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The evolution of intelligence in mammalian carnivores

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Although intelligence should theoretically evolve to help animals solve specific types of problems posed by the environment, it is unclear which environmental challenges favour enhanced cognition, or how general intelligence evolves along with domain-specific cognitive abilities. The social intelligence hypothesis posits that big brains and great intelligence have evolved to cope with the labile behaviour of group mates. We have exploited the remarkable convergence in social complexity between cercopithecine primates and spotted hyaenas to test predictions of the social intelligence hypothesis in regard to both cognition and brain size. Behavioural data indicate that there has been considerable convergence between primates and hyaenas with respect to their social cognitive abilities. Moreover, compared with other hyaena species, spotted hyaenas have larger brains and expanded frontal cortex, as predicted by the social intelligence hypothesis. However, broader comparative study suggests that domain-general intelligence in carnivores probably did not evolve in response to selection pressures imposed specifically in the social domain. The cognitive buffer hypothesis, which suggests that general intelligence evolves to help animals cope with novel or changing environments, appears to offer a more robust explanation for general intelligence in carnivores than any hypothesis invoking selection pressures imposed strictly by sociality or foraging demands.

1. Introduction

The cognitive demands imposed on animals in their natural habitats vary considerably among species. Accordingly, behavioural ecologists and evolutionary psychologists have proposed that intelligence comprises an aggregate of special abilities that have evolved in humans and other animals in response to specific environmental challenges [1–3]. For example, spatial memory is very well developed in squirrels [4] and seed-caching birds [5]. These domain-specific cognitive mechanisms or 'modules' are activated under particular circumstances, enhancing fitness by improving the animal's ability to solve specific types of problems posed by the environment. At the neurological level, modules are often conceptualized as dedicated brain areas serving domain-specific cognitive functions or behaviour patterns that can be selectively activated or inhibited; for example the suprachiasmatic nucleus mediates time-keeping in mammals [6], and sleep is mediated by a cluster of ventrolateral preoptic neurons that innervate the tuberomammillary nucleus [7]. Abundant evidence shows that certain species are exceptionally good at solving some types of socio-ecological problems, but not others [8,9], and that these specialized abilities enhance fitness [10,11]. Thus there is a great deal of empirical support for the evolution and maintenance of domain-specific cognitive abilities in both humans [12] and non-human animals.

Interestingly, there is also a great deal of evidence that is incompatible with a strictly modular view of intelligence, suggesting that domain-general

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processes evolve in animals as well as domain-specific ones [13] (reviewed by [14]). We define general intelligence as the suite of cognitive mechanisms that appear to enhance an animal's ability to engage in flexible, innovative behaviours when confronted with a problem [15]. Both domain-specific abilities and domain-general cognitive processes have been well documented in humans [12,14,16–18]. Human performance across tasks in various cognitive domains is positively correlated, and factor-analytical procedures applied to datasets documenting individual performance across tasks consistently reveal a single 'general factor', called 'g', that loads positively overall and can explain a significant amount of variation [14,19,20]. Interestingly, g better predicts life outcomes in humans than does any specific cognitive ability [21]. In recent years, g has also been calculated in various animal species using psychometric factor-analytical approaches like that used in humans, and as in humans, g accounts for 17–48% of the intraspecific variance in performance on multiple tasks (e.g. rodents [22,23], primates [24,25], domestic dogs [26,27], birds [28,29]). Importantly, g does not simply reflect anxiety, personality traits, motivational states or other non-cognitive processes, nor is it merely a statistical artefact [14,30,31].

Despite considerable interest in the evolution of intelligence, it remains unclear which selective pressures promote the evolution of improved cognitive abilities and large brains relative to body size. Brain size is positively correlated with many different behavioural indicators of intelligence, including learning ability, tool use, ability to control inappropriate impulses and behavioural innovation [24,32,33]. Brain size is, therefore, often used as a proxy for intelligence. It also remains unknown how general intelligence evolves from or along with domain-specific cognition. Several hypotheses have been proposed to explain the evolution of superior cognitive abilities and larger brains in primates and other animals, but of these only four remain truly viable. It is important to emphasize that these hypotheses are not mutually exclusive and that multiple factors probably affect the evolution of intelligence.

The first hypothesis posits that large brains evolved to cope with complexity in the physical environment. 'Complexity' in the physical environment is most often couched in terms of finding, capturing or extracting food from the environment as well as the memory-related and navigational challenges associated with these efforts (e.g. [34–36]). The second hypothesis, commonly known as the 'social complexity' hypothesis [37,38], suggests that large brains and great intelligence evolved to cope with complexity in the social environment. This hypothesis has received a great deal of support to date, particularly in data from primates [24,39–42], but also to a lesser extent in data obtained from other taxa [43–46]. Both the first and second of these hypotheses posit that general intelligence evolves as a by-product of selection for the domain-specific cognitive abilities of foraging efficiency or social agility, respectively.

The 'cultural intelligence' hypothesis [14,42,47,48] suggests that culture, which entails social learning of specialized skills, promotes the evolution of general intelligence and larger brain size. The cultural intelligence hypothesis can be construed as a specialized version, or extension, of the social complexity hypothesis because it requires sustained social interaction, at least during early ontogeny. The development of culture is only likely in species with protracted ontogenetic development, long lives and social tolerance. Burkart *et al*. [14] argue that fundamental preconditions for the evolution of large brains and considerable general intelligence include a slow life history and high survivorship; these are possible only in species not subject to unavoidable extrinsic mortality such as high predation pressure [42]. The cultural intelligence hypothesis suggests that species relying more systematically on social learning can construct adaptive skills, such as learning which stimuli in the environment merit attention, more efficiently than other species during ontogenetic development [14,41,42,48,49]. Burkart *et al*. argue that this is because social influences are so powerful that they can effectively canalize domain-general cognitive processes such that they become second nature to the animals involved. For example, selective attention, widely considered to be a core executive function in cognitive hierarchies [50], should be honed in species in which youngsters follow their mother's example when learning which stimuli in their environment they must attend to in order to survive. Enhanced selective attention should in turn enhance survivorship over that of youngsters who learn only from direct experience with environmental stimuli. Whereas the cultural intelligence hypothesis might thus explain the relatively large brains and striking general intelligence observed in bears [36,51–53] and certain other solitary carnivores (e.g. raccoons [54–57]), several troubling exceptions remain that this hypothesis cannot explain. For example, solitary weasels have some of the largest relative brain sizes in the entire carnivore order [58], yet they are born in large litters, mature very rapidly, have no allo-parenting, and lead totally solitary lives except when mating [59,60].

Finally, the 'cognitive buffer' hypothesis posits that large brains evolved to allow animals to cope with novel socio-ecological challenges and thus reduce mortality in changing environments [61–65]. The cognitive buffer hypothesis posits that domain-general intelligence is favoured directly by natural selection to help animals cope with novel or unpredictable environments, where general intelligence is adaptive because it enables individuals to exhibit flexible behaviour, and thus find innovative solutions to problems threatening their survival and reproduction. Whereas the foraging and cognitive buffer hypotheses can potentially explain the impressively large brains found in such fast-developing, short-lived, solitary carnivores as weasels, the social complexity and cultural intelligence hypotheses cannot.

Here we first review our tests of predictions of the social complexity hypothesis using data documenting behaviour and brain volumes of one highly gregarious carnivore, the spotted hyaena, *Crocuta crocuta*. Spotted hyaenas share many aspects of their social lives and life histories with cercopithecine primates, and these similarities, which have been detailed elsewhere [11,66], suggest that cognitive abilities should also converge between the two taxa. We briefly summarize a great deal of evidence indicating that spotted hyaenas do indeed exhibit many of the same abilities in the domain of social cognition as those documented in primates.

We then 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 suggests convergent evolution in these two distantly related taxa, and is consistent with the hypothesis that the demand for social agility has driven the evolution of brains as well as specific cognitive abilities. 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 largely

consistent with some of the other hypotheses outlined above, which 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, although our findings here are consistent with predictions of the foraging hypothesis.

Next, we review our work addressing the question of whether social complexity might have shaped the evolution of general intelligence as well as social problem solving in mammalian carnivores. We first describe presentation of spotted hyaenas with a simple food-acquisition problem, and then our presentation of this same problem, scaled to accommodate variation in body size, to a large array of zoo-housed carnivores [33]. The results of our zoo study are much more strongly consistent with the cognitive buffer hypothesis than with the social complexity hypothesis.

Finally, we describe how we are now using spotted hyaenas to test predictions of the cognitive buffer hypothesis, and suggest that scientists interested in the evolution of brains and intelligence in animals have much to learn from computer scientists modelling the evolution of modular and general intelligence *in silico*.

2. Social cognition in spotted hyaenas converges with that in primates

Cercopithecine primates possess well-developed cognitive abilities that make them unusually adept at predicting outcomes of behavioural interactions among their group mates [9,39,67,68]. They recognize individual conspecifics based on their voices and faces, discriminate kin from non-kin, and can even recognize paternal kin despite the fact that there is no paternal care [69–72]. Nepotism is common in most primates, and kin also form stronger bonds than do non-kin [71,73]. 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 [74,75]. They know that group mates vary in their value as social partners, and they also attempt to repair valuable relationships when those are damaged [68,71,74,76–78]. Monkeys clearly remember outcomes of earlier encounters with particular conspecifics, and they modify their social behaviour on the basis of interaction histories [71,74,79,80]. Furthermore, they possess knowledge about both the social ranks of, and the social relationships among, their group mates [81–83], and they base their decision-making in social situations upon this knowledge. Since the early 1990s, we have found that spotted hyaenas share all these capabilities with cercopithecine primates.

Like monkeys, spotted hyaenas can recognize individual group mates using cues from multiple sensory modalities [84]. For example, they can identify individual conspecifics based on their long distance 'whoop' vocalization [85–90], and they use olfactory cues to discriminate sex, reproductive state, clan membership and familiarity of conspecifics [91–94]. As in monkeys, nepotism is common among spotted hyaenas, social bonds are stronger among kin than non-kin [95–97], and individuals direct affiliative behaviour most frequently towards kin [97–99]. Male hyaenas do not participate in parental care, but sires can nevertheless recognize their offspring and vice versa [100], as also occurs in monkeys [49]. Furthermore, hyaena littermates not only recognize one another as such, but can distinguish full- from half-siblings [99]. When deciding whether or not to join on-going fights, hyaenas support close kin most often, and the density of cooperation networks increases with genetic relatedness; nevertheless, as in primates, kinship fails to protect hyaenas from coalitionary attacks [101]. Based on both kinship and social rank, spotted hyaenas can recognize third-party relationships among their clan-mates [102]; these relationships involve interactions and relationships in which the observer is not directly involved [68]. For example, 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 [102].

As in monkeys, young hyaenas learn their positions in their clan's dominance hierarchy via a process of 'maternal rank inheritance' [103–106], and non-littermate hyaena siblings assume relative ranks that are inversely related to age in a primate-like pattern of 'youngest ascendency' [75,104,107]. In fact, hyaena cubs learn about rank relationships just as monkeys do [108]. Learning is a critical aspect of rank acquisition in spotted hyaenas, which clearly remember outcomes of earlier encounters with particular group mates. As in primates, coalitions play an important role in acquisition and maintenance of social rank in spotted hyaenas [104–106,109].

Like monkeys, spotted hyaenas recognize that their social partners vary in relative value to them, and based on this knowledge, they make adaptive choices regarding with which clan-mates to associate [97,110]. Males prefer to associate most closely and mate with the highest-ranking females, whose offspring survive far better than do offspring of low-ranked females [111], so this preference by males appears highly adaptive. Adult hyaenas of both sexes prefer to associate with non-kin holding ranks similar to their own [97]. Spotted hyaenas use unsolicited appeasement and greeting behaviours to reconcile their fights [98,112,113], as is also true in many primates [76]. Furthermore, patterns of non-conciliatory greeting behaviour in spotted hyaenas mimic primate patterns of social grooming in which individuals prefer to spend time with, and direct affiliative behaviour towards, high-ranking non-kin [98,114,115].

Like primates, spotted hyaenas make flexible decisions regarding whether to cooperate or compete with conspecifics, modifying their behaviour based on multiple types of information about their immediate social and ecological circumstances [101]. Furthermore, like chimpanzees, which also live in fission–fusion societies, spotted hyaenas are able to make flexible decisions regarding whether to engage in aggressive interactions with unfamiliar conspecifics [116]. That is, hyaenas decide whether to engage in interactions with strange conspecifics based on whether or not their current subgroup size is larger than that of their potential opponents; they engage only when they outnumber their opponents [85].

Thus, overall we find striking similarities in social cognition between spotted hyaenas and cercopithecine primates, as predicted by the social complexity hypothesis. Some social cognitive abilities exist in monkeys that we have not yet tested in hyaenas (e.g. whether hyaenas, like baboons, classify their clan-mates hierarchically based on multiple traits concurrently [117]), but to date the behaviour of our hyaena subjects has indicated that they can solve, without exception, all the social problems we have posed for them that monkeys can also solve.

3. Brain size and frontal cortex size in hyaenas and other carnivores

The social complexity hypothesis considered specifically in relation to nervous systems, dubbed 'the social brain hypothesis' [40,118,119], predicts that non-primates 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 compared with those of most non-primate mammals [120–122]. The mammalian brain comprises a number of functionally distinct systems, and natural selection acting on particular behavioural capacities may cause size changes selectively in the systems mediating those capacities [123]. Frontal cortex is known to mediate complex social behaviour in humans and other mammals [124,125]; the neocortex disproportionately covers the frontal area in primates [40], and social complexity is strongly correlated with neocortical volume [126]. Thus, social complexity in primates appears to be related broadly to greater brain volume and specifically to expansion of frontal cortex. In the light of all this, the social brain hypothesis predicts that we should find larger brains and greater frontal cortex volumes in gregarious carnivores than in closely related solitary species. We tested these predictions in mammalian carnivores using virtual brains generated with computed tomography (CT) in combination with cytoarchitectonic analysis [127].

Our first goal was to conduct accurate volumetric assessments of 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 comprise the extant Hyaenidae, span a wide spectrum of social complexity. The aardwolf is solitary except when breeding [128]. The striped hyaena is usually solitary, but females may rear their cubs at the same den as that used concurrently by female relatives [129], and striped hyaenas may be found with up to four conspecifics [130–132]. The brown hyaena lives in small clans that may contain up to 11 individuals [133]. Spotted hyaenas occur sympatrically with all three of these other species in Africa, but uniquely live in complex, hierarchically structured groups containing up to 130 individuals. The four hyaena species last shared a common ancestor approximately 11 Ma [134].

Because it is extremely difficult to find actual hyaena brains that have been properly preserved, we used CT analysis of skeletal material from adult members of the four extant hyaenid species collected in the wild (32 spotted hyaenas, eight brown hyaenas, 11 striped hyaenas and five aardwolves) [127,135] 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, including 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 [11,127,135,136].

We found that spotted hyaenas had much larger corrected brain volumes than did the other three species in the family Hyaenidae [135]; this is consistent with predictions of the social complexity hypothesis. However, the relative brain volumes of striped hyaenas, brown hyaenas and aardwolves did not differ significantly, a result that contradicts predictions of the social complexity hypothesis. We also found that frontal cortex volume relative to total brain volume in the spotted hyaena was significantly larger than those in the other three species, and that frontal cortex volume in aardwolves was significantly smaller than that in any other hyaenid species [135]. These results are consistent with the idea that expansion of frontal cortex is driven by social complexity, but they are also consistent with the foraging and cognitive buffer hypotheses. Spotted hyaenas actively hunt and kill antelope and many other types of living prey [137]; they also hunt both alone and in groups [138]. By contrast, both striped and brown hyaenas eat carrion, and aardwolves eat termites [139]. Furthermore, 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, as predicted by the cognitive buffer hypothesis. Spotted hyaenas must be able to find, and anticipate the behaviour of, large agile antelope to capture them, whereas neither termites nor carrion present the other members of the family Hyaenidae with comparably diverse or novel challenges. Enlarged brains should be adaptive in novel and unpredictable environments because they enable individuals to exhibit more flexible behaviour [63,64,140,141].

Although we found no sex difference in total endocranial volume (relative to skull length) in 23 female and 22 male adult spotted hyaenas, frontal cortex volume was significantly greater in males than females [136]. This sex difference cannot be explained by differential demands of foraging because male and female hyaenas are equally proficient at hunting vertebrate prey [138] and forage over similarly large areas [142,143]. However, the sex difference observed in frontal cortex 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 these things only in the natal clan [143]. 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 [124,125]. An interpretation of this sex difference based on the need for social acumen, or for adjustment to novel conditions, is consistent with results from cercopithecine primates, in which males also disperse while females are philopatric.

In an attempt to assess the relative contributions of social and multiple other variables to brain evolution in carnivores, we next expanded our CT-based analysis of whole brains and brain regions to a larger array of mammalian carnivores [58]. 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.

This 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 in this order of mammals. 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 [58]. We found no support for a role of social complexity in overall encephalization, which is consistent with results from earlier carnivore studies [144]. 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) familes, most of which are solitary, than in other extant families [58]; this finding is also consistent with those from earlier comparative analyses [145,146].

4. The problem of general intelligence

A major shortcoming of the social complexity hypothesis is its apparent inability to explain the common observation that species with high socio-cognitive abilities also excel in general intelligence [24,147]. There is, in fact, a longstanding 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 [24,148]. Although our own data strongly support the notion that social selection pressures can shape the evolution of social cognition in carnivores, it remains unclear 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 non-social problems. We were particularly interested to know whether the social complexity hypothesis or the cognitive buffer hypothesis [63,64] best predicts success when carnivores attempt to solve novel foraging problems.

We began by presenting wild spotted hyaenas with a simple extractive foraging problem, presentation of a wrought iron puzzle box baited with meat, and inquiring which aspects of performance in each individual's first trial predicted whether it would eventually be successful at extracting the bait from the box [149]. Subjects could potentially emit from 0 to 5 different behaviour patterns when they first interacted with the puzzle box. We found that those individuals exhibiting a greater diversity of initial exploratory behaviours were more successful problem solvers. We also found that neophobia reduced success at problem solving. 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 wild 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 colony at the University of California in Berkeley, 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 did wild hyaenas [150]. To date, we have also been able to test three striped hyaenas in captivity, but none of them have opened the box [33]. 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; this finding is consistent with both social complexity and cognitive buffer hypotheses. Our work with captive hyaenas next prompted us to conduct comparable tests of problem solving ability in a wider range of carnivore species.

To extend our findings from spotted hyaenas regarding measures that predict success at solving simple extractive foraging problems outside the social domain, we presented our puzzle boxes, scaled according to subject body size, to myriad carnivores housed in nine North American zoos [33]. Because we were testing animals that ranged in size approximately from 2 to 300 kg, we used small and large steel mesh boxes. We videotaped all trials and extracted performance measures from videotapes using methods described elsewhere [33,149,150]. We then brought together data on success and performance measures during zoo trials with data documenting total brain size [144], the relative volumes of different brain regions and average group size for each species tested [58], and used phylogenetic generalized least-squares regressions [151,152] to identify the variables predicting success or failure in solving this non-social problem (detailed methods are available in [33]).

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 at opening the box varied among families, with species in the bear family (Ursidae, 69.2% of trials), the raccoon family (Procyonidae, 53.8% of trials) and the weasel family (Mustelidae, 47% of trials) being most successful at opening the puzzle box, and those within the mongoose 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 [58]. Carnivore species with larger brain volumes relative to their overall body mass were significantly better than others at opening the puzzle box [33]. 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 [58], are remarkably like those obtained by MacLean *et al*. [32] in a comparative study of problem solving by a wide array of birds and mammals on two tasks requiring self-control, another important executive function in the general domain. 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 either success in problem solving or brain size in either primates or carnivores.

Our comparative data are inconsistent with the idea that general intelligence evolves as a by-product of selection for social dexterity. Furthermore, these data are only partially

consistent with the physical complexity and cultural intelligence hypotheses. However, our data do not appear to contradict in any way predictions of the cognitive buffer hypothesis [63,64], which suggests that exposure to new socio-ecological challenges or novel environments represents direct selection pressure favouring general intelligence and brain enlargement in carnivores. 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 [153–157]. 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 [140]. Furthermore, in both primates and birds, innovation rates are better correlated with brain size than are social variables such as group size [141,158–160]. Our zoo study offers important empirical support for the relationship in mammalian carnivores between relative brain size and their ability to solve novel technical problems.

5. Conclusion and future directions

Over 20 years of fieldwork on social cognition have revealed strong and consistent evidence that the abilities of spotted hyaenas in the domain of social cognition have evolved convergently with those in primates. However, to date the convergence we have demonstrated appears to be limited to social cognition, and does not appear to extend to other cognitive domains. Overall, although some lines of evidence from our work with hyaena brains appear consistent with the social brain hypothesis, others appear more consistent with competing hypotheses. Furthermore, research conducted by other investigators has identified various phenomena in carnivores for which the social brain and cultural intelligence hypotheses 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 by a corresponding increase in carnivore brain size, and this covariation occurs in solitary as well as gregarious carnivores [121].

In both primates [32] and carnivores [33], strong, phylogenetically corrected comparative data now show that brain size predicts ability to solve non-social problems, and that diet better predicts brain size in both taxa than does social complexity [32,58,144]. To date, we have found no support for the idea that general intelligence evolves as a by-product of selection for social agility. Instead our data on brain size support the idea that foraging demands shape intelligence, and our data on general problem solving are most consistent with the cognitive buffer hypothesis. It is relatively straightforward to quantify social complexity based on group size or numbers of differentiated relationships in which individual animals are involved [161]. Similarly it is possible to assign animal diets to at least crude categories of complexity (as in [58]). However, it is currently very challenging to quantify the novel socio-ecological challenges confronting different species or different populations of conspecifics.

Our current research focuses on testing specific predictions of the cognitive buffer hypothesis, focusing on the idea that general intelligence is favoured directly by natural selection to help animals cope with novel environments. General intelligence might be expected to have particularly strong effects on fitness in cities, which represent some of the most extreme novel environments confronted by animals today [162,163]. In cities, animals need to exploit new food resources, cope with new suites of predators and competitors, develop new navigation strategies and adjust their communication to cope with new noise [162,164,165]. Recent work consistent with the cognitive buffer hypothesis has suggested that urban animals might be better at problem solving than conspecifics inhabiting rural areas [166,167].

We are currently testing predictions of the cognitive buffer hypothesis in the context of urbanization by presenting a psychometric test battery, focusing on several elementary cognitive abilities, to adults in each of seven clans of wild spotted hyaenas occupying rural, urban and transitional habitats in Africa. We will not only compare performance on each specific task among clans and habitat types, but also adopt a psychometric factor-analytical approach that will permit statistical derivation of a general intelligence measure, g, for individuals within each population. This work should allow us to determine whether specific cognitive abilities correlate within groups, the extent to which g can describe overall variation in test performance, how performance on the test battery varies among clans and among habitat types, and the extent to which individual cognitive abilities and g are affected by exposure to novel urban environments. Exposing hyaenas in the three habitat types to the test battery will also permit assessment of the respective roles played by developmental plasticity and evolution *per se* in facilitating adaptation to city life. That is, availability of transitional study clans currently undergoing rapid urbanization should permit discrimination between developmental plasticity within the hyaenas' current reaction norm and evolutionary modification of their reaction norm.

The four hypotheses discussed in this paper suggesting functional explanations for the evolution of large brains and great intelligence are not mutually exclusive, and much of the work described above in fact suggests that multiple variables must surely shape the evolution of intelligence in mammalian carnivores and other animals. However, many important questions remain unanswered, particularly regarding the evolution of general rather than domain-specific modular intelligence. In addition to study of domain-specific cognitive abilities, like Thornton *et al.* [168] and Burkart *et al.* [14], we also encourage assessment of general intelligence. We recommend that other workers adopt psychometric approaches to assess general intelligence in animals, so that we can start to understand general intelligence in a broader comparative context. Finally, we urge those interested in the evolution of animal brains and intelligence to consider these phenomena in the light of recent discoveries in scientific computation germane to the evolution of both modular [169] and general intelligence [170]. Computer simulations of evolving organisms have revealed that modularity evolves in neural and other networks as a by-product of selection for minimizing connection costs among nodes [169]. However, general intelligence has proved more challenging to evolve *in silico* than domain-specific cognition.

Research in artificial intelligence has yet to produce agents that acquire many available skills in non-trivial environments; instead most current algorithms produce agents that specialize on only one or a few specific tasks. Stanton & Clune [170] have recently developed a new evolutionary algorithm yielding digital organisms that acquire as many skills as possible during their lifetime. We hope that the ability to evolve

such creatures *in silico* will open new pathways for assessment of hypotheses suggesting variables favouring enlargement of animal brains, and a broader understanding of the circumstances under which general intelligence evolves.

Ethics. This work was conducted under research permit no. NACOSTI/P/14/2154/1323, issued by the Kenyan National Council on Science, Technology and Innovation. All fieldwork with spotted hyaenas was approved by Michigan State University Institutional Animal Care and Use Committee (IACUC) under Approval 05/14-087-00, approved most recently on 29 April 2014. The zoo work was approved under Approval 03/08-037-00 and also the IACUCs at all nine zoos (St Louis Zoo, Bergen County Zoo, Binder Park Zoo, Potter Park Zoo, Columbus Zoo, The Living Desert, Wild Canid Survival and Research Center, Turtle Back Zoo, and Denver Zoo) where testing was done.

Authors' contributions. K.E.H. and S.B.-A. conducted the fieldwork described in this paper, and both drafted the manuscript. Both authors gave final approval for publication.

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