rank than either of the participants, any tendency to join should be inhibited and s/he should discreetly leave the scene, because the subordinate participant in the ongoing encounter may be able to redirect the attack of the dominant animal, forming a new coalition against a lower ranking hyena. Alternatively, if our observing hyena is dominant to the animal being attacked, s/he can safely join in a coalition attack, reinforcing the lower status of the target animal and, perhaps, solidifying his/her own relationship with the higher ranking hyena. In this case, social facilitation appears to drive the tendency to attack, but it is always modulated or differentiated by the prior social history of the individuals involved.

MEETING CEREMONIES

Spotted hyenas have much more elaborate meeting ceremonies than do brown hyenas *(Hyaena brunnea)*[2] or striped hyenas *(Hyaena hyaena).*[28] This might well correlate with the greater complexity of social relationships in spotted hyenas as well as the daily transition from solitary to social existence. In the spotted hyena meeting ceremony, the participants approach one another, stand head to tail, and engage in intense olfactory investigation of the external genitalia, anal scent glands, and surrounding tissues. Data obtained by Kruuk,[1] Mills,[2] and East *et al.*[27] suggest that hyena etiquette has firm rules: the subordinate hyena lifts its hindleg first and offers its erect penis or clitoris for inspection by the dominant animal, which will usually then reciprocate. Many authors have called attention to the potential role of the meeting ceremony in maintaining group cohesion and speculated that the hypertrophied clitoris of the female spotted hyena might have been naturally selected as the result of benefits that accrued from participation in the meeting ceremony.[1,27]

In a study that involved a captive group of 10 subadult hyenas, Krusko and her collaborators[29] found that following a 4-hour period during which the animals were divided into two groups of five hyenas and separated in areas without visual or olfactory contact, a marked increment was noted in frequency of meeting ceremonies at the time of reunion. Moreover, the subjects apparently had kept track of who they had been separated from during the 4-hour interval, for each hyena engaged in a proportionally greater number of meeting ceremonies with the five animals from which they had been separated than the four animals with which they had resided during the interval. Krusko *et al.*[29] also observed that merely releasing the entire group of 10 animals from a semienclosed sleeping area to a somewhat larger outside

area resulted in an increment in the number of meeting ceremonies, albeit a much less dramatic increment than that observed accompanying reunion after separation. This appeared to be a simple excitement-induced enhancement of meeting ceremony activity. Finally, as in nature, subordinate animals initiated meetings with dominant animals more frequently than the reverse. If dominance rank (as determined by threats, displacement, and subordinate postures during group competitive feeding[18]) was correlated with proportion of meetings received, there was an inverse correlation (rho = -0.85): high ranking animals received proportionally more meeting ceremonies than subordinate members of the group. Dominant animals also participate in more meeting ceremonies than do subordinates (rho = -0.74). As suggested by Kruuk[1] and substantially amplified by East *et al.*,[27] meeting ceremonies provide a crucial behavioral mechanism facilitating the transition between solitary and social existence, reinforcing dominance relationships that are of critical importance in the daily life of the clan, and adding to the cohesiveness of topranking members of the clan. The more frequent meeting ceremonies observed in situations involving tension or excitement suggest that these ceremonies may also operate as a device promoting reconciliation after, e.g., squabbles over food.

INTEGRATING AFFILIATION AND AGGRESSION

Affiliativeand aggressive behavior was recorded in both cohorts of captive hyenas during an extended subadult period (from 11-21 months of age). A critical incident sampling procedure was employed, using a standardized list of behavioral definitions, with trained observers dictating an account of social interactions during evening observation periods. The auditory record from a voice-operated tape recorder was then entered into a computer database and analyzed in 30-second bins by way of an SAS package. The existence of this dataset provides an opportunity for examination of the relation between dominance and various patterns of affiliative behavior among members of the social group. It seemed possible that highly aggressive, dominant hyenas would be unable to surmount their aggressive tendencies and fully participate in the affiliative activities. Alternatively, it was also possible that given the apparent cohesion observed within high-ranking matrilines in nature, high-ranking members of our cohorts would engage in more affiliative behavior than low ranking hyenas.

Data bearing on these hypotheses are presented in TABLE 1. Although substantial variation exists in the magnitude of correlations observed in the two cohorts, results clearly support the second hypothesis. The correlational matrices show a strong tendency for positive correlations among measures of social (olfactory) investigation, participation in meeting ceremonies, scent-marking (“pasting”), and play. Moreover, all of these affiliative behaviors are positively related to dominance rank, as determined in a competitive feeding situation,[18] and dominance in hyenas is transsituational. Within our cohorts, there was a strong positive correlation between dominance rank determined in tests of competitive feeding and relative frequencies of giving (as opposed to receiving) aggression during spontaneous nightly, nonfeeding activities (Zabel, unpublished observations). If the power of statistical evaluation is increased by combining correlation coefficients from the two cohorts,[30,p.157-158] only the relationship between play and scent-marking fails to achieve statistical significance. Similar cohesiveness among high-ranking animals recently was described in the field.[31]

TABLE 1. Rank-Order Correlation Coefficients among Measures of Social Behavior[a]

	Social Investigation	Meeting Ceremonies	Scent-Marking	Play	Dominance
		Cohort I (n = 10)			
Social investigation	–	0.40	0.47	0.63*	0.49
Meeting ceremonies	0.65*	. . .	0.71	0.13	0.66*
Scent-marking	0.53	0.60	. . .	0.23	0.60
Play	0.76*	0.86*	0.63*	.	0.59
Dominance	0.50	0.85*	0.74*	0.80*	–
		Cohort II (n = 10)			

* $p < 0.05$.

[a] Values for hyenas in cohort I are represented in the upper right potion of the table; Cohort II, the lower left section of the table.

ANDROGENS, DOMINANCE, AND AFFILLATION

It is common to associate the presence of androgens with aggressive behavior and social dominance.[32] However, in the ordinary case, that is obviously not incompatible with the sarne subjects also exhibiting high levels of affiliative behavior. As long as behavior remains "differentiated," that is, sensitive to the details of the social context and individual relationships, affiliative and aggressive behavior patterns can not only coexist, but also facilitate one another. We suspect that in spotted hyenas, dominance resulting (in part) from aggression and supported by coalition formation both permits and encourages high ranking animals to display affiliative behavior and forge cohesive social bonds.

SOME CONCLUDING THOUGHTS

A century ago, Morgan[33] described a process of social learning in chicks that were stimulated to peck by the presence of an experienced tutor. He referred to the process as *instinctive imitation* and allowed that it was a fundamental characteristic of social behavior. In its modem guise as social facilitation, such behavioral tendencies remain a fundamental substrate of social organization, albeit that they are modulated by a broad array of cognitive mechanisms, including histories of individual social relationships.

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