

Field studies of social cognition in spotted hyenas

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Considered in relation to body size, the brains of primates are relatively large and complex compared to those of other animals, including most non-primate 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 (*sensu* 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 non-primate 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 as do 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, that have prompted many observers to claim that these predators must possess extraordinary intellectual powers (e.g., Guggisberg 1962), and 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 or not hyenas exhibit some of the same cognitive abilities as those 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, failure to obtain such evidence would suggest that the social complexity hypothesis should either be 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 will 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