The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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45 Field Studies of Social Cognition in Spotted Hyenas

Kay E. Holekamp and Anne L. Engh

Considered in relation to body size, the brains of primates are relatively large and complex compared with those of other animals, including most nonprimate mammals (Macphail 1982; Harvey and Krebs 1990). In particular, the primate neocortex is very large in relation to the rest of the brain (Barton and Dunbar 1997). Furthermore, primates appear to be endowed with cognitive abilities that are superior to, and qualitatively different from, those observed in most other mammals (reviewed in Byrne and Whiten 1988; Harcourt and de Waal 1992; Tomasello and Call 1997).

Two different types of selection pressures have been hypothesized to favor the evolution of large brains and great intelligence (as defined by Kamil 1987) in primates. The first hypothesis suggests that intelligence has been favored in primates by selection pressures associated with complexity in the physical environment, particularly that confronted when navigating through a three-dimensional arboreal world (e.g., Povinelli and Preuss 1995) or when finding and obtaining food (e.g., Milton 1981). The second hypothesis suggests instead that the key selection pressures have been imposed by complexity associated with the labile social behavior of conspecific group members (Byrne and Whiten 1988). Predictions of this social complexity hypothesis have now been confirmed in a number of Old World primate species, suggesting that the evolution of intelligence has been more strongly influenced by social pressures than by nonsocial aspects of the environment (reviewed in Byrne 1994; Tomasello and Call 1997). Unfortunately the generality of this hypothesis is severely limited by the current dearth of information about social cognition in animals other than primates (Harcourt and de Waal 1992). In fact, most work in this area has focused exclusively on cercopithecine primates and great apes. The social complexity hypothesis, however, predicts that nonprimate animals that share with primates most salient features of their social life and resource distribution should possess many of the same features of social intelligence found in monkeys and apes.

Like most primates, many mammalian carnivores live in permanent, complex social groups that contain both males and females from multiple, overlapping generations. Gregarious carnivores also engage in a variety of behaviors, such as cooperative hunts of large vertebrate prey, which have prompted many observers to claim that these predators must possess extraordinary intellectual powers (e.g., Guggisberg 1962). The size of the carnivore neocortex is positively correlated with group size (Dunbar and Bever 1998). However, the cognitive abilities of carnivores have seldom been the subject of systematic study, and they are currently very poorly understood (e.g., Byrne 1994).

In our own research we are examining the cognitive mechanisms underlying social behavior and communication in one gregarious carnivore, the spotted hyena (*Crocuta crocuta*). Our ultimate objective is to determine whether hyenas exhibit some of the same cognitive abilities that are observed in primates. Evidence for the existence of shared cognitive abilities would suggest convergent evolution in these two distantly related taxa and would strongly support the social complexity hypothesis. In contrast, the failure to obtain such evidence would suggest that the social complexity hypothesis should be either rejected or revised. We use three different methods to investigate the cognitive abilities of gregarious carnivores: (1) comparative analysis based on literature review, (2) field experiments in the natural habitat, and (3) controlled observations of free-living hyenas. Here we summarize our work to date using each of these methods, although we hope readers will bear in mind the fact that much of it is still in progress.

Comparative Analysis of Group Travel

Here we sought to understand whether coordinated movements by gregarious carnivores reveal the operation of complex mental abilities. Like many primates (e.g., Boinski and Garber 2000), gregarious carnivores frequently travel with other members of their social groups. Group hunts by lions, spotted hyenas, and other carnivores often appear to involve intelligent coordination and division of labor among hunters (e.g., Guggisberg 1962; Stander 1992a,b). Studies of carnivore predatory behavior reveal that their group hunts represent more complexly organized phenomena than mere opportunistic grabs at prey. However, although myriad observers have claimed that the group hunting activity of large carnivores requires the operation of humanlike mental processes, coordinated hunting behavior by lions, hyenas, and social canids can in fact be most parsimoniously explained by the operation of a few simple mental rules of thumb, such as "Move wherever you need to in order to keep the selected prey animal between you and another hunter" (Holekamp et al. 2000). Currently there is no evidence that gregarious carnivores use mental algorithms more complex than simple rules of thumb to surround and capture prey. Disproving the rules of thumb hypothesis will require experimental evidence, not only that individual carnivores monitor both their prey and their fellow hunters (e.g., Stander 1992b), but also that they accurately anticipate the behavior of the latter based on knowledge of their goals.

Another form of group travel that reveals the mental operations of gregarious carnivores takes place when young cubs or pups are moved from one den site to another (Holekamp et al. 2000). Whereas group hunts make carnivores look very smart, den moves make them appear very stupid. When gregarious carnivores move infants (N) to a new den, they always make at least one extra trip ($N + 1$) to the old den, suggesting that instead of being able to count, during den moves carnivores operate according to a rule of thumb that says "Revisit the old den until you find no more of your infants there." Thus the mental processes required to initiate and maintain seemingly complex movements need not be particularly sophisticated in carnivores. Interestingly, it appears that much coordinated group travel in primates, including cooperative hunting behavior by chimpanzees (e.g., Boesch and Boesch 1989), might also be explained effectively by these same simple rules of thumb.

Field Experiments and Controlled Observations of Spotted Hyenas

Many primates demonstrate the ability to form mental representations of tertiary, or third-party, relationships among conspecific group members (Tomasello and Call 1997). These involve interactions and relationships in which the observer is not directly involved. For example, adult male hamadryas baboons make adaptive decisions about whether to challenge a rival male based on their assessment of the strength of the social bond between the rival and his female associates (Bacchman and Kummer 1980). Tomasello and Call (1997) hypothesize that an ability to understand third-party relationships is unique to primates, and furthermore, that this distinguishes their mental abilities from those of all other animals. Indeed, the ability to recognize third-party relationships has not been documented in nonprimate mammals, even in species living in complex, stable societies such as elephants (Moss 1988), dolphins (Connor et al. 1992), or lions (Packer 1994). However, few published studies of these other gregarious mammals have focused on the cognitive abilities of these animals, so it remains unclear whether the absence of evidence that any of these nonprimate mammals can recognize tertiary relationships actually means that this ability is also absent. Our own field work has attempted to determine whether a primate-like ability to recognize tertiary relationships is exhibited by the spotted hyena, a carnivore whose social life is remarkably similar in most respects to that of many Old World primates.

The Social Lives of Hyenas and Old World Monkeys

Both spotted hyenas and Old World monkeys usually live in permanent social groups that commonly contain multiple adult males and multiple matrilines of adult female kin with offspring. Males leave their natal groups, whereas females are usually philopatric (Cheney and Seyfarth 1983; 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 access to resources varies with social rank (Tilson and Hamilton 1984; Andelman 1985). 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 extended periods. Juvenile hyenas of both sexes acquire ranks immediately below those of their mothers (Holekamp and Smale 1991), and they do this via the same associative learning mechanisms as those documented in cercopithecine primates (Horrocks and Hunte 1983; Engh et al. 2000). Thus social status is often not determined by size, strength, or fighting ability in either of these taxa, as it is in many mammals (e.g., Clutton-Brock et al. 1982). Instead, juvenile monkeys and hyenas both learn during early life that they can dominate individuals ranked lower than their mothers. In both monkeys and hyenas, kin associate more closely than do non-kin, and individuals direct affiliative behavior more frequently toward kin than non-kin (Seyfarth 1980; 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; Holekamp et al. 1997). Furthermore, the patterns of greeting behavior in *Crocuta* follow primate patterns of social grooming (East et al. 1993), in which individuals prefer to direct affiliative behavior toward high-ranking non-kin (Seyfarth and Cheney 1984). This suggests that hyenas, like monkeys, may recognize that some group members are more valuable social partners than others. Finally, triadic and more complex interactions (e.g., coalitions) appear to play important roles in both maintenance and reversals of social rank in free-living *Crocuta* (Zabel et al. 1992; Smale et al. 1993), as they do in many cercopithecine primates (Walters 1980; Datta 1986; Chapais 1992).

Playback Experiments on Vocal Recognition

The similarities between the social lives of spotted hyenas and Old World primates present an ideal opportunity for comparative analysis of their social knowledge. In our first attack on this problem (Holekamp et al. 1999), we conducted a series of playback experiments with hyenas in the field and compared the hyenas' behavioral responses during these experiments with those observed earlier in vervet monkeys (Cheney and Seyfarth 1990) and in other cercopithecine primates (e.g., Gouzoules et al. 1995).

In the vervet experiments (Cheney and Seyfarth 1980), the distress scream of a juvenile was played through a hidden loudspeaker to groups of females that contained the juvenile's mother as well as other adult breeding females (controls). The mothers responded more strongly to screams than the control females, and the controls often responded by looking at the mother without any apparent cues from the mother herself. Thus vervets behaved as though they recognized the close associative relationships existing among group members unrelated to themselves (Cheney and Seyfarth 1980, 1990).

We used playback experiments to determine whether hyenas are capable of identifying individual conspecifics on the basis of their long-distance "whoop" vocalizations and whether they recognize tertiary relationships among non-kin members of their clan, as occurs in vervets. Although the results obtained during our playback experiments showed clearly that hyenas can recognize the whoops of specific individuals, they yielded no evidence that hyenas can recognize third-party relationships (Holekamp et al. 1999). In contrast to vervets, after the playback, the control females in our experiments were no more likely to look at the mother of the whooping cub than at other control females. Although this result suggests that spotted hyenas do not recognize third-party relationships, it remains possible that they do recognize them, but that their orientation responses during playback experiments are poor indicators of this ability. If this alternative hypothesis is correct, then other social situations, in which actions based on social knowledge will unambiguously improve fitness outcomes for the actor, should reveal that hyenas can indeed recognize third-party relationships. Therefore we recently turned our attention to these other types of social situations.

Coalition Formation

Coalitions play an important role in the acquisition and maintenance of social rank in spotted hyenas (Zabel et al. 1992; Smale et al. 1993; Engh et al. 2000). When aggression between two hyenas escalates, one or more others may join the skirmish by forming a coalition with the attacker against the target individual. Typically, animals joining to form coalitions are all dominant to the victim. Thus when attempting to displace a larger subordinate animal from food, a hyena might benefit, for example, by delaying its attack until the arrival of a potential coalitionary ally who is higher ranking than the target animal.

We are currently analyzing changes in rates of aggression directed against subordinates after the arrival of hyenas of high and intermediate rank in order to learn more about hyenas' abilities to recognize tertiary relationships (Engh et al. in preparation). If hyenas increase their rates of aggression only after higher-ranking hyenas arrive on the scene, then they may be following a simple rule of thumb, such as "Only attack a larger subordinate when another individual is present who is higher ranking than yourself." Alternatively, if the attack rate also increases following the arrival of an individual who is dominant to the victim but subordinate to the attacker, then the attacking hyena must recognize the relative ranks of the other two individuals. In the latter case, the hyenas would be indicating to us that they can indeed recognize tertiary relationships. Although we are still in the early stages of this study, the preliminary results suggest that hyenas increase their rates of aggression only when animals higher ranking than themselves arrive, indicating once again that they are probably using simple rules of thumb to make decisions, rather than knowledge of complex relationships.

Reconciliation and Redirected Aggression

Affiliative gestures functioning to repair social relationships damaged during a fight are called "reconciliation behaviors" (de Waal 1993). Reconciliation occurs in many primates during friendly reunions between former opponents shortly after aggressive conflicts (reviewed by Aurlei and de Waal 2000). Similarly, spotted hyenas appear to reconcile after 10 to 15 percent of fights, often by the loser lifting its leg in a friendly "greeting" gesture directed at its former opponent (Hofer and East 2000; Wahaj et al. 2001). After fights, Old World primates are known to reconcile, not only with their former opponents, but also with the kin of former opponents (e.g., Cheney and Seyfarth 1989), indicating that the conciliatory monkeys recognize those tertiary relationships. In contrast, we rarely observe hyenas reconciling with any animals but their former opponents. This suggests that even though the ability to recognize tertiary relationships under these circumstances might well enhance their fitness, hyenas do not behave as though they possess this ability.

In many primates, an animal that has been involved in a fight will redirect aggression and threaten a third, previously uninvolved individual (e.g., Cheney and Seyfarth 1989). Often such redirected aggression is directed toward a close relative of the prior opponent. Thus patterns of redirected aggression in primates resemble those seen in kin-based reconciliation, and both indicate that monkeys can recognize third-party relationships. Although we have not yet begun work on redirected aggression in spotted hyenas, it is very common in this species, and we plan in the near future to use these interactions to ask once again whether hyenas can recognize third-party relationships.

Conclusions

Much of our work is still in progress, but the initial results from our studies of social cognition in hyenas suggest that even though these predators live in the same types of complex, stable groups as many primates do, they lack some of the mental abilities common in monkeys and apes. If spotted hyenas cannot recognize third-party social relationships, then features of the social environment common to both primates and spotted hyenas may be necessary, but cannot be sufficient, to account for the evolution of the primates' ability to recognize relationships among unrelated group members. Our data to date suggest that hyenas may accomplish many of the same social feats as monkeys do by following simple rules. If it is confirmed in our ongoing studies, the finding that hyenas cannot recognize third-party relationships will suggest that the social complexity hypothesis should be modified to focus only on those aspects of primate social life that are not shared with gregarious carnivores.

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