Chapter 5
The Evolution of Brains and Cognitive Abilities

Christopher Mitchell

Abstract Humans place great significance in intellectual abilities, and because of this, biologists have been interested in the cognitive abilities of animals since Aristotle. The difficulties in defining intelligence in a way that can be applied to taxonomically distant animals have resulted in most studies using relative brain size as a directly measurable metric of intelligence. This approach has received criticism but persists in the literature as it has proved to be informative despite imperfections. Large brain size and, by inference, arguably complex cognition have evolved independently in several lineages including primates, corvids, cetaceans, cephalopods and hymenopteran insects. In these varying taxa, the evolutionary history of intelligence is still hotly debated. Proponents of the social intelligence hypothesis suggest that the cognitive challenges of group living have driven the evolution of large brains whereas other researchers have suggested ecological drivers such as seasonal challenges, dietary differences and energetic constraints. Here I review the study of the evolution of intelligence with particular focus on the widely cited social intelligence hypothesis and cognitive buffering hypothesis. I begin by summarising the study of animal intelligence and the methods employed. I will then go on to briefly review the current state of knowledge concerning cognitive evolution in some of the most heavily studied taxa. Finally, I will summarise and evaluate the social intelligence hypothesis and the cognitive buffering hypothesis. I propose that the weight of evidence suggests that social intelligence is limited to relatively few taxa, such as primates and cetaceans, and that across other taxa, a variety of other factors have driven the evolution of advanced intelligence in animals.

C. Mitchell (✉)
Institute of Integrative Biology, Biosciences Building, University of Liverpool,
Crown Street, Liverpool L69 7ZB, UK
e-mail: cmitch@liv.ac.uk

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5.1 Defining and Studying Intelligence in Animals

Intelligence is defined in humans as an individual's performance on a variety of cognitive tasks, often compiled into a metric such as the intelligence quotient (IQ). Researchers investigating animal intelligence are addressing a slightly different phenomenon than IQ by trying to assess species typical intelligence. Most definitions of intelligence employed in the study of animals are similar in that they emphasise the importance of behavioural flexibility and problem-solving abilities (Reviewed in Roth 2015). Dicke and Roth (2016) define intelligence as "the ability of an organism to solve problems occurring in its natural and social environment, culminating in the appearance of novel solutions that are not part of the animal's normal repertoire". This definition has the advantage that intellectual abilities of animals will be observable in the wild and, if tests can be designed that can be applied to a wide variety of species, testable under laboratory conditions.

In order to study intelligence in animals comparatively, a metric that can be applied across taxa is necessary. The most obvious and easily measurable potential index of intelligence is brain size. Absolute brain size is broadly considered not to be a reliable indicator of cognitive ability as most of the variation in brain mass can be attributed to variation in body mass. However, a recent study in which over 500 individuals from 36 species ranging from pigeons to chimpanzees were tested on problem-solving tasks that required self-control showed that absolute brain size is the best predictor of performance on the tasks (MacLean et al. 2014) raising the possibility that absolute brain size may be informative. The majority of researchers prefer to consider measures of brain size independent of body size and thus attempt to control for the confounding effect of body size on brain size statistically. The vast majority of studies on brain size and intelligence use either encephalization quotient (EQ) or relative brain size. EQ uses the allometric relationship between body size and brain size to derive a relative measure of brain size (Jerison 1973). EQ relies on accurately determining the nature of the allometric relationship between brain and body size. Studies of mammals have variously placed the exponent of this relationship (the slope of the line on a log–log plot of body mass and brain mass) at 0.67 and 0.75 (Boddy et al. 2012). Variation in the scaling relationship between body and brain size between groups can be problematic. In a study of cetacean brain size, Manger (2006) used the scaling parameter of all mammals to calculate EQs for cetaceans. In fact, cetacean brain mass scales quite differently to terrestrial mammals, having a scaling parameter of 0.376 (Manger 2006), possibly due to their aquatic lifestyles (Marino 1998). Improper use of EQs in this manner can drastically alter the results of subsequent statistical analysis as was pointed out in this case by Marino et al. (2008) who advocate the use of relative brain size instead.

Using relative brain size is a slightly different methodology. Relative brain size takes account of the correlation between brain and body size in statistical models and allows researchers to identify any effects down to variation in brain size, independent of body size. There is a vast literature using relative brain size as indicative of intelligence (Reviewed in Healy and Rowe 2007), but this is not without criticisms. Studying brain size as a metric of cognition assumes that any increase in size results in an increase in function or complexity and increases in relative size of specific brain regions may not be detectable by changes in whole brain size (Healy and Rowe 2007).

Some authors prefer to emphasise behavioural flexibility and thus use reported incidences of cognitively advanced behaviours as a quantitative measure of intelligence (Ducatez et al. 2015; Lefebvre et al. 2004; Reader and Laland 2002). For primates and birds, the behavioural ecology literature contains many examples of innovative behaviour because both groups are well studied and researchers are inclined to report their observations. As a result, primate intelligence has been studied using the reported incidences of innovation, tool use, social learning, extractive foraging and tactical deception (Reader et al. 2011; Reader and Laland 2002; Byrne and Corp 2004), and bird intelligence has been studied using foraging and technical innovations (Ducatez et al. 2015; Overington et al. 2009). Similar observations of apparently cognitively complex behaviours from other groups are sparse. In cetaceans for example, there are numerous behavioural observations of a small number of well-studied species but not enough to allow large-scale comparative analysis. This approach focuses on behaviour and, in doing so, addresses some of the concerns of Healy and Rowe (2007). Most significantly, this approach attempts to study intelligence directly by using complex behaviour as a direct consequence of cognitive complexity and therefore circumvents issues concerning the use of indirect measures such as brain size. Nevertheless, using reports of complex behaviours may be biased towards well-studied species, potentially overestimating the complexity of species such as chimpanzees and bottlenose dolphins which are heavily studied for their behavioural repertoires. In such cases, it may be appropriate to correct for research effort in much the same way as brain size is corrected for body size (Reader and Laland 2002).

5.2 Intelligent Animals

Non-human primates have attracted the most attention in the study of animal intelligence due to their close relation to humans and their relatively large brains compared to other mammals. Primates are known for their capacity for cultural transmission (Yamamoto et al. 2013), tool use (Ottoni and Izar 2008; Boesch and Boesch 1990), behavioural innovation (Reader and Laland 2002), tactical deception (Byrne and Corp 2004) and potentially theory of mind (the ability to attribute mental states to others) (Tomasello et al. 2003). The complexity of the behavioural repertoire of primates correlates well with relative brain size, and this has been used to argue in favour of a general intelligence (Reader et al. 2011).

Amongst birds, two lineages are held up as possessing cognitive abilities comparable to those observed in primates. Corvids (crows, jays and magpies) have been described by researchers as “feathered apes” because of striking similarities in the cognitive abilities of some corvids and those of the great apes (Emery 2006).

Parrots are often held up alongside corvids as extremely intelligent birds and are famous for prodigious vocal learning capacities (Emery 2006). Corvids have been shown to make and use tools (Weir et al. 2002), possess precursors of theory of mind (Bugnyar 2011) and exhibit analogical reasoning (Smirnova et al. 2015) and casual reasoning (Taylor et al. 2010). Scrub-jays use cognitively complex strategies to protect their caches from thieves (Emery et al. 2004), and some have argued that crows and parrots can solve problems by insight (Pepperberg 2004; Bird and Emery 2009). The similar levels of cognitive complexity of corvids, parrots and primates have been attributed to convergent evolution (Emery and Clayton 2004).

Cetaceans (whales, dolphins and porpoises) possess some of the largest brains of any animal. Despite the common perception that cetaceans are some of the most intelligent non-human animals, researchers are in fact deeply divided on the question of cetacean intelligence. Bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*) in particular are thought to be highly intelligent based on numerous observations in captivity and in the wild of apparently complex behaviours such as male–male alliances similar to those of chimpanzees (Connor 2007), tool use (Krutzen et al. 2014; Smolker et al. 1997) and communication of identity information analogous to names (Janik et al. 2006). Conversely, some authors assert that despite their relatively large brains, claims of advanced cognition in cetacea are overstated (Manger 2013). Roth (2015) describes experiments on dolphin cognition as generating “mixed and often disappointing results” whereas Manger (2013) asserts that the evidence in favour of complex cetacean cognition becomes considerably less impressive when placed within a broader comparative framework as many of the reputedly complex behaviours occur throughout vertebrates and often invertebrates as well. Such critics generate strong responses from cetacean researchers (Marino et al. 2007, 2008) who argue that the weight of evidence in favour of complex cognitive abilities in cetaceans is convincing. Controversy over the intellectual status of cetaceans remains unresolved.

Carnivora, a mammalian order containing approximately 300 terrestrial species and around 30 aquatic species (known as pinnipeds), have been quite well studied, and as a result, data on brain size are available for most species. As a whole, the behavioural repertoires of wild carnivorans have not been assessed in a similar manner to primates or birds, making inferences concerning their behavioural complexity difficult. However, a recent study of captive carnivores has shown that relative brain size reliably predicts the ability of a carnivoran to solve a novel problem (Benson-Amram et al. 2016). This would seem to indicate that relative brain size is a reliable metric of cognitive ability.

The cephalopods (octopuses, cuttlefish, squid and nautiluses) have remarkably large and complex brains, especially octopuses which possess the largest, most complex brain of any invertebrate (Roth 2015). Octopuses have demonstrated abilities such as spatial learning and memory (Boal et al. 2000), observational learning (Fiorito and Scotto 1992) and potentially tool use (Finn et al. 2009).

Rarely considered in studies of intelligence, insects are often thought of as cognitively very simple. However, the neural architecture of insects is relatively well known, and in particular, the structure known as the mushroom body (*corpora* *pedunculata*) has been of particular interest. The mushroom body has been shown to play a major role in many of the behavioural markers of complex cognition including associative learning in *Drosophila* (McGuire et al. 2001), spatial memory in cockroaches (Mizunami et al. 1998) and selective attention in *Drosophila* (Xi et al. 2008). Special attention has been given to the apparently structurally complex mushroom bodies of the hymenoptera which are argued to be the seat of complex cognitive behaviours such as spatial orientation and social behaviour (Roth 2015).

5.3 The Evolution of Brains and Cognition

Hypotheses purporting to explain variation in brain size, and hence cognitive complexity, are numerous and have been the subject of much debate in the literature. These competing hypotheses mostly fall into two schools of thought. Ecological theories propose a direct link between cognitive ability and environmental challenges, supposing that given features of the environment favour increased cognitive abilities to deal with the cognitive challenges posed. By contrast, social theories propose that living in large or complex social groups presents cognitive challenges and so selection pressures that favour grouping will also result in increases in cognitive ability. The social and ecological schools of thought differ on one key point. The crux of this debate is which selection pressure is directly responsible for evolutionary increases in cognitive ability.

5.3.1 The Social Intelligence Hypothesis

The most broadly cited hypothesis for the evolution of large brains is the social intelligence hypothesis, which posits that large brains and intelligence are an adaptation to social living (Humphrey 1976). Living as a group provides numerous benefits to animals. Living in a social group is also thought to present a variety of cognitive challenges such as navigating a hierarchy, keeping track of interactions and cooperative behaviour patterns (Dunbar 1998). The social intelligence hypothesis states that these problems are solved or managed by having a larger brain and more advanced cognitive abilities to allow animals to cope with increased competition for food and matings.

The social intelligence hypothesis was initially developed as an explanation for large brains in primates, many of which live in large complex groups. Social group size is limited in primates by the relative size of the neocortex which is thought to be the part of the brain most involved with complex cognition (Dunbar 1992; Kudo and Dunbar 2001). These primate findings have formed the basis of much of the research into the social intelligence hypothesis. However, similar relationships have not been found to be widespread in animals.

Amongst fishes, cichlids have been shown to exhibit cooperative hunting behaviour and other potentially complex social behaviours (Bshary et al. 2002; Roth 2015). In some cases, these behaviours show some resemblance to primates, particularly observations of social learning and traditions in a variety of species (Bshary et al. 2002). Social group size has been linked to brain size in the cichlid species of Lake Tanganyika (Pollen et al. 2007) supporting the social intelligence hypothesis. Some studies of brain size in cartilaginous fish have found larger, more complex brain structures in social species such as carcharhinid and sphyrnid sharks (Yopak et al. 2007).

Studies of carnivores have shown that the social African lion (*Panthera leo*) exhibits sex-specific differences in neocortex size that are absent in the solitary cougar (*Puma concolor*) suggesting a link between sociality and brain organisation (Arsznov and Sakai 2012). In support of the social brain hypothesis, Perez-Barberia et al. (2007) argued for a tight coevolutionary relationship between sociality and relative brain size in carnivorans. However, detailed reconstructions of living and extinct lineages of carnivorans reveal no relationship between sociality and brain size throughout the history of Carnivora (Finarelli and Flynn 2009). In fact, Finarelli and Flynn (2009) determined that the relationship between sociality and brain size in carnivores is limited to the Canidae family and removal of this lineage from their analysis invalidates the claims of Perez-Barbeira et al. (2007). Furthermore, studies of hyaenas have shown that the predictions of the social brain hypothesis (that social species will have larger relative brain sizes) do not apply (Holekamp et al. 2015). Even the highly social spotted hyaena (*Crocuta crocuta*), which has a social system comparable to cercopithecine primates such as baboons, relies much more on relatively simple forms of social learning such as facilitation than primates, seemingly indicating a relatively simple degree of social intelligence (Holekamp et al. 2007). Across Carnivora, relatively large brains are also found in mustelids (weasels, martens, badgers and otters), some of the smaller cats and bears, which all share predominantly solitary lifestyles (Finarelli and Flynn 2009).

It is important to note that the social intelligence hypothesis is not directly concerned with group size but rather with the complexity of social living. The complexity of primate groups is a subject of significant study with considerable variety throughout the clade (Kasper and Voelkl 2009), and the underlying assumption that larger social group sizes imply a more complex social lifestyle has been questioned (Bergman and Beehner 2015). Some efforts have been made to study social network dynamics, and the results are less clear. Lehmann and Dunbar (2009) used network cohesion and found that in primates with larger neocortex ratios, females tend to live in fragmented, smaller grooming clans. To counter this, Lehmann and Dunbar (2009) suggest that the complexities of living within highly fragmented social systems, also known as fission–fusion groups, and maintaining social cohesion drove the evolution of advanced intelligence of primates.

The assumption that larger social groups are more complex seems to hold within primates but not necessarily when we consider other lineages such as ungulates and birds which occasionally gather in herds or flocks numbering in the thousands or more. These very large groups are not always complex as individuals will typically not engage in complex interactions. In birds, group size shows no relationship to forebrain size (Beauchamp and Fernandez-Juricic 2004). Emery and colleagues (2007) note that birds with long-term pair bonds tend to have the largest brains, possibly supporting the social brain hypothesis. This combined with the observation that bird flocks are much less stable than primate groups suggests that it is the cognitive challenges of forming and maintaining long-term bonds that drove the evolution of cognitive abilities in birds. However, other factors influencing intelligence have also been identified including ecological generalism (Overington et al. 2011) and a resident lifestyle as opposed to migratory (Sol et al. 2005).

A wealth of comparative analyses of brain evolution in bats has revealed a complex picture. One such analysis demonstrated that monogamous bat species have the largest brains with polygynous species also having relatively large brains, but promiscuous species have relatively small brains (Pitnick et al. 2006). Similar results in birds have been used to argue in favour of the social intelligence hypothesis (Shultz and Dunbar 2010), but Pitnick et al. (2006) suggest that mate fidelity in bats and high relative brain size are both the product of an evolutionary trade-off between brain size and testes size and thus the correlation between brain size and mating system is a by-product of sexual selection. This scenario presents a possible confounding factor in the study of sociality and brain size and casts doubt on some interpretations of links between mating system and brain size. There is some debate concerning these results as Shultz and Dunbar (2007) assert that in fact, the mating system–brain size relationship is a direct causal relationship and that the correlation between brain size and testes size is a by-product of both traits being closely related to mating size. Similarly, equivocal evidence comes from ungulates where gregarious species have been shown to have larger brains (Perez-Barberia and Gordon 2005), but other studies have shown that brain size can be predicted by both mating system and ecological factors such as habitat use (Shultz and Dunbar 2006).

Observations of behavioural complexity in hymenopterans (bees, ants and wasps) (Roth 2015) could be assumed to support the social brain hypothesis. However, Farris and Schulmeister (2011) tested the social brain hypothesis in hymenopterans and found that a parasitoid life history rather than a social life history is associated with large, complex mushroom bodies. This leads to their interpretation that the cognitive demands of locating a host drove the enlargement of the mushroom body in this lineage, possibly serving as a pre-adaptation for the subsequent evolution of social living (Farris and Schulmeister 2011).

An extension of the social intelligence hypothesis is the cultural intelligence hypothesis (van Schaik and Burkart 2011). Under this hypothesis, the selective advantages of social learning, such as the rapid spread of novel solutions between individuals, drive increases in behavioural flexibility and general cognitive ability. Thus, non-social cognitive skills such as tool use could be a consequence of general increases in intellectual abilities brought about by social living, particularly the social learning aspect of group living which is the underlying mechanism of culture. Evidence in favour of this hypothesis comes from Reader and colleagues (2011) who used observations of primates reported in the literature and identified a general intelligence factor with social, ecological and technical intelligence very closely correlated.

The observation that primate intelligence is not modular but instead contains a mix of social and technical skills has also been advanced as evidence against the social brain hypothesis. Based on strong correlations between cerebellum size and extractive foraging and tool use but not group size, Barton (2012) proposes the embodied cognition theory of primate brain evolution. This hypothesis proposes that ecological pressures drove the evolution of complex technical skills in parallel to the established idea that social factors drove evolution of social cognition in the neocortex. However, under this evolutionary scenario, we might expect a degree of modularity in primate cognition with the pre-frontal cortex as the seat of social cognition and the cerebellum as the principal component of technical cognition. This seems to be contradicted by Reader's (2011) general intelligence factor which is closely correlated to the neocortex ratio and includes both extractive foraging and tool use. In fact, the cerebellum has been linked to nest complexity in birds (Hall et al. 2013), and within mammals, the largest cerebellums relative to body size belong to elephants and odontocetes (Maseko et al. 2012) which are thought to be amongst the most intelligent mammals behind some primates. Furthermore, in humans and other great apes, the cerebellum contains four times the neurons of the neocortex and has expanded considerably more rapidly than the neocortex in the evolution of the ape lineage (Barton and Venditti 2014). These observations challenge an exclusively social interpretation of primate cognition.

5.3.2 Ecological Drivers of the Evolution of Intelligence

Ecological explanations for large brains and complex cognition are varied and have attributed observed patterns of variation in brain size to many factors. The expensive tissue hypothesis states that brain tissue is metabolically very expensive to maintain and evolutionary changes in diet must occur to allow the expansion of the brain (Aiello and Wheeler 1995). Studies of diet in primates and small mammals have found that folivores have smaller brains than generalists (Harvey et al. 1980), but further work showed that dietary quality, an index calculated from the relative components of each species' diet, does not account for variation in relative brain size in platyrrhine primates (Allen and Kay 2012). Furthermore, brain size in phytophagous bats is larger than in animalivorous bats (Eisenberg and Wilson 1978) which goes against the expectation that high-energy diets are needed to support large brains (Harvey et al. 1980). The larger brains of phytophagous bats have been argued to be the result of the complexity of the foraging habitat in which for bats foraging in dense vegetation provides much greater sensory challenges (Safi and Dechmann 2005). These findings would suggest a strong influence of ecology on the evolution of brain size in bats. Thus, despite the intuitive appeal of the expensive tissue hypothesis, diet alone is insufficient to explain the variation in brain size.

Melin and colleagues (2014) provide evidence in favour of the hypothesis that seasonality in foraging demands, specifically the seasonal dependence on extractive foraging which requires accessing food embedded within a substrate which may require tool use or planning of behaviour, has been selected for increased "sensorimotor" intelligence in primates. Strong seasonal fluctuations in food abundance require the ability to respond flexibly and thus are argued to explain the observed instances of tool use and innovative problem-solving in primates.

In cetacea, it has been suggested that the relatively large brains of odontocetes (toothed whales) are closely related to their sensory ecology (Jerison 1986). All extant odontocete cetaceans echolocate, as did all known fossil odontocetes but mysticete whales (baleen whales), and other aquatic mammals such as pinnipeds (seals and walruses), do not. The processing demands of echolocation could be argued to explain the high degree of encephalization observed in odontocetes compared to mysticetes. However, it has been pointed out that other echolocating animals such as bats are not highly encephalized (Marino 2007) and therefore echolocation by itself does not explain the large brains of some cetaceans. Another hypothesis proposes that living in cold water has driven the evolution of large brains in cetaceans and large brains in these species have no relation to cognitive abilities at all (Manger 2006). The so-called thermogenesis hypothesis states that the thermal challenges of living in cold waters can in part be solved by expanding the proportion of thermogenic glial cells in the brain and thus generating more heat from the brain without necessarily increasing cognitive function. This hypothesis has been heavily criticised for the dismissal of cetacean species as not exhibiting advanced cognition despite behavioural observations to the contrary (Marino et al. 2008) although these observations are themselves the subject of considerable debate (Manger 2013).

A more general hypothesis is the cognitive buffering hypothesis, which proposes that having a large brain gives an organism the ability to respond flexibly in the face of novel, unpredictable challenges posed by the environment (Sol 2009). At first glance, the cognitive buffer hypothesis may appear to be a very broad hypothesis applicable to almost any animal with a large brain in almost any situation. In fact, the hypothesis makes a clear, testable prediction. The key prediction of this hypothesis is that advanced cognitive abilities have significant survival value and this has been shown in birds where the behavioural flexibility of a species predicts the success of invasion (Sol and Lefebvre 2000). Further support for this idea comes from the fact that large-brained animals have greater longevity (Gonzalez-Lagos et al. 2010). When presented with a model predator, female guppies (*Poecilia reticulata*) with large brains evaluate the risk and habituate faster than those with small brains (Bijl et al. 2015), suggesting that a general cognitive ability is an important factor in anti-predator behavioural responses. Evidence in support of the cognitive buffer hypothesis can even be found in primates, famed for their social intelligence. A study of catarrhine primates showed that species with large relative brain sizes experienced less seasonality in their dietary intake than species in similarly seasonal habitats with smaller brains, suggesting that cognitive buffering allowed these primates to adjust to changing food availability and maintain their energetic intake (van Woerden et al. 2012).

In marsupial mammals, analysis of brain sizes across the group revealed that species living in the relatively aseasonal environment of New Guinea have larger brains (Weisbecker et al. 2015). The reduced nutritional pressure on these animals is thought to be a factor allowing the development of large brains. The correlation between brain size and litter size in marsupials (Weisbecker and Goswami 2010) is also taken into account in hypotheses of marsupial brain evolution and leads researchers to conclude that marsupials living in environments with reliable food sources invest more in lactation which allows the brains of the young to grow larger. Crucially, no evidence has been found for any behavioural driving force for the evolution of large brains in marsupials (Weisbecker et al. 2015). This stands in stark contrast to the social brain hypothesis and other hypotheses that propose that the challenges of certain lifestyles (social living, unpredictable environments, etc.) drive the evolution of advanced cognitive abilities to deal with such challenges. Instead, in conditions that allowed large brains to grow, animals that grew large brains, and by inference developed greater intelligence/behavioural flexibility, had a fitness advantage. Weisbecker et al. (2015) interpret this as support for the cognitive buffer hypothesis as the general framework for brain evolution in mammals, contradicting claims that the social intelligence hypothesis should be considered as a general hypothesis for mammals (and birds) (Dunbar 2009).

5.4 Conclusion

Studying animal cognition is a difficult task. The consensus of many studies is that despite well-known problems and pitfalls, variation in relative brain size does predict performance on cognitive tasks. Therefore, considerable gains in knowledge can be attained from studying brain size. However, it should be noted that taking relative brain size as a measure of cognitive ability is clearly a flawed approach as whole brain size will also correlate with sensory processing abilities and other non-cognitive tasks. This leads to the conclusion that component parts of the brain may be a more promising avenue of research. This approach has been used very successfully in some groups but can make comparisons between distantly related groups difficult, especially when analogous brain structures may be difficult to identify.

The evidence suggesting that brain size and sociality are causally related, once considered strong and taxonomically widespread, appears to have been weakened by recent research. Although sociality has been strongly linked to cognition in primates and perhaps cetaceans, across mammals, there is only weak support for the social intelligence hypothesis. Uncertainty around the interpretations of different lines of evidence could be resolved by using a reliable measure of social complexity that can be generalised across species such as the number of relationships in a social network. Nevertheless, studies in carnivores, marsupials, bats and social insects have failed to support the social intelligence hypothesis, suggesting that the relationship between group living and cognition may be limited to certain clades.

The cognitive buffering hypothesis provides a good paradigm in which to consider the evolution of intelligence. Under this paradigm, if there is a survival advantage to having a large brain and complex cognitive abilities, then we will observe greater survival, longevity, invasion success and adaptation to shifting climates in large-brained species. Some studies of birds and mammals have found such patterns as reviewed here and elsewhere. Although the cognitive buffering hypothesis gives an excellent description of how we expect large brains to evolve in circumstances where there are survival advantages, it does not propose a specific factor that may drive the evolution of large brains. This feature of the cognitive buffer hypothesis leaves open the possibility that different factors may have favoured the evolution of advanced cognitive abilities in different lineages. Therefore, the cognitive buffering hypothesis does not stand directly opposed to the social brain hypothesis. Rather, it provides a framework that can be applied across animals to understand the multiple convergent evolutions of large brains and intelligence.

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