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Brains, brawn and sociality: a hyaena's tale

Kay E. Holekamp [a, b, *], Ben Dantzer [c, d], Gregory Stricker [a], Kathryn C. Shaw Yoshida [e], Sarah Benson-Amram [f, g]

[a] *Ecology, Evolutionary Biology and Behavior, Michigan State University, East Lansing, MI, U.S.A.*
[b] *BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI, U.S.A.*
[c] *Department of Psychology, University of Michigan, Ann Arbor, MI, U.S.A.*
[d] *Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.*
[e] *Las Vegas Natural History Museum, Las Vegas, NV, U.S.A.*
[f] *Department of Zoology and Physiology, University of Wyoming, Laramie, WY, U.S.A.*
[g] *Program in Ecology, University of Wyoming, Laramie, WY, U.S.A.*

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Theoretically intelligence should evolve to help animals solve specific types of problems posed by the environment, but it remains unclear how environmental complexity or novelty facilitates the evolutionary enhancement of cognitive abilities, or whether domain-general intelligence can evolve in response to domain-specific selection pressures. The social complexity hypothesis, which posits that intelligence evolved to cope with the labile behaviour of conspecific group-mates, has been strongly supported by work on the sociocognitive abilities of primates and other animals. Here we review the remarkable convergence in social complexity between cercopithecine primates and spotted hyaenas, and describe our tests of predictions of the social complexity hypothesis in regard to both cognition and brain size in hyaenas. Behavioural data indicate that there has been remarkable convergence between primates and hyaenas with respect to their abilities in the domain of social cognition. Furthermore, within the family Hyaenidae, our data suggest that social complexity might have contributed to enlargement of the frontal cortex. However, social complexity failed to predict either brain volume or frontal cortex volume in a larger array of mammalian carnivores. To address the question of whether or not social complexity might be able to explain the evolution of domain-general intelligence as well as social cognition in particular, we presented simple puzzle boxes, baited with food and scaled to accommodate body size, to members of 39 carnivore species housed in zoos and found that species with larger brains relative to their body mass were more innovative and more successful at opening the boxes. However, social complexity failed to predict success in solving this problem. Overall our work suggests that, although social complexity enhances social cognition, there are no unambiguous causal links between social complexity and either brain size or performance in problem-solving tasks outside the social domain in mammalian carnivores.

Despite the huge metabolic costs of neural tissue (Aiello & Wheeler, 1995), primates have larger brains for their body size than most other mammals, and many cognitive abilities are best developed in primates (Byrne & Whiten, 1988; Tomasello & Call, 1997). The 'social complexity' hypothesis suggests that the primary selective force favouring advanced cognition and big brains in primates was the need for mental agility in the social domain (Humphrey, 1976; Jolly, 1966). According to this hypothesis, selection favours the individuals best able to anticipate, appropriately respond to, and manipulate the social behaviour of conspecifics (Byrne & Whiten, 1988). The social complexity hypothesis predicts that, if indeed the large brains and great intelligence found in primates evolved in response to selection pressures associated with life in complex societies, then cognitive abilities and nervous systems with primate-like attributes should have evolved convergently in nonprimate mammals living in large, elaborate societies in which individual fitness is strongly influenced by social dexterity.

de Waal and Tyack (2003) suggested that the most challenging societies are those in which animals live in stable multigenerational

* Correspondence: K. E. Holekamp, 288 Farm Lane, Room 203, Michigan State University, East Lansing, MI 48824-1115,U.S.A.
E-mail address: holekamp@msu.edu (K. E. Holekamp).

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units, group members recognize one another individually, group members cooperate as well as compete for resource access, and a substantial amount of learning occurs during social development. In addition to these characteristics, we further suggest that the most complex societies are those containing multiple genetic lineages such that individuals live in close proximity to, and frequently interact with, nonkin as well as their genetic relatives. Theoretically, computing the costs and benefits of cooperating or competing exclusively with kin should be considerably less demanding than in groups of mixed relatedness. Therefore, we would expect genetic heterogeneity to interact with group size as synergistic determinants of social complexity more effectively than other characteristics of social groups, such as their cohesiveness (e.g. Amici, Aureli, & Call, 2008).

Mammalian carnivores represent an excellent group of nonprimate mammals in which to evaluate relationships among cognitive abilities, brain size and social complexity. Although most carnivores are solitary, some species form social groups that are comparable in size and complexity to those of primates (e.g. Gittleman, 1989a; Smith, Swanson, Reed, & Holekamp, 2012; Stankowich, Haverkamp, & Caro, 2014). Gregarious carnivores engage in a variety of behaviours that appear highly intelligent, such as cooperative hunts of large vertebrate prey. However, the cognitive abilities of carnivores other than domestic dogs have seldom been the subject of systematic study, and they remain poorly understood (e.g. Vonk, Jett, & Mosteller, 2012). Carnivores and primates last shared a common ancestor 90–100 million years ago (Springer, Murphy, Eizirik, & O'Brien, 2003, 2005), so the carnivores offer us an opportunity to test, as independently as possible within the class Mammalia, the hypothesis that demands imposed by living in stable groups of mixed relatedness have driven the evolution of both cognition and nervous systems.

Here we test predictions of the social complexity hypothesis using data documenting behaviour and brain volumes of one highly gregarious carnivore, the spotted hyaena, *Crocuta crocuta*. We first summarize the aspects of their social lives and life histories that spotted hyaenas share with many Old World primates, then inquire whether or not these hyaenas also exhibit some of the same specific cognitive abilities as those found in primates, as predicted by the social complexity hypothesis. We find that spotted hyaenas do indeed exhibit many of the same abilities in the domain of social cognition as those documented in primates. We next review our work comparing brains among members of the hyaena family, and also comparing brains in a larger array of mammalian carnivores. Evidence for the existence of shared cognitive abilities and neural traits would suggest convergent evolution in these two distantly related taxa, and would be consistent with the hypothesis that the demand for social agility has driven the evolution of brains as well as specific cognitive abilities. We find that, although social complexity may have affected the evolution of brain size and regional brain volumes within the family Hyaenidae, our data from this family are also consistent with alternative hypotheses that logically compete with the social complexity hypothesis. We also find no relationship between social complexity and brain measures in a wider array of mammalian carnivores. Finally, we address the question of whether social complexity might have shaped the ability to solve nonsocial as well as social problems in mammalian carnivores by presenting zoo-dwelling individuals from 39 species with a simple food acquisition problem. Interestingly, the results of our zoo study are much more strongly consistent with the cognitive buffer hypothesis, which suggests that large brains facilitate the construction of novel or altered behaviour patterns through domain-general cognitive processes (Sol, 2009a, 2009b), than with the social complexity hypothesis.

SPOTTED HYAENAS AND MONKEYS LIVE IN SIMILARLY COMPLEX SOCIETIES

Like baboons and vervet monkeys, spotted hyaenas are large-bodied mammals that occur throughout sub-Saharan Africa. Spotted hyaenas exhibit many remarkable similarities to these monkeys with respect to their life histories and to the size and complexity of their social groups. Although they consume different things, the foods of both hyaenas and cercopithecine primates generally occur in rich, scattered patches appearing unpredictably in space and time. Like female primates, female hyaenas produce tiny litters at long intervals, and their offspring require an unusually long period of nutritional and social dependence on the mother; in both taxa mothers continue to help their offspring long after weaning (e.g. Holekamp, Smale, Berg, & Cooper, 1997), and this assistance enhances offspring fitness (Watts, Tanner, Lundrigan, & Holekamp, 2009). Like many primates, hyaenas have a long life span. The complexity of spotted hyaena societies is also comparable in most respects to that found in troops of cercopithecine primates, and far exceeds that found in the social lives of any other terrestrial carnivore (e.g. Gittleman, 1989a, 1989b, 1996). We have detailed these similarities elsewhere (Holekamp, Sakai, & Lundrigan, 2007a, 2007b; Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012), so here we merely recapitulate the highlights, and note recent discoveries.

Spotted hyaenas live in permanent complex social groups, called clans (Kruuk, 1972). All members of a hyaena clan recognize one another, cooperatively defend a common territory and rear their cubs together (Boydston, Morelli, & Holekamp, 2001; Henschel & Skinner, 1991; Kruuk, 1972). Like cercopithecine primates, spotted hyaenas establish enduring relationships with clan-mates that may last many years, often spanning multiple decades (Ilany, Booms, & Holekamp, n.d.). Group size on the prey-rich plains of eastern Africa (Holekamp & Dloniak, 2010) is at least the same as that of sympatric baboon troops (e.g. Holekamp et al., 2012; Sapolsky, 1993); in fact, we currently have one study clan in Kenya containing 130 individuals. Like baboon troops, hyaena clans contain multiple adult males and multiple matrilines of adult female kin with offspring, including individuals from several overlapping generations. Breeding males in both taxa are usually immigrants born elsewhere. As in virtually all cercopithecines, male hyaenas disperse voluntarily from their natal groups after puberty, whereas females are usually philopatric (Boydston, Kapheim, Van Horn, Smale, & Holekamp, 2005; Cheney & Seyfarth, 1983; Henschel & Skinner, 1987; Honer et al., 2007; Mills, 1990; Smale, Nunes, & Holekamp, 1997). As in many monkeys, relatedness is high within hyaena matrilines but, on average, clan members are only very distantly related due to high levels of male-mediated gene flow among clans (Van Horn, Engh, Scribner, Funk, & Holekamp, 2004). Thus, both monkeys and hyaenas interact on a daily basis, not only with their kin, but also with individuals who are no more closely related to them than are the five authors of this paper to one another.

Like many primates, hyaenas within each clan can be ranked in a linear dominance hierarchy based on outcomes of agonistic interactions, and priority of resource access varies with social rank (Frank, 1986; Rodriguez-Llanesa, Verbekeb, & Finlayson, 2009; Tilson & Hamilton, 1984). As in female cercopithecine primates, dominance ranks of female hyaenas are not correlated with size or fighting ability; instead, power in hyaena society resides with the individuals having the strongest network of allies, and ally network size declines with rank (Smith et al., 2011, 2010). In both hyaenas and cercopithecine primates, members of the same matriline occupy adjacent rank positions in the group's hierarchy, and female dominance relations are extremely stable across contexts and time.

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