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Brains, brawn and sociality: a hyaena's tale

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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.

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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

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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 non-primate 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.

One interesting difference between hyaenas and cercopithecine primates in regard to rank is that adult female hyaenas dominate adult males (Kruuk, 1972), whereas male cercopithecines dominate females. Adult natal male hyaenas dominate adult females ranked lower than their own mothers as long as they remain in the natal clan, but when males disperse they behave submissively to all new hyaenas encountered outside the natal area, and thus allow themselves to be dominated by all natal animals in their new clan (Smale, Frank, & Holekamp, 1993; Smale et al., 1997). When a male joins a new clan, he assumes the lowest rank in that clan's dominance hierarchy (Holekamp & Smale, 1998; Smale et al., 1997). Immigrant male hyaenas rarely fight amongst themselves; instead they form a queue in which the immigrant who arrived first in the clan holds the highest rank in the male hierarchy, and the most recently arrived male the lowest (East & Hofer, 2001; Smale et al., 1997).

Like vervets and baboons, spotted hyaenas are plural breeders, but reproductive success in both sexes varies with social rank (Frank, Holekamp, & Smale, 1995; Hofer & East, 2003; Holekamp, Smale, & Szykman, 1996). Male primates and male spotted hyaenas use both male–male aggression and endurance rivalries in competition for mates, but primates rely far more heavily on the former (e.g. Carpenter, 1942; MacCormick et al., 2012; Rodriguez-Llanesa et al., 2009) while spotted hyaenas compete mainly via endurance rivalry (Curren, 2012; Curren, Linden, Heinen, McGuire, & Holekamp, 2015). However, in females the mechanisms mediating rank-related variation in reproductive success are remarkably similar between Old World primates and spotted hyaenas (Fig. 1). In both taxa dominant females can use aggression or displacement to gain access to better resources. As in various primates (e.g. Thierry, Singh, & Kaumanns, 2004), high-ranking female spotted hyaenas start breeding at younger ages, produce more surviving offspring per unit time, and enjoy longer life spans than do their low-ranking counterparts, and these differences have profound long-term fitness consequences (Hofer & East, 2003; Holekamp et al., 1996; Holekamp et al., 2012). However, as in female baboons (e.g. Silk et al., 2009, 2010), the fitness of female spotted hyaenas is strongly affected by sociability as well as by dominance rank. For example, after controlling for social rank, gregariousness has positive effects on life span among female spotted hyaenas (Fig. 2). Life span is a major determinant of fitness in this species (Swanson, Dworkin, & Holekamp, 2011), and highly gregarious females have longer life spans than others (Shaw, 2012). We also found significant positive relationships between sociability and reproductive success in low-ranking, but not high-ranking, female hyaenas (see Supplementary Material), suggesting that hyaenas, like monkeys, can use social strategies to offset costs of low rank.

Finally, patterns of intragroup cooperation in spotted hyaenas are surprisingly similar to those documented among cercopithecine primates. Spotted hyaenas often help both kin and nonkin allies defend their kills against lions or other hyaenas, and by doing so may risk serious injury or death (Hofer & East, 1993; Kruuk, 1972; Mills, 1990). Clan-mates also often cooperate to hunt ungulate prey; the probability of successfully making a kill increases by approximately 20% with the presence of each additional hunter (Holekamp, Smale, et al., 1997). As in baboons (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012), female hyaenas form long-lasting affiliative relationships with a subset of other females in their clan, with the strongest bonds occurring among close matrilineal kin (Holekamp et al., 2012; Smith et al., 2011). Thus, as in many primates, hyaenas have enduring cooperative relationships that affect survival and reproduction of individual group members.

Clearly, spotted hyaenas share many aspects of their biology with Old World primates. Although some primatologists claim that primate societies are more complex than those of other mammals (e.g. Dunbar, 2009), the characteristics of hyaena societies reviewed here suggest otherwise (see also Drea & Frank, 2003). The striking similarities between cercopithecines and spotted hyaenas suggest that there may be convergence in the underlying mechanisms, namely cognitive processes and nervous system organization. Next we review abilities in the domain of social cognition that are exhibited by both Old World primates and spotted hyaenas.
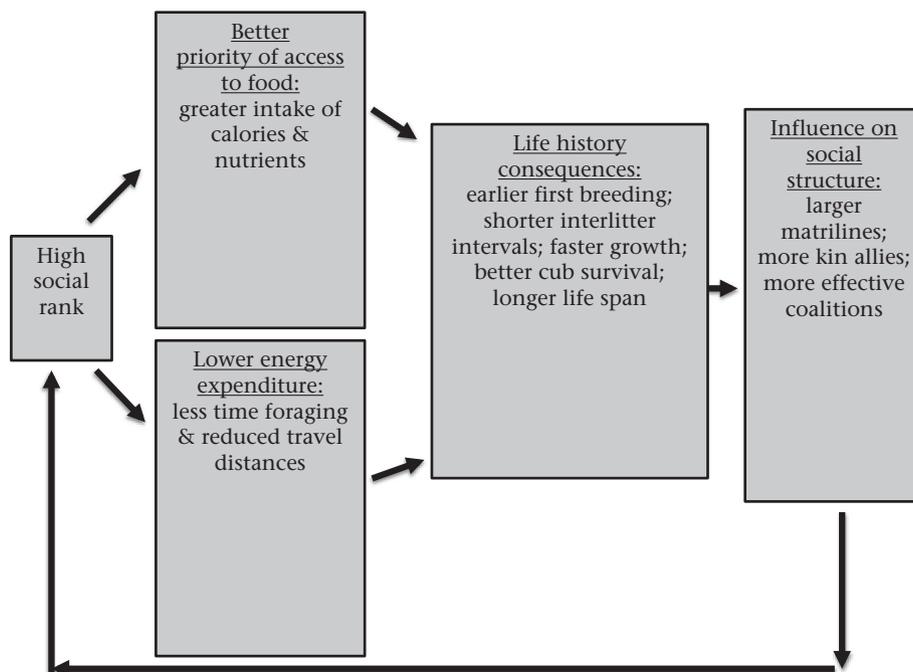
Figure 1. Mediation of the relationship between female social rank and reproductive success in spotted hyaenas. Modified from Holekamp et al. (2012).
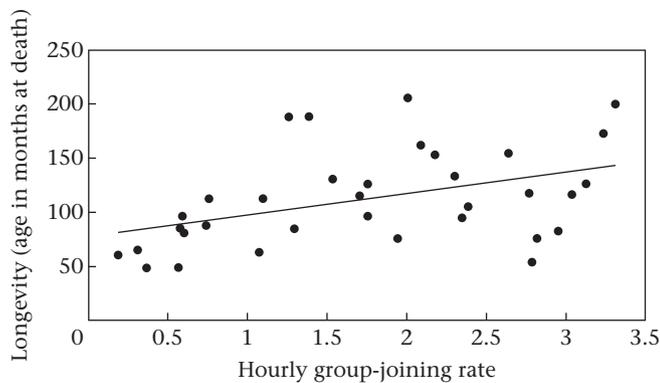
Figure 2. Relationship between sociability and fitness among female spotted hyaenas. Longevity is our measure of fitness, and mean lifetime joining rate is our measure of sociability. Group-joining rate significantly predicted age at death; hyaenas that joined groups more often lived longer than did those that joined groups less often (19.82 ± 7.35, $N = 34$; generalized linear model: $t_{31} = 2.695$, $P = 0.011$). Methodological details, which are available in online supplementary materials, are drawn from a study of hyaena personality traits by Shaw (2012).

SPOTTED HYAENAS AND MONKEYS CAN SOLVE THE SAME SOCIAL PROBLEMS

Cercopithecine primates possess well-developed cognitive abilities that make them unusually adept at predicting outcomes of behavioural interactions among their group-mates (e.g. Byrne, 1994; Byrne & Whiten, 1988; Cheney & Seyfarth, 1986; Tomasello & Call, 1997; de Waal & Tyack, 2003). They recognize individual conspecifics based on their voices and faces, discriminate kin from nonkin, and may even be able to recognize paternal kin in the absence of paternal care (e.g. Buchan, Alberts, Silk, & Altmann, 2003; Cheney & Seyfarth, 1980, 1990; Seyfarth & Cheney, 2010; but see Moscovice et al., 2010). Nepotism is common in most primates, and kin also form stronger bonds than do nonkin (e.g. Cheney & Seyfarth, 1990; Silk et al., 2012). As they mature, monkeys assume their places in the troop's dominance hierarchy through a protracted process of associative learning during interactions with group-mates (e.g. Cheney & Seyfarth, 2007; Horrocks & Hunte, 1983). They know that group-mates vary in their value as social partners, and they attempt to repair valuable relationships when those are damaged (e.g. Aureli & de Waal, 2000; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Cheney & Seyfarth, 1990, 2007; Cords, 1988; Tomasello & Call, 1997). Monkeys clearly remember outcomes of earlier encounters with particular conspecifics, and they modify their social behaviour on the basis of interaction histories (Cheney & Seyfarth, 1990, 2003, 2007; Clarke, Halliday, Barrett, & Henzi, 2010). Furthermore, they possess knowledge about the social ranks of their group-mates (Silk, 1999) and about the social relationships among their group-mates (e.g. Wittig, Crockford, Seyfarth, & Cheney, 2007; Wittig, Crockford, Wikberg, Seyfarth, &Cheney, 2007), and base their decision making in social situations upon this knowledge. Here we argue that spotted hyaenas share all these capabilities with cercopithecine primates.

Spotted hyaenas can recognize individual group-mates using visual, acoustic or olfactory cues (Kruuk, 1972). For example, they can identify individual conspecifics, and distinguish kin from nonkin, on the basis of their long-distance 'whoop' vocalizations, and whoops also convey information about the caller's age, sex and motivational state (Benson-Amram, Heinen, Dryer, & Holekamp, 2011; East & Hofer, 1991a, 1991b; Gersick et al., 2015; Holekamp et al., 1999; Theis, Greene, Benson-Amram, & Holekamp, 2007). Hyaenas also have a keen olfactory sense; each clan has a unique scent signature, mediated in part by volatile products of

metabolism in the symbiotic microbes inhabiting the hyaenas' scent glands (Hofer, East, Sammang, & Dehnhard, 2001; Theis, Schmidt, & Holekamp, 2012, Theis et al., 2013), and hyaenas can distinguish scents of their clan-mates from those of hyaenas from other clans (Theis, 2007). Spotted hyaenas also use olfactory cues to discriminate sex, reproductive state and familiarity of conspecifics (Drea, Vignieri, Cunningham, & Glickman, 2002; Drea, Vignieri, Kim, Weldele, & Glickman, 2002; Theis, 2007).

Nepotism is common among spotted hyaenas, social bonds are stronger among kin than nonkin (Holekamp, Cooper, et al., 1997, Holekamp et al., 2012; Smith, Memenis, & Holekamp, 2007), and individuals direct affiliative behaviour most frequently towards kin (East, Hofer, & Wickler, 1993; Smith et al., 2007; Wahaj et al., 2004). Although male hyaenas do not participate in parental care, sires can recognize their offspring, and vice versa; this most likely occurs via phenotype matching (Van Horn, Wahaj, & Holekamp, 2004). Furthermore, full-sibling littermates associate more closely, and direct more affiliative behaviour towards one another, than do half-sibling littermates (Wahaj et al., 2004). When deciding whether or not to join ongoing fights, female spotted hyaenas support close kin most often, and the density of cooperation networks increases with genetic relatedness; nevertheless, as in primates, kinship fails to protect females from coalitionary attacks (Smith et al., 2010). As in monkeys, hyaenas are more likely to attack the relatives of their opponents after a fight than during a matched control period, and after a fight they are more likely to attack relatives of their opponents than to attack other lower-ranking animals unrelated to their opponents (Engh, Siebert, Greenberg, & Holekamp, 2005).

Young hyaenas learn their positions in their clan's dominance hierarchy via a process of 'maternal rank inheritance' (Engh, Esch, Smale, & Holekamp, 2000; Holekamp & Smale, 1991, 1993; Smale et al., 1993), and nonlittermate hyaena siblings assume relative ranks that are inversely related to age in a primate-like pattern of 'youngest ascendency' (Holekamp & Smale, 1993; Horrocks & Hunte, 1983; Jenks, Weldele, Frank, & Glickman, 1995). In fact, hyaena cubs learn about rank relationships just as monkeys do (e.g. Cheney, 1977), but they do so with considerably less information than young monkeys, because cubs live at dens and spend relatively little time with their mothers. Learning is a critical aspect of rank acquisition in spotted hyaenas, and they clearly remember outcomes of earlier encounters with particular group-mates (e.g. Fig. 3). As in primates, coalitions play an important role in acquisition and maintenance of social rank in spotted hyaenas (Engh et al., 2000; Holekamp & Smale, 1993; Smale et al., 1993; Zabel, Glickman, Frank, Woodmansee, & Keppel, 1992).

Multiple lines of evidence indicate that spotted hyaenas recognize that their social partners vary in relative value to them, and that they make adaptive choices regarding which clan-mates to associate with (Smith et al., 2007). For example, although interactions between male and female spotted hyaenas are almost exclusively initiated and maintained by males, females often mate with their closest male associates (Szykman et al., 2001). Males prefer to associate most closely with the highest-ranking females, whose offspring survive far better than do offspring of low-ranked females (Watts et al., 2009), so this preference by males appears highly adaptive. We do not yet know how males discriminate female rank. Adult hyaenas of both sexes prefer to associate with nonkin holding ranks similar to their own (Smith et al., 2007). Furthermore, patterns of greeting behaviour in spotted hyaenas follow primate patterns of social grooming in which individuals prefer to spend time with, and direct affiliative behaviour towards, high-ranking nonkin (East et al., 1993; Seyfarth &Cheney, 1984 ; Smith et al., 2011).

Spotted hyaenas use unsolicited appeasement and greeting behaviours to reconcile their fights (East et al., 1993; Hofer & East, 2000; Wahaj, Guze, & Holekamp, 2001). As is also true in many
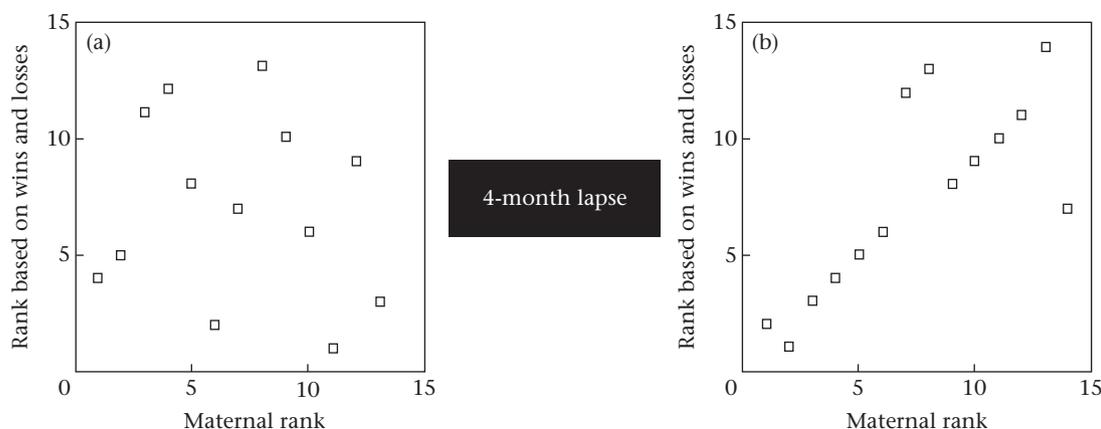
Figure 3. Results from two 'bone tests' administered to the same cohort of 13 hyaena cubs at the communal den after the cubs had lived at the communal den for (a) a few weeks and (b) several months. Cub ranks based on wins and losses during each test are plotted against maternal rank. Cub ranks became isoporphic with those of their mothers after living at the communal den for several months. Modified from Holekamp and Smale (1993).

primates, victims in hyaena fights are significantly more likely to reconcile than are aggressors (Aureli & de Waal, 2000; Wahaj et al., 2001). Furthermore, spotted hyaenas can recognize third-party relationships among their clan-mates. Third-party relationships involve interactions and relationships in which the observer is not directly involved (Tomasello & Call, 1997). Hyaenas can recognize third-party relationships based on either social rank or kinship, and they use this knowledge in adaptive decision making (Engh et al., 2005). Hyaenas clearly make flexible decisions regarding whether or not to cooperate or compete with conspecifics, modifying their behaviour based on multiple types of information about their immediate social and ecological environments (Smith et al., 2010).

To summarize, we find many striking similarities in social cognition between spotted hyaenas and cercopithecine primates, as predicted by the social complexity hypothesis, which has also been supported in various studies of social cognition in primates (e.g. Bachmann & Kummer, 1980; Byrne & Whiten, 1988; Cheney & Seyfarth, 1990) and birds (e.g. Paz-y-Mino, Bond, Kamil, & Balda, 2004; West, 2014). Some social cognitive abilities exist in monkeys that we have not yet sought in hyaenas (e.g. Bergman, Beehner, Cheney, & Seyfarth, 2003), but the hyaenas' behaviour has indicated that they have been able to solve, without exception, all the social problems we have posed for them.

BRAIN SIZE AND FRONTAL CORTEX IN MAMMALIAN CARNIVORES

Because social complexity is expected to shape nervous systems as well as behaviour, we next turned our attention to assessment of hyaena brains. The social complexity hypothesis considered specifically in relation to nervous systems has been dubbed 'the social brain hypothesis' (Barton & Dunbar, 1997; Brothers, 1990; Dunbar, 2003), which predicts that nonprimates living in complex societies should possess neural structures mediating social behaviour that have evolved convergently with those in primates. In relation to body size, the brains of primates are relatively large and complex compared to those of other animals, including most nonprimate mammals (Harvey & Krebs, 1990; Jerison, 1973; Macphail, 1982). The mammalian brain comprises a number of functionally distinct systems, and natural selection acting on particular behavioural capacities causes size changes selectively in the systems mediating those capacities (Barton & Harvey, 2000). The frontal cortex is known to mediate complex social behaviour in humans and other mammals (Adolphs, 2001; Amodio & Frith, 2006), so the social

brain hypothesis predicts we should find larger frontal cortex volumes in gregarious species than in closely related solitary species.

Among primates, the neocortex disproportionately covers the frontal area (Dunbar, 2003), and social complexity is strongly correlated with neocortical volume (Lehmann & Dunbar, 2009). Thus, social complexity in primates appears to be related broadly to greater brain volume and specifically to expansion of the frontal cortex. If the social brain hypothesis is correct, we should find similar patterns in the brains of nonprimate mammals that, although closely related to one another, vary with respect to the complexity of their social lives. We recently tested predictions of the social brain hypothesis in mammalian carnivores using virtual brains generated with computed tomography (CT) in combination with cytoarchitectonic analysis (Sakai, Arsznov, Lundrigan, & Holekamp, 2011a). Here we first review our analysis of the four extant species within the family Hyaenidae (Arsznov, Lundrigan, Holekamp, & Sakai, 2010; Sakai, Arsznov, Lundrigan, & Holekamp, 2011b), then we summarize our larger analysis of 36 species of terrestrial carnivores whose societies vary greatly with respect to complexity (Swanson, Holekamp, Lundrigan, Arsznov, & Sakai, 2012).

Our first goal was to conduct accurate volumetric assessments of the frontal cortex in relation to total brain volume in spotted hyaenas, and compare these measurements with those obtained from their closest living relatives, which are aardwolves, *Proteles cristatus*, striped hyaenas, *Hyaena hyaena*, and brown hyaenas, *Parahyaena brunnea*. These four species, which constitute the extant Hyaenidae, span a wide spectrum of social complexity. The aardwolf is solitary except when breeding (Richardson, 1988). The striped hyaena is usually solitary, but may be found with two or three conspecifics (Kruuk, 1976; Wagner, Creel, Frank, & Kalinowski, 2007, Wagner, Frank, & Creel, 2008), and closely related females may rear their cubs together at shared dens (Califf, 2013). The brown hyaena lives in small clans that may contain up to 11 individuals (Mills, 1990). Spotted hyaenas occur sympatrically with all three of these other species in Africa. The four hyaena species last shared a common ancestor approximately 11 MYA (Koepfli et al., 2006).

Using skeletal material from the four extant Hyaenids, we used CT to generate virtual three-dimensional hyaena brains with which we could examine the relationship between frontal cortex volume and social complexity. We measured overall endocranial volume relative to the size of the skull from which each brain was scanned. We also measured the volume of each of four gross brain regions in

each virtual brain. That is, overall endocranial volume was subdivided into (1) cerebrum anterior to the cruciate sulcus (AC), (2) cerebrum posterior to the cruciate sulcus (PC), (3) total cerebrum (AC+PC) and (4) hindbrain, which includes both cerebellum and brainstem (Cb+Bs). The AC is made up mainly of frontal cortex. Overall endocranial volume was corrected for size of the skull from which it came, and the volume of each brain region was corrected for the overall endocranial volume. Further methodological details can be found elsewhere (Arsznov et al., 2010; Sakai et al., 2011a, 2011b; also see Supplementary Material).

We found that spotted hyaenas had much larger corrected brain volumes than did the other three species in the family Hyaenidae (Sakai et al., 2011b). However, the relative brain volumes of striped hyaenas, brown hyaenas and aardwolves did not differ significantly, which fails to conform to predictions of the social complexity hypothesis. We also found that AC volume relative to total brain volume in the spotted hyaena was significantly larger than those in the other three species, and that AC volume in aardwolves was significantly smaller than that in any other hyaenid species. The frontal cortex comprises 25% of the total endocranial volume in spotted hyaenas but only 17–18% in both striped and brown hyaenas, and 10% in aardwolves (Sakai et al., 2011b). These data are consistent with the idea that expansion of frontal cortex is driven by social complexity, but they are also consistent with two competing hypotheses. The first suggests that diet shapes frontal cortex size: spotted hyaenas hunt antelope; striped and brown hyaenas eat carrion; and aardwolves eat termites. The second hypothesis, known as the 'cognitive buffer' hypothesis, posits that large brains evolved to help animals cope with novel or unpredictable environments (Reader & MacDonald, 2003; Richardson & Boyd, 2000; Sol, 2009a, 2009b). Enlarged brains should be adaptive in novel and unpredictable environments because they enable individuals to exhibit more flexible behaviour. With respect to both their foraging and their social lives, spotted hyaenas are likely to experience more novel and unpredictable environments than are the other species in the family Hyaenidae.

Interestingly, although we found no sex difference in total endocranial volume (relative to skull length) in 23 female and 22 male adult spotted hyaenas, AC volume was significantly greater in males than in females (Arsznov et al., 2010). This sex difference cannot be explained by differential demands of foraging because male and female hyaenas are equally proficient at hunting vertebrate prey (Holekamp, Smale, et al., 1997) and forage over similarly large areas (Holekamp, Ogutu, Frank, Dublin, & Smale, 1993). However the observed sex difference in AC volume is consistent with both the social brain hypothesis and the cognitive buffer hypothesis because the intellectual demands imposed by male transfer to new social groups should be so much greater than those imposed by female philopatry. That is, male spotted hyaenas must learn to forage efficiently in a new clan's territory and learn the identities of, and relationships among, members of at least two different clans, whereas females do this only in their natal clan. Interestingly, male hyaenas must inhibit their aggressive behaviour, and behave submissively to all natal animals in the new clan, for successful transfer between clans at dispersal. Frontal cortex should theoretically be strongly involved in the mediation of both these types of social cognition (Adolphs, 2001; Amodio & Frith, 2006). An interpretation of this sex difference based on the need for social acumen is consistent with results from primates. Lindenfors and colleagues (Lindenfors, 2005; Lindenfors, Nunn, & Barton, 2007) suggested that social agility may generally be of greater value to female than male primates, corresponding to a sex difference in relative neocortex size; neocortex size scales with social complexity among female primates but not among male primates (Lindenfors, 2005). Males disperse in most cercopithecine primates

as they do in spotted hyaenas, but Lindenfors et al. (2007) argued that the brain regions that are enlarged in male primates are more directly involved in mediation of male–male fighting than social agility; these include brain structures involved in autonomic function and sensory-motor skills. Enhanced fighting ability is of little use to male spotted hyaenas (East, Burke, Wilhelm, Greig, & Hofer, 2003; East & Hofer, 2001), so perhaps sexual selection has favoured the evolution of brains over brawn in male hyaenas. In future studies perhaps we should consider mode of competition for key resources along with diet, ecological novelty and social complexity as important variables affecting brain evolution.

Overall, although some lines of evidence from our work with hyaena brains appeared consistent with the social brain hypothesis, others appeared more consistent with competing hypotheses. Furthermore, various phenomena have been identified in carnivores for which the social brain hypothesis cannot account. For example, the brain sizes of mammalian carnivores and their ungulate prey covary through geological time, with each increase in ungulate brain size being followed later by a corresponding increase in carnivore brain size, and this covariation apparently occurred in solitary as well as gregarious carnivores (Jerison, 1973).

In an attempt to assess the relative contributions of social and multiple other variables to brain evolution in carnivores, we expanded our CT-based analysis of whole brains and brain regions to a larger array of mammalian carnivores (Swanson et al., 2012). We did this specifically because most research on brain evolution addresses only one hypothesis at a time, despite the demonstrated importance of considering multiple factors simultaneously. We used phylogenetic comparative methods to investigate simultaneously the importance of several factors previously hypothesized to be important in neural evolution among mammalian carnivores, including social complexity, forelimb use, home range size, diet, life history, phylogeny and recent evolutionary changes in body size. We also assessed the roles of these variables in shaping the relative volume of the same four brain regions as those measured in our study of the Hyaenidae.

Our larger comparative study, in which we analysed CT data from 36 carnivore species in seven families, revealed that sociality is only one of multiple variables shaping brain evolution. Diet also has important effects: carnivore species that primarily consume vertebrates have the largest brains, omnivores are intermediate, and carnivores that specialize on insects have the smallest brains relative to their body size (Swanson et al., 2012). We found no support for a role of social complexity in overall encephalization, which is consistent with results from earlier carnivore studies (e.g. Finarelli & Flynn, 2009). Interestingly, although many carnivores are highly gregarious, we found that relative brain size was substantially greater in members of the ursid (bear) and mustelid (weasel) families, most of which are solitary, than in other extant families (Swanson et al., 2012), a finding consistent with those from earlier comparative analyses (Dunbar & Bever, 1998; Gittleman, 1986). Although overall brain size was not predicted by social complexity in our own comparative data set, we found that relative cerebrum volume (AC+PC) was predicted by social complexity in carnivores (Swanson et al., 2012). Nevertheless, this larger analysis of brains and brain regions in mammalian carnivores highlighted some major cracks in the armour of the social brain hypothesis.

## PROBLEMS FOR THE SOCIAL COMPLEXITY HYPOTHESIS

Although data from various comparative studies on features of the nervous system, social cognition, or both are consistent with the social complexity hypothesis (e.g. Dunbar & Bever, 1998; Shultz & Dunbar, 2010), it is now widely agreed that the social complexity hypothesis has two major shortcomings (e.g. Holekamp, 2007; van

Schaik, Isler, & Burkart, 2012). First, this hypothesis appears unable to account for grade shifts in relative brain size or relative cortex size among animal groups (e.g. Finarelli & Flynn, 2009; Jerison, 1973). When plotting the allometric relationship between brain size and body size, or between cortex size and overall brain size, a grade shift occurs when the slopes or the *Y* intercepts of the curves differ markedly for two animal taxa. For example, Bush and Allman (2004) compared mammalian carnivores and primates with respect to the relationship between frontal cortex and total cortex volumes, and found that the slope of the curve for primates was considerably steeper than that for carnivores. We have recently suggested that one factor contributing to such grade shifts might be differential evolvability of neural tissue in these two taxa. We found that brain size is considerably more variable within and between primate families than it is in carnivore families (Fig. 4). Because variability is the very stuff on which natural selection acts, it has strong effects on trait evolvability. We hypothesize that constraints imposed by demands of locomotion or feeding, affecting the nervous system during ontogenetic development, might influence the variability in brain size found within any particular taxonomic group (Holekamp, Van Meter, & Swanson, 2013). However, social complexity appears unrelated to this variability.

The second shortcoming of the social complexity hypothesis is its apparent inability to explain the common observation that species with high sociocognitive abilities also excel in general intelligence (e.g. Byrne, 1997; Reader, Hager, & Laland, 2011). There is, in fact, a long-standing debate as to whether animal behaviour is mediated by cognitive specializations that have evolved to fulfil specific ecological functions, or instead by domain-general

mechanisms (e.g. Reader et al., 2011; Thornton, Clayton, & Grodzinski, 2012). Although it appears that social selection pressures can shape the evolution of social cognition, it is not clear whether social complexity also affects the ability to solve problems outside the social domain. Therefore we initiated a line of inquiry aimed at identifying the variables that predict success when hyaenas and other carnivores are confronted with nonsocial problems. We were interested to know whether the social complexity hypothesis or the cognitive buffer hypothesis (Sol, 2009a, 2009b) best predicts success when carnivores attempt to solve a novel foraging problem.

We began by presenting wild hyaenas with a wrought-iron puzzle box baited with meat, and inquiring which aspects of performance in each individual's first trial predicted whether or not it would eventually be successful at getting the bait out of the box (Benson-Amram & Holekamp, 2012). We found that those individuals exhibiting a greater diversity of initial exploratory behaviours were more successful problem solvers. We also found that neophobia reduced problem-solving success. Although juveniles and adults were equally successful in solving the problem, juveniles were significantly more diverse in their initial exploratory behaviours, and more persistent and less neophobic than adults. We found no significant effects of social rank or sex on success or on any performance measure. Our results suggested that the diversity of initial exploratory behaviours, akin to some measures of human creativity, might be an important determinant of problem-solving success in our study animals. Surprisingly, however, only 9 of 62 hyaenas tested (14.5% of subjects) were ever able to open the puzzle box. We then took advantage of the existence of the captive hyaena
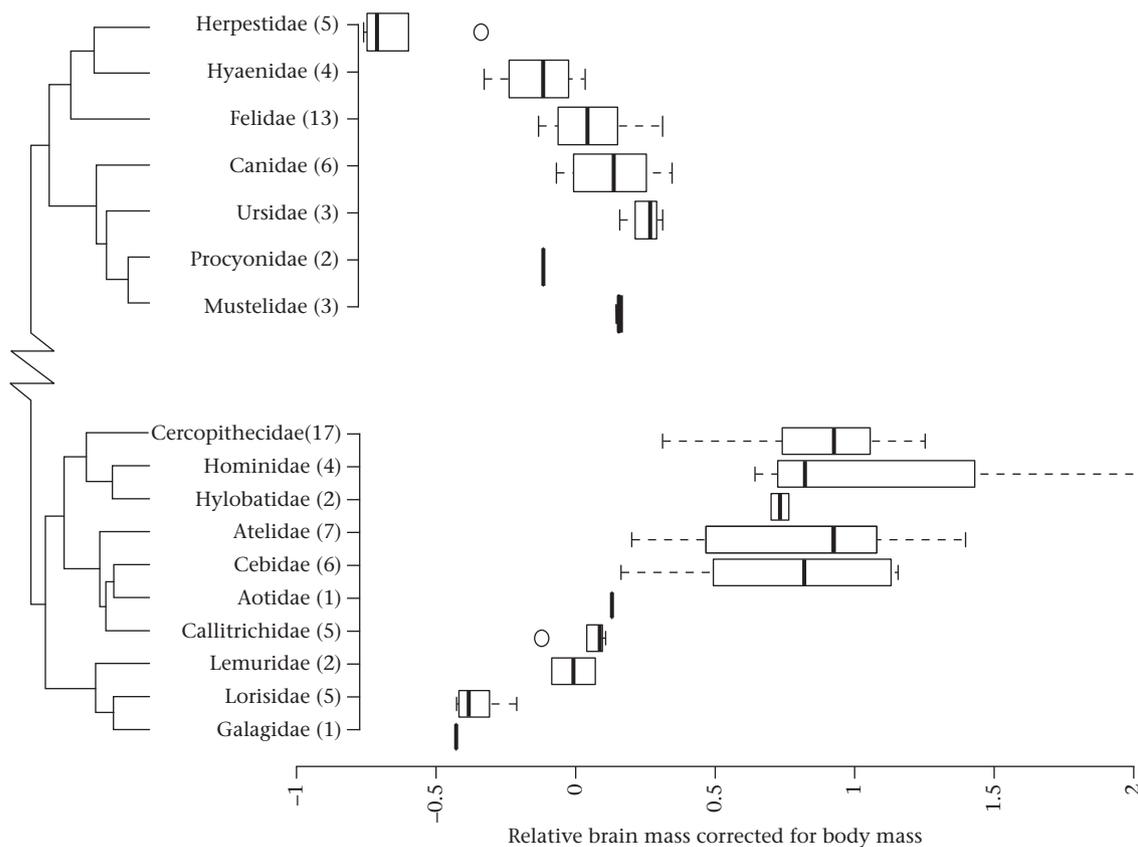
Figure 4. Phylogeny for seven families in the order Carnivora and 10 families in the order Primates taken from Bininda-Emonds et al. (2007). Horizontal box plots display relative brain mass corrected for body mass using phylogenetic regression. Branch lengths on phylogenies are not shown to scale, but the relative brain mass values for the two orders are scaled to be comparable. Sample sizes, representing species within each family, are given in parentheses following each family name. Boxes indicate interquartile range, and whiskers spread to the furthest points outside the interquartile range, but within 1.5 times the interquartile range from the median. From Holekamp et al. (2013).

colony in Berkeley, CA, and found that 73.7% of hyaenas tested in the captive environment ($N = 19$) were able to open the box, apparently because they were more accustomed to interacting with man-made metal objects and had fewer competing demands on their time than do wild hyaenas (Benson-Amram, Weldele, & Holekamp, 2013). To date we have also been able to test three striped hyaenas in captivity, but none of them have opened the box (Benson-Amram, Dantzer, Stricker, & Holekamp, n.d.). Preliminary data suggest that spotted hyaenas might be more innovative than striped hyaenas, even though both species are equipped with exactly the same morphological tools with which to open the puzzle box (Fig. 5); this preliminary result is consistent with both the social complexity hypothesis and the cognitive buffer hypothesis. Our work with captive hyaenas next prompted us to conduct comparable tests of problem-solving ability in a wider range of carnivore species.

PROBLEM SOLVING IN ZOO-HOUSED CARNIVORES

To extend our findings from spotted hyaenas regarding measures predicting success at solving simple problems outside the social domain, in 2007–2009, we presented our puzzle boxes, scaled according to subject body size, to myriad carnivores housed in nine North American zoos (Benson-Amram et al., n.d.). Because we were testing animals that ranged in size from roughly 2 kg–300 kg, we used small and large steel-mesh boxes. We videotaped all trials, and extracted performance measures from videotapes using methods described elsewhere (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013; Benson-Amram et al., n.d.). This work was approved by the Institutional Animal Care and Use Committee (IACUC) of Michigan State University (approval number 03/08-037-00) and also by IACUCs at all nine zoos where testing was done. We then brought together data on success and performance measures during zoo trials with data documenting total brain size (Finarelli & Flynn, 2009), the relative volumes of different brain regions and average group size for each species tested (Swanson et al., 2012), and used phylogenetic generalized least squares

regressions (Freckelton, Harvey, & Pagel, 2002; Pagel, 1999) to identify the variables predicting success or failure in solving this nonsocial problem (detailed methods are available in Benson-Amram et al., n.d.; also see Supplementary Material).

We evaluated puzzle box success in 146 individuals from 39 species in nine families of mammalian carnivores. Of the 146 individuals tested, 48 individuals (32.8%) from 23 species succeeded at opening the puzzle box. The proportion of individuals within each species that succeeded in opening the box varied among families, with species in the families Ursidae (69.2% of trials), Procyonidae (53.8% of trials) and Mustelidae (47% of trials) being most successful at opening the puzzle box, and those within the family Herpestidae (0%) being the least successful.

Total brain volume corrected for body mass varied among the species tested, with canid and ursid species having the largest brains, and viverrid, hyaenid and herpestid species having the smallest brains (Swanson et al., 2012). Carnivore species with larger brain volumes relative to their overall body mass were significantly better than others at opening the puzzle box (Benson-Amram et al., n.d.). Species with large average group sizes such as banded mongoose, *Mungos mungo* (average group size = 23.67 individuals) tended to be less successful at opening the puzzle box than were solitary species such as black bears, *Ursus americanus* (group size = 1) and wolverines, *Gulo gulo* (group size = 1).

The results from this zoo study, particularly when taken together with our earlier data on brain volumes (Swanson et al., 2012), are remarkably like those obtained recently by MacLean et al. (2014) in a comparative study of problem solving by a wide array of birds and mammals on two inhibition tasks. In both studies the best performance was observed in the species with the largest brains (either mass-corrected or uncorrected brain volume), and social complexity failed to predict success either in problem solving or in brain size in both primates and carnivores.

Interestingly, our data support the 'cognitive buffer' hypothesis (Sol, 2009a, 2009b), which suggests that behavioural innovation is an important factor affecting brain evolution in carnivores. We found that carnivore species in which tested individuals used a greater diversity of behaviours were significantly more successful at opening the puzzle box than were others (Benson-Amram et al., n.d.). When animals are faced with novel or unpredictable environments, the ability to produce new behaviours and to innovate solutions to problems not previously encountered is hypothesized to have critical effects on their survival and reproduction (Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005; Sol, Bacher, Reader, & Lefebvre, 2008; Sol & Lefebvre, 2000; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Szekely, Liker, & Lefebvre, 2007). In particular, innovation is likely to facilitate the invasion of novel habitats by allowing animals to exploit new resources. Indeed, the ability to respond to environmental change is thought to be an important component of human brain evolution (Richardson & Boyd, 2000). Furthermore, in both primates and birds, innovation rates are better correlated with brain size than are social variables such as group size (Lefebvre, Reader, & Sol, 2004; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader & Laland, 2002; Reader & MacDonald, 2003). Similarly, the results from our zoo study show that, across carnivores, the most innovative individuals are the most successful at solving a novel technical problem.

Although previous links have been established between brain size and cognitive capacity, as reflected in innovation frequency (Reader & Laland, 2002), in our zoo work we cannot assume that carnivores that solved our puzzle box problem possessed elevated cognitive abilities without testing the underlying mechanisms (Thornton et al., 2012). Indeed, although some of our zoo subjects appeared to give serious 'intellectual' consideration to the problem of opening the box, others appeared to use brawn rather than
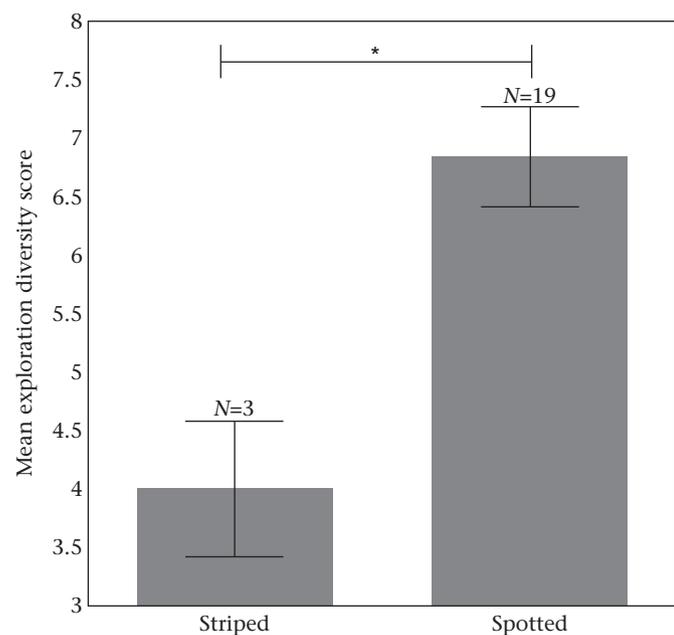
Figure 5. Comparison of behavioural diversity measures scored for spotted and striped hyaenas in puzzle box trials administered to captive animals (Mann–Whitney U test: $U = 3.5$, $P = 0.016$). None of the three striped hyaena subjects opened the box, whereas 73.7% of the 19 spotted hyaenas did.

brains to get it open (see video clips in online supplementary materials associated with Benson-Amram et al., n.d.). Nevertheless, as suggested nearly 50 years ago by Glickman and Sroges (1966), our results indicate that zoos and other animal sanctuaries might offer useful venues for some types of large-scale comparative study in future.

CONCLUSIONS

The social complexity hypothesis posits that big brains and great intelligence have been favoured by selection pressures imposed by life in challenging social environments, but our data suggest the story is considerably more complicated than this. Nearly 20 years of fieldwork on social cognition in spotted hyaenas have revealed strong and consistent evidence that abilities in the domain of social cognition have evolved convergently in spotted hyaenas with those in primates. Our work has revealed that spotted hyaenas live in social groups just as large and complex as those of cercopithecine primates, that they experience an extended early period of intensive learning about their social worlds like primates, that their need for social dexterity is no less than that in primates, and that the same sociocognitive abilities have evolved in carnivores as in primates. Much remains to be learned about social cognition in spotted hyaenas, but they appear to be capable of solving every social problem we have posed for them to date, which is strongly consistent with the social complexity hypothesis.

On the other hand, impressive knowledge about relationships among conspecifics has also been documented in various animals that lead solitary lives (e.g. Bond, Kamil, & Balda, 2007; Grosenick, Clement, & Fernald, 2007). Furthermore, support is quite weak for the notion that social complexity affects the size of brains or gross brain regions; it might apply at the level of the family in carnivores (e.g. Sakai et al., 2011b), but fails at the level of the order (Bush & Allman, 2004; Swanson et al., 2012). Overall, although it seems reasonable to expect that some brain areas in some animals have evolved to deal with specifically social problems, it seems unlikely that selective changes in frontal cortex size have occurred to enhance the isolated ability to manage social relationships (Charvet & Finlay, 2012). Nevertheless, when we inquired whether, in addition to improving social cognition, social complexity might also favour the evolution of superior problem-solving abilities in the nonsocial domain, we could find no support at all except perhaps when comparing two very closely related hyaena species, and those data were merely preliminary. In other pairs of closely related carnivore species in our zoo study, the less gregarious species greatly outperformed the more gregarious one (Benson-Amram et al., n.d.). In any case, in both primates (MacLean et al., 2014) and carnivores (Benson-Amram et al., n.d.), strong, phylogenetically corrected comparative data now show that brain size predicts the ability to solve nonsocial problems, but that diet better predicts brain size in both taxa than does social complexity (Finarelli & Flynn, 2009; MacLean et al., 2014; Swanson et al., 2012). Our comparative data are broadly consistent with the idea that the demand for innovative problem solving might be imposed more strongly in carnivores by feeding ecology than by social variables, whereas the opposite might be true in primates (but see Melin, Young, Mosdossy, & Fedigan, 2014). In any case, there appear to be no unambiguous causal links between selection pressures favouring social dexterity and performance in problem-solving tasks outside the social domain in mammalian carnivores.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.01.023.

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