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Review

# The economics of brain size evolution in vertebrates

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## SUMMARY

**Across the animal kingdom, we see remarkable variation in brain size. This variation has even increased over evolutionary time. Traditionally, studies aiming to explain brain size evolution have looked at the fitness benefits of increased brain size in relation to its increased cognitive performance in the social and/or ecological domain. However, brains are among the most energetically expensive tissues in the body and also require an uninterrupted energy supply. If not compensated, these energetic demands inevitably lead to a reduction in energy allocation to other vital functions. In this review, we summarize how an increasing number of studies show that to fully comprehend brain size evolution and the large variation in brain size across lineages, it is important to look at the economics of brains, including the different pathways through which the high energetic costs of brains can be offset. We further show how numerous studies converge on the conclusion that cognitive abilities can only drive brain size evolution in vertebrate lineages where they result in an improved energy balance through favourable ecological preconditions. Cognitive benefits that do not directly improve the organism's energy balance can only be selectively favoured when they produce such large improvements in reproduction or survival that they outweigh the negative energetic effects of the large brain.**

## Introduction

Organisms cannot afford to be in negative energy balance for long and are therefore expected to avoid unnecessary caloric expense. Following the principle of energy conservation, each trait or body function inevitably requires a certain number of calories for its maintenance[1]. Each individual's ability to acquire these calories is limited, at least most of the time, and storing energy brings its own challenges. Therefore, to understand the fitness effects of adaptive traits, we must also consider their energetic costs and benefits. Understanding the interplay of costs and benefits is especially relevant when investigating brain size evolution because few tissues use as much energy per unit weight as brain tissue[2–4]. Yet, there is a remarkable amount of variation in brain size across species[5]. A longstanding question therefore is how brains could often evolve to be so large and manage to get even larger over evolutionary time: more recently evolved lineages tend to have larger brains than the ones from which they emerged, and within lineages new species tend to have larger brains as well[5,6] (Figure 1). This question is especially pressing given that our own species has, in terms of cortical neuron numbers and relative to body size, the largest brains[7].

Brain size is closely linked to cognition and there is substantial evidence that brain size can be used as a proxy for intelligence (i.e., cognitive performance) across species[8,9]. Advanced cognitive performance underpinned by large brains is suggested to increase the ability of individuals to utilize the resources in their habitat more efficiently and exploit new ones. To mention a few examples, relative to species with smaller brains, bigger-brained and thus more intelligent vertebrate species live in larger or more complex habitats, supposedly due to improved spatial memory[10–13], are better at gaining continuous access to difficult-to-extract but nutrient-rich food resources by using more sophisticated foraging techniques[14,15], are relatively more successful in colonising new areas, perhaps due to greater behavioural flexibility[16–19], and experience lower mortality rates, presumably because of better predator and parasite avoidance[20]. Furthermore, more encephalised species tend to live in larger groups, likely because they may deal better with competition and cooperation by monitoring and remembering social relationships and anticipating the actions of others[21].

These cognitive benefits of larger brains are the main focus of the majority of studies on brain size evolution[10,14,15,22–25]. However, these benefits explain only a part of the variation we see in brain size across lineages, even if variation in body size and neuron densities is taken into account[26]. For instance, group-living lemurs experience similar social challenges to monkeys but are clearly smaller brained[27]. Across carnivore species, brain size does not correlate with the cognitive demands of the foraging niche[13]. And larger-brained lizard and snake species do not inhabit more complex habitats than smaller-brained ones[28]. These are only a few of a long list of discrepancies that suggest that our understanding of brain size variation is incomplete if we just focus on the cognitive benefits of large brains.

Therefore, over the past few decades, the high energetic costs of brains have become the topic of an increasing number of studies[3,29–35]. Universally across all vertebrates, brain tissue is

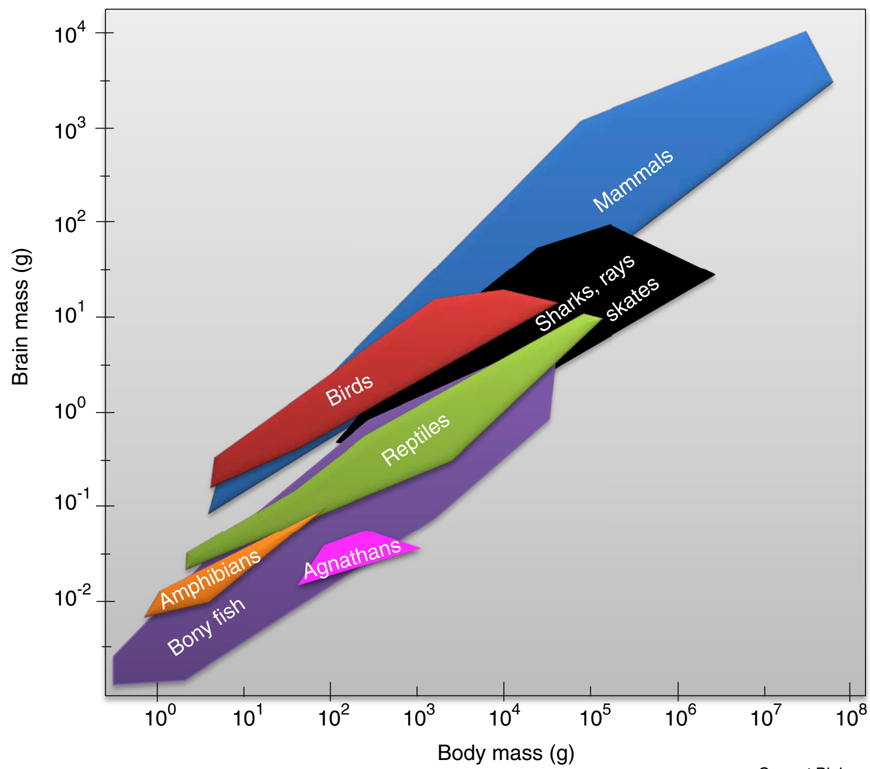


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**Figure 1. Vertebrate species show considerable brain size variation.**
Brain size variation across the main vertebrate groups in relation to their body mass (modified from[5]).

among the most energetically expensive tissues in the body[3]. For instance, the brain of an adult human at rest is responsible for about 20–25% of the body's total daily energy expenditure but makes up only 2% of the body's weight[36,37]. In other words, the human brain uses 10 times the energy predicted by its weight alone. The exceptionally high energy demand of brains is linked to the high energy costs of electrical signalling processes, of which synaptic transmission uses the largest proportion of energy[38]. The need to keep the brain supplied with a constant stream of energy requires that its needs are prioritized over those of other organs[2,39]. These high energy costs are exacerbated during brain development: per unit weight, immatures devote even more energy to nourishing their brains than adults, sometimes over 50% of their total energy intake[2,4,40]. Inevitably, these high costs mean that brain development competes with that of somatic and reproductive functions, which ultimately slows down overall development, resulting in a later onset of reproduction.

Despite a surge of interest, studies on the costs of brains and their consequences are still underrepresented. Increased brain size in response to any cognitive benefit can only evolve in lineages where its positive fitness effects due to various cognitive benefits outweigh the negative fitness effects of the increase in energetic costs and reduction in reproductive lifespan due to slower development[26,41]. The same potential cognitive benefit may therefore lead to an increase in relative brain size in some lineages but not in others. In lineages where the costs of sustaining a large brain are exorbitant such as in fast-flying bats, these high costs may even result in an evolutionary decrease in brain size[6,35]. Differences in the ability to offset these costs may therefore account for the part of the variation in brain size across vertebrate species that cannot be explained by benefits[5] (Figure 1). Consequently, merely studying the evolution of a trait by focusing on its adaptive benefits may not lead to a comprehensive understanding of brain size evolution.

In this review, we provide an overview of how the costs and benefits of brains help to explain brain size variation across vertebrates. We show how studies on a large variety of different lineages, conducted by many different researchers, lead to the strikingly coherent conclusion that cognitive abilities could only become prominent in vertebrate lineages where the evolution of large brains was enabled by favourable ecological preconditions.

## Paying for larger brains

Brain size varies considerably among vertebrate species even after statistically controlling for body size correlations[5]. Given the ubiquitous benefits of having a large brain, the *Expensive Brain Hypothesis* postulates that each animal species would benefit from a brain that is as large as possible, subject to the strong constraint that the required energy is constantly available[29] (see Table 1 for a list and description of hypotheses). Therefore, from a given ancestral state there are two complementary pathways towards increased encephalisation (Figure 2). First, a stable increase in energy input makes more energy available to the organism and so allows selection to favour an increase in brain size. Second, at constant energy inputs, selection favours a redirection of energy allocation away from other bodily functions to the brain.

### *Increasing and stabilizing net energetic input*

The first evolutionary pathway towards a larger brain is a permanent increase in net energy intake. Among the evidence for this pathway is the positive correlation between brain size and basal metabolic rate (BMR) found across mammals and especially primates[42]. BMR is often used as an index of daily energy expenditure[43]. This idea is also consistent with the finding that humans, which are arguably the most encephalized species, spend up to 800 kcal more per day than our closest relatives, the chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*) and orang-utans (*Pongo* spp.)[44]. This increased energy expenditure in large-brained species is accompanied by higher energetic demands. A higher energy input can be achieved by a change of diet toward food items with higher caloric value or food whose energy can be drawn more easily, i.e., that is easier to digest[45]. Fruits, insects, and meat are higher-quality food types relative to grass or leaves. Accordingly, numerous large-scale comparative studies across primates[10,31,46–48], bats[49], rodents[50], insectivores[50] and lagomorphs [50] found that frugivorous

**Table 1. Hypotheses used to explain the evolution of large brains.**

| Hypothesis | Definition | References |
|---|---|---|
| Expensive Brain Hypothesis | The energetic costs of an evolutionary increase in brain size must be met by any combination of increased total energy turnover or reduced energy allocation to other expensive functions such as body maintenance or production (growth and reproduction). | [29] |
| Expensive Tissue Hypothesis | The evolution of a larger brain was made possible by a diet-related reduction in the size of the digestive tract. | [69] |
| Maternal Energy Hypothesis | The total amount of maternal energetic investment during development constrains the offspring's brain size and thus ultimately also the species' brain size. | [99,100] |
| Ecological Brain Hypothesis | Solving essential ecological problems, such as finding or extracting hidden food sources or moving efficiently through complex habitats or large home ranges, requires higher levels of cognition and ultimately drove the evolution of enlarged brains. | [12,87,88,130,131] |
| Cognitive Buffer Hypothesis | Larger brains provide the cognitive abilities that allow for increased behavioural flexibility to buffer the effects of habitat seasonality. | [86–88] |
| Social Brain Hypothesis | Larger brains evolved in response to the cognitive demands of living in large, stable and thus complex societies and/or intense forms of pair-bonding. | [21,144,175] |
| Cultural Intelligence Hypothesis | Selection on social learning abilities over evolutionary time improves individual learning ability. Species with more opportunities for social learning may therefore evolve to become more intelligent, reflected by larger brain size. | [162,176,177] |

and faunivorous species have on average larger brains than grazers or browsers, even when controlling for possible confounding factors such as body mass.

But an evolutionary increase in brain size does not simply require higher caloric input to the brain; the higher supply of energy also needs to be constantly available. Temporary disruption of the energy supply to brain synapses leads to brain damage, and thus potentially catastrophic loss of cognitive performance[38,39]. In periods of starvation, brain energy requirements are partly covered by metabolising fat[51]. Thus, fat deposits can help to buffer against short-term seasonal or unpredictable lean periods[52], but their ability to fill the energy gap is limited for two reasons. First, fat is metabolically less efficient because the detour through fat metabolism increases the average amount of energy intake needed per day[53]. In addition, metabolizing fat ketones can only provide around 60 to 70% of the energy needs of the brain[51]. In the complete absence of food ingestion and hence glucose intake, ketones are therefore incapable of maintaining or restoring normal cerebral function[54]. Fat deposits are thus unable to sustain large brains through long-term starvation. Second, although adipose tissue itself does not use much energy, fat animals have more difficulty escaping from predators and experience elevated energetic costs, most likely because the extra weight increases locomotion costs[55,56] and decreases hunting success due to reduced agility and speed[57–59]. This energy is then lacking for potential brain expansion.

As expected, brain size in amphibians and both eutherian and marsupial mammals is therefore constrained in highly seasonal habitats where food availability is periodically too low to sustain a large brain[30–33,60,61]. Such periodic troughs in energy intake reach their nadir in hibernating species, which have no or minimal food intake for several months. Accordingly, a large study across 1,104 mammalian species found that hibernators have smaller relative brain sizes than non-hibernating relatives[62]. Longer periods of hibernation in species of toads and in extinct cave bears[63–65] are related to brain size reduction. Even in non-hibernators, there is a reduction in brain size in species that experience occasional periods of dramatic food scarcity, such as Bornean orang-utans (linked to long periods of scarcity due to mast fruiting[66]), or extinct dwarf hippos, and Balearic Islands cave goats (linked to the inability to disperse during occasional periods of starvation on small islands[67,68]). All these studies corroborate the idea that environmental seasonality (where *in extremis* survival is only possible with hibernation) or unpredictable periods of extreme food scarcity impose energetic challenges, and thus act as an evolutionary constraint on brain size.

## Changing energy allocation

The second pathway to meet the costs of increased brain size is to reduce energy allocation to other body functions and shunt it to the brain. This can be achieved by reducing maintenance costs or the costs of reproduction.

### *Brain size and maintenance costs*

The well-known *Expensive Tissue Hypothesis* suggests that large brains evolved at the expense of the size of the digestive tract[69]. This hypothesis found support through studies on guppies (*Poecilia reticulata*)[70], cichlid fishes[71], and frogs and toads[72]. However, in homoeothermic animals such as birds[73], bats[49], primates[74,75], and mammals in general[76,77], there is little or no evidence for negative co-evolution of brain and gut size. Similarly, inconclusive results were found for a trade-off between large brains and the size or performance of the immune system. Whereas large brains correlate with a reduction in the immune response in guppies[78] and bats[79], this pattern was not confirmed in birds[80] or rodents[81]. In addition, costly sexual tissues such as large testes favoured under sperm competition have been proposed to compete with energetic investment in brain tissue. Whereas there is evidence for such a trade-off in bats[82,83], no such evidence was found for other mammals, including rodents,

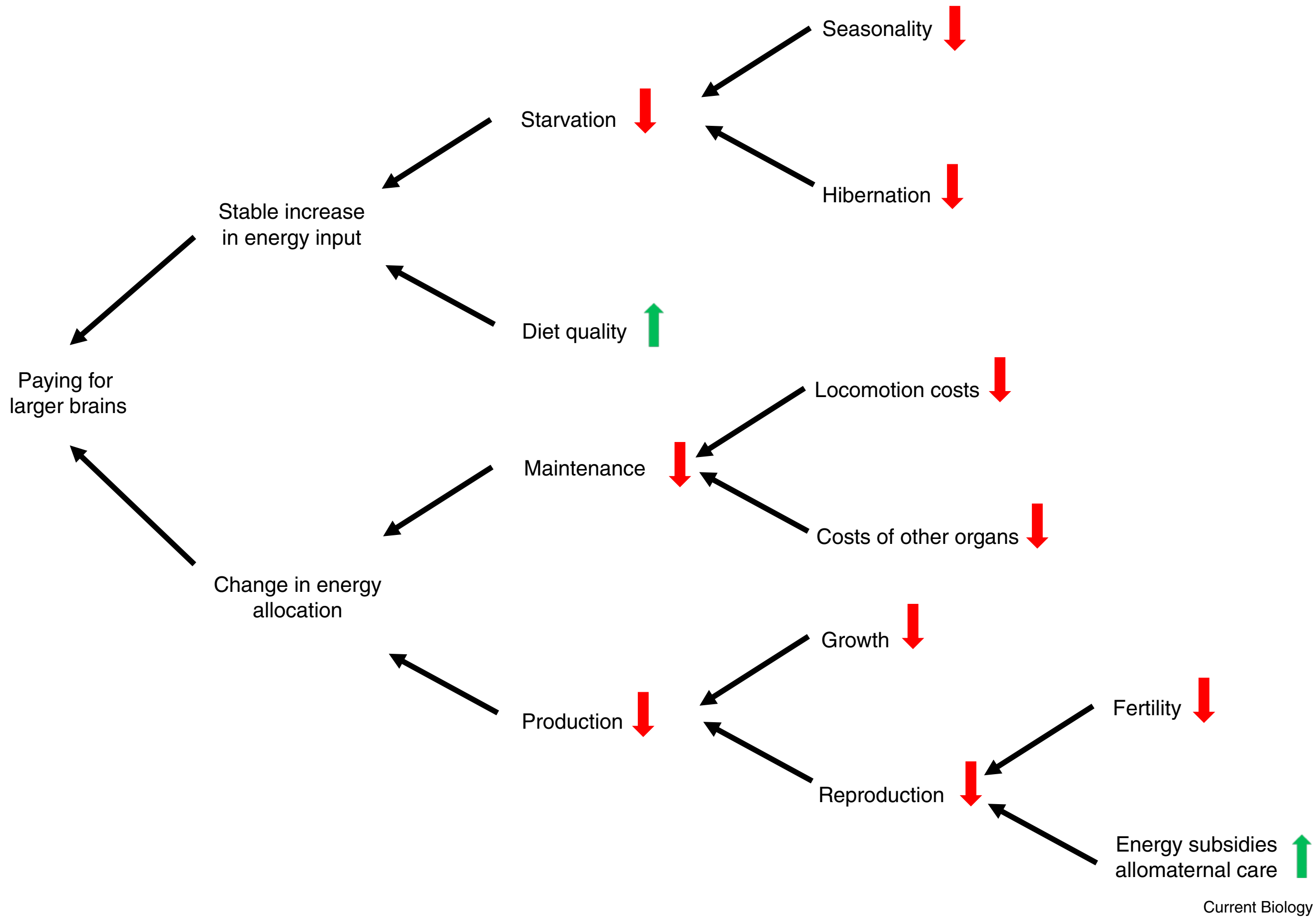


**Figure 2. The *Expensive Brain Hypothesis*.**
An adaptive increase in brain size is energetically affordable through two non-exclusive pathways: when energy inputs are stabilized on a higher level by increasing diet quality[10,31,46–48,50] and avoiding starvation[30–33,60–64,66–68] and/or through a reduction of energy allocation to other functions such as body maintenance[34,69,70,73,76,84,91,92] or production[2,29,70,94–96,98,103–105].

ungulates, primates, carnivores, or across combined mammalian orders[83].

Instead, across mammals, other energy targets were found to correlate negatively with brain size. Comparative studies, each covering more than 100 mammal species, found negative correlations between the amount of body fat and brain size[76,84]. These findings are consistent with the costs of adipose deposits described above and suggest that the ability to avoid starvation appears to be associated with one of two major evolutionary pathways[84,85]. On the one hand, species may rely on storing fat to survive lean periods at the expense of being less active (because of higher costs of locomotion) and facing an increased predation risk (due to reduced agility). On the other hand, animals may use increased cognitive abilities (i.e., large brains) to prevent starvation by innovative ways of acquiring alternative foods (so-called cognitive buffering[86–88]). Given that brain and fat tissue are both metabolically expensive and because investment into fat-storage reduces the net cognitive benefit of a large brain without reducing its cost, there are likely strong evolutionary constraints on simultaneous increases in brain size and fat stores. One exception to this are humans: we have both an extremely large brain and a high amount of body fat[89]. This human distinctiveness might reflect our economical terrestrial bipedal locomotion[76,84] in combination with our uniquely high energy acquisition through hunting and gathering[90].

Besides a brain size reduction due to other costly tissues and functions, periods of intense locomotion, with its attendant energy costs, may also select for smaller brains. Among birds and bats, migratory species have smaller brains than sedentary species[34,91,92] and, indeed, the longer the migration distance a bird species has to fly, the smaller is its brain[92]. Moreover, in birds, brain mass is also negatively correlated with pectoral muscle mass, an indicator of the costs of flight[73], whereas in bats, narrow-winged species, which have low relative costs of flight and thus increased flight efficiency, have larger brains than species with broad and large wings, which render them highly manoeuvrable but make them inefficient flyers[35].

### *Brain size and production from an energetic perspective*

The alternative way of decreasing costs in order to make energy available for brain enlargement is to reduce the energetic costs of growth and reproduction, as these are among the most energetically costly processes within an individual's lifetime[93]. For instance, brains of human children consume so much energy that glucose is diverted from the rest of the body, which slows down growth[2]. Likewise, comparative studies across mammals and birds show that larger-brained taxa have longer gestation and lactation periods and also grow and develop more slowly, apparently to ensure sufficient energy for brain development[29,94–96]. Accordingly, relatively large brained mammals[29], birds[96,97], amphibians[98], and fish[70] have been shown to reproduce later and less often compared to their smaller brained relatives. This pattern suggests that benefits of an increase in reproductive rate due to enhanced cognition in larger-brained species are outweighed by the reproductive slowdown larger brains impose.

The *Maternal Energy Hypothesis* proposes that the amount of energy that the mother can provide during development constrains the offspring's brain size development and thus ultimately also the species' brain size[99,100]. This pattern predicts that reducing the energetic burden of reproduction for mothers by, for example, distributing the costs of offspring production over more individuals may favour the evolution of larger brains (or alternatively, lead to higher rates of reproduction). Indeed, energy subsidies to the mother or the dependent offspring during breeding in the form of help from the father or other non-breeding group members alleviates the trade-off between reproduction and brain size in fish[71,101], birds[102], and mammals including marsupials[103–105]. This is most impressively exemplified by humans which likely achieved a combination of extremely large brains and high reproductive rates by relying on support from fathers and other family and group members[105,106].

A study disentangling the sources of allomaternal help in mammals suggests that care provided by the breeding male was most likely the driving force of evolutionary brain enlargement, supposedly because it is more stable and reliable than care by other helpers[105]. Breeding males help consistently and dependably with the rearing of their offspring. In contrast, assistance from other group members, such as older siblings, may vary with demographic conditions and also fluctuates as they adjust their investment depending on both food availability and their own reproductive opportunities[107–109]. Therefore, as predicted by the *Expensive Brain Hypothesis*, we find increased brain size only if the increase in energy available to the female is predictable and constant, which is the case for male care but not for care provided by other group members. In agreement with these findings, a comparative study across mammals showed that reproducing females in species with any sort of care from other helpers can afford to reduce the amount of energy stored in the form of body fat[110]. Corroborating the importance of male care, paternal care reduced the breeding females' reliance on body fat more than care by other helpers.

To investigate the effects of parental and alloparental care and its different forms on brain size evolution in more detail, future studies should look beyond mammals, to fishes, reptiles and amphibians: In these lineages, simple forms of parental care have evolved multiple times[111–113], but in contrast to birds and especially mammals, parental provisioning is rare[114].

### *Brain size and production from a time perspective*

On top of their high energetic costs, large brains also impose time costs on the developing individual in terms of a need for extended growth and maturation. Timewise, brains need to be fully developed and differentiated before the rest of the body in order to guarantee a fully functional organism[115]. However, the speed at which brains can be developed is seriously constrained by the fact that the energy flow to the brain needs to be held constant to avoid brain starvation and the resulting permanent cognitive damage[29,39]. In general, large brains take longer to develop than small ones, not just because of the difference in volume but also because they have more complex patterns of neural connectivity[116]. Therefore, high energetic investment into brain growth during development goes along with a delay in the physical development of the body[95,98,117].

An additional cause of the delayed development of large-brained species may be that their motor and in particular their foraging skills take a long time to develop[41,94,118–121], which means that for most of the developmental period, the developing brain will hardly be able to pay for its high energetic costs. This problem is most acute for the largest-brained species: as adults, they often develop complex foraging skills which take especially long to acquire[15,41,118,122–125], in part because they pass through a uniform and linear/successive development sequence that cannot be cut short[41].

As a consequence of their slowed down development, large-brained species mature and therefore also reproduce later and have longer intervals between births[29,94,95,98]. This slowdown commonly leads to reduced maximum reproductive rates (known in ecology as $r_{max}$) despite a longer adult life expectancy brought about by higher survival with increasing brain size[126,127]. In other words, as brain size increases, the resulting time delay in reproduction might not be sufficiently offset by the prolonged reproductive life span. The strength of this effect varies between species. For example, high extrinsic mortality through predation that cannot be reduced through cognitive means and so results in shorter lifespans in many small-bodied species may prevent large brains from evolving in these lineages[26].

## Benefiting from brains

As outlined above, brains are tremendously expensive to develop and maintain. So why do animals invest in such a costly organ? The answer to this question must lie in the numerous benefits a large brain provides to its owner. Indeed, there is substantial evidence that brain size can be used as a proxy for cognitive performance or intelligence[8,9,17,128,129] and that larger-brained and thus more intelligent species profit from a wide range of benefits in both the ecological and social domains (Figure 3). However, the *Expensive Brain Hypothesis* offers predictions as to the nature of these cognitive benefits.

### *Ecological benefits of large brains*

The high energetic costs of maintaining large brains and the trade-offs with other functions and organ sizes suggest that the cognitive benefits large brains bring are slanted toward energy-generating actions. Nonetheless, whether brain size evolution is mainly driven by ecological or social benefits has been subject to an ongoing debate. If increased cognition brings in more calories, the extra brain tissue required can energetically pay for itself. Direct benefits to survival or reproduction are thus very likely. The *Ecological Brain Hypothesis* therefore proposes that solving ecological problems, such as finding or extracting hidden food sources or moving efficiently through complex habitats or large home ranges, requires higher levels of

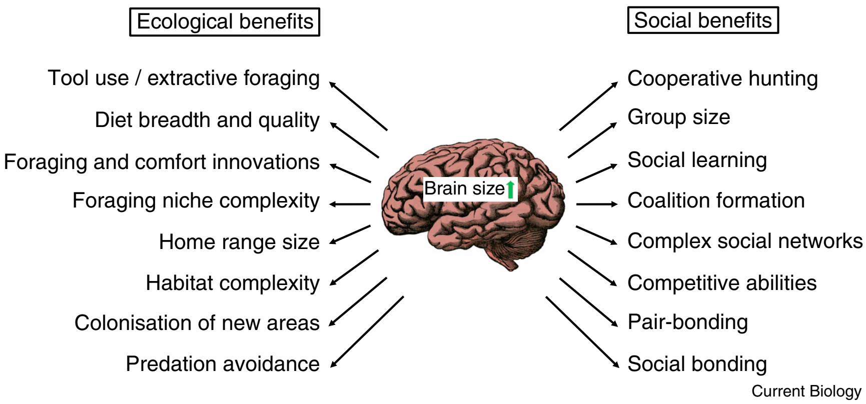


**Figure 3. Ecological and social benefits of large brains.**
Large brains are presumed to have been favoured by natural selection because they provide a wide range of benefits in both the social and ecological domain. Among other benefits in the ecological domain, large-brained and thus more intelligent species may profit from a broader and higher quality diet[10,31,46,47,50,134], a higher innovation frequency[23,135,136], more sophisticated motor skills such as extractive foraging and tool use[15,41,130], larger home ranges[10,134], more complex habitat and foraging niches[11,13,132,133,137] as well as being more successful in colonising new areas[16–19]. Social benefits for large-brained species may comprise living in intense forms of pair-bonds[102,149], large group sizes[21,48,147,148], or complex societies in general. Furthermore, social benefits of large brains include being better at social learning[31] as well as solving social challenges of competition and cooperation including forming coalitions and hunting cooperatively[21,31].

cognition and ultimately drove the evolution of enlarged brains[10,46,88,130,131].

In line with this hypothesis, larger brains and spatial cognition are correlated with habitat complexity in rodents[132], frogs[133] and birds[11] and with larger home ranges in primates[10,134]. Moreover, mammal and bird species with larger overall brain or forebrain sizes are more likely to invent novel foraging techniques, such as innovative predation techniques, commensal foraging, tool use, or extractive foraging[23,135,136]. Primate species with larger brain sizes or larger ventromedial prefrontal cortexes (a small part of the frontal lobe critical for episodic memory and decision making) have additionally been shown to be able to live in more complex foraging niches[13,137] and to master more sophisticated foraging strategies including more sophisticated motor skills[15,41]. As an example, aye-ayes (*Daubentonia madagascariensis*) have a highly enlarged auditory cortex and cerebellum[138] (and thus also overall brain size) to support their unusual tap-foraging strategy. Besides large brains allowing for specializations in the foraging domain, larger relative brain sizes are also generally correlated with enhanced sensory information (e.g. vision in primates[139,140] and olfaction in primates, bats and insectivores[141]) and thus neocortex size. Mammal[16], bird[17,18], amphibian[19], and reptile[19] species with larger brains are also more successful in colonizing new areas, presumably because large-brained species are able to adapt their behaviour more flexibly in response to novel environments. Finally, studies have reported correlations between brain size and various other ecological variables such as diet[10,46,47,50,134], terrestriality[50,142] and activity period[10,47,50].

### *Social benefits of large brains*

Improved social cognition could also lead to fitness benefits. Historically, flexible social strategizing has been seen as a hallmark of primates and has been linked to the fact that they are the mammalian lineage with the largest brains[143–145]. Thus, the *Social Brain Hypothesis* postulates that larger brains, in particular large neocortices, evolve in response to the complexities of living in groups[21]. Its rationale is that large-brained species can deal better with the social challenges of competition and cooperation, because they are better at monitoring and remembering social relationships and anticipating the actions of others[21]. The social benefits of larger brains and the resultant ability to live in stable, personalized groups further include increased protection against predators, access to potential mates, increased foraging efficiency, and the access to and transfer of social information[146]. In line with this hypothesis, overall brain size and relative neocortex volume correlate with social group size in primates and cetaceans[48,147,148] and with pair-bonding in bats, ungulates, carnivores, and birds[102,149]. However, the results of other studies are not conclusive regarding the link between brain size and sociality, mainly because several large-brained taxa are not as social as predicted and vice versa[25,28,150,151]. Furthermore, the *Social Brain Hypothesis* does not hold in the most encephalized primate family, the great apes[152]. Byrne[152] therefore proposed that to explain variation in this large-brained taxon, caloric benefits of more efficient foraging, gained through so-called technical intelligence, should be considered.

The *Expensive Brain Hypothesis* can explain the mixed support for social benefits. In many cases, increased social cognition does not lead to a direct increase in energy acquisition, which means that even though they potentially lead to a higher fitness, these socio-cognitive skills will not directly contribute to support the energetic needs of the larger brain that make these skills possible. However, examples where socio-cognitive skills may lead to higher net energetic yields include species where social rank determines access to resources[153–155] or correlates with energy expenditure, for example, through less favourable spatial positioning in the group[156–158]. Overall, brain size increases in response to benefits in the social domain are expected to be less common, because most socio-cognitive adaptations can only be favoured when a reduced allocation to maintenance or reproductive investment is possible. However, socio-cognitive adaptations that do produce energetic benefits should be widespread, such as the ones that increase individuals' ability to compete over food[159–161]. As the *Cultural Intelligence Hypothesis* proposes, increased social learning ability does likely lead to a faster acquisition of complex ecological skills[162].

### *Social or ecological benefits of large brains?*

Over the last fifteen years it has become increasingly clear that many birds and mammals show domain-general cognitive flexibility: species showing advanced cognitive performance in one domain also perform better in another, with cognitive performance being closely linked to brain size[8,9,23,129,163]. The presence of domain general cognition suggests that selection on larger brains equally improves cognitive abilities in the ecological and social domains, irrespective of the nature of the selective agent[164]. This of course premises that the energetic costs of an overall increase of brain size can be offset by the overall increase in cognitive performance. Thus, we risk mistaking the cognitive consequences of brain size for the selective agents that favoured the evolution of larger brains. This risk is real: most of our comparative methods can only establish correlated evolution, which often amounts to co-evolution in which causes and consequences feedback on each other. Some studies have tended to interpret all correlates of increased brains as selective agents, which may explain why we found conflicting evidence for social factors influencing brain size evolution[25,28,150,151].

The next step in disentangling the drivers of brain size evolution would therefore be a new conceptual approach which includes both social and ecological variables while systematically distinguishing between selective drivers and evolutionary consequences of brain size.

## Conclusions and future directions

In conclusion, the strong comparative support for the *Expensive Brain Hypothesis* from numerous studies implies that an economic perspective is of great heuristic value in the quest to understand brain size variation. We noted that brain size is especially likely to increase over evolutionary time in animal species that are able to achieve a stable increase in energy input, a reduced energy allocation to other competing functions, or a change in their lifestyle to ameliorate the trade-off between reproduction and brain size. All these findings in support of the *Expensive Brain Hypothesis* affirm the role of ecology as a selective driver in brain size expansion. Diet quality, substrate use, and intense seasonality of habitats leading to high body fat stores, hibernation or migration are all ecological factors shown to strongly impact brain size evolution. The social factors found to support the *Expensive Brain Hypothesis* also tend to concern energy balance, for instance by reducing the costs of reproduction or leading to increased foraging efficiency. Thus, when it comes to the economics of the brain, above all, we need to take the energetic cost of running it into consideration.

Although much progress has been made in recent years showing that the energetic costs of maintaining larger brains play a decisive part in enabling brain enlargement, most of this work has focused on primates, with other mammals and birds second. Far less work has concerned ectothermic vertebrates such as fishes, reptiles, and amphibians, and it remains unclear to what extent the theoretical framework developed for birds and mammals applies to them. Ectothermic organisms rely on environmental heat sources and are thus heavily affected by variation in ambient temperature, both seasonally and diurnally. Consistent with the *Expensive Brain Hypothesis*, ectothermy may therefore exacerbate the effects of seasonality as besides fluctuations in food availability, lower temperatures may have additional negative effects on a species' energy balance and thus on its brain size. Furthermore, we have not reviewed another ectothermic group, the invertebrates, for which we are even less sure whether the present theoretical framework holds. Synthetic work on these animal groups is therefore welcome to further enhance our understanding of the influence of energy supply on brain size evolution.

Besides current research being heavily biased towards mammals and especially primates, most studies to date focus on overall brain size and not on particular brain regions. This is in part due to data availability, in part due to the high collinearity of regions and overall brain size, and in part because from an energetic perspective, it is warranted to focus on the size of the brain as a whole rather than on specific regions. New methods, such as high-resolution computed tomography (CT) images, have made it much easier to characterize the individual components of brains. One very recent example of a study applying this method to measure the sizes of different brain regions of fossils showed that in early members of modern mammal groups there was a large increase in the neocortex over evolutionary time, whereas the proportion of the brain devoted to olfaction decreased[165]. The authors therefore concluded that encephalisation was driven by the expansion of brain regions mediating more complex ranges of senses and motor skills but not olfaction. Such studies are needed to test hypotheses for specific brain regions, to assess the degree to which they complement the broad studies using overall brain size, and to help to delineate the role of domain-specific cognitive adaptations.

Another understudied aspect of brain size economics are the developmental costs of brains. Larger brains develop slower and produce cognitive benefits much later than smaller brains. In a recent study we showed that infants of large-brained primates take longer to learn hand and finger movements[41]. This was not just because they had to learn more complex skills than small-brained species, but mainly because larger-brained species did not begin learning these skills until much later. We also showed that the neural development of these motor skills follows extremely rigid patterns. However, it remains unclear whether these findings also apply to the learning of other skills and/or to other mammalian groups and to what extent long developmental periods are driven by underlying constraints imposed by brain size growth. Future studies correlating brain growth to the timing of the ontogenetic emergence of particular skills across species with various brain sizes will yield new insight into (shared and divergent) phylogenetic patterns of the costs of brain development in association with skill learning.

Brain development is also costly due to the high energetic requirements associated with tissue growth. Based on this fact, the *Maternal Energy Hypothesis*[99,100] suggests that the brain size of a species is as large as the mother can afford to produce. While this idea did not generate much interest as the majority of studies have focused on adult brain size, and early tests were unfavourable[166,167], a reformulated version, focusing on all components of parental provisioning, is very promising (cf.[168]). Other vertebrate groups, such as fishes, amphibians, and reptiles have a much more diverse array of mechanisms for nourishing offspring, including yolk, uterine milk, oophagy, uterine cannibalism, and placentotrophy, and also exhibit a wide range of relative brain sizes. A promising direction for future research would therefore be to relate these different maternal provisioning strategies or just different egg sizes to brain size variation across vertebrate species in the frame of an expansion to the current *Maternal Energy Hypothesis*.

Not only on the cost side of brain evolution but also on the benefit side many questions also remain to be explored. For instance, several earlier studies have suggested that benefits in access to mates may have affected brain size evolution (Pitnick *et al.*[82] and Lemaître *et al.*[83], but see Dechmann and Safi[169]). While the general idea is plausible, these benefits do not improve the energy balance and thus do not support the increased energetic needs of enlarged brains. Moreover, because the sexes often differ in the extent of contest competition, benefits associated with access to mates would most likely primarily lead to sex differences in brain size within species rather than between species. Such sex differences have been described in several species such as sticklebacks or pinnipeds and are attributed to sexual selection[70,170,171]. In primates, female social networks have been suggested to have an influence on brain size on the species level[172], but this has never been tested systematically so far. However, a study investigating the influence of male–male coalitions on brain size in primates found no evidence for such an effect[173]. Therefore, additional detailed intraspecific studies are needed to resolve the role of sexual selection on brain size.

Lastly, to move towards a mature synthesis in the field of brain evolution, we argue that we need a better framework for causal inference. Decades of work have been dedicated to unravelling which ecological and social factors have driven the evolution of the brain without yielding any consensus. Given the evidence for domain-general intelligence, we risk mistaking the cognitive consequences of brain size for the selective agents that favoured the evolution of larger brains. Recent phylogenetic methods such as phylogenetic path analysis[174] and yet to be developed methods may provide us with tools to determine the drivers and consequences of brain size evolution.

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## DECLARATION OF INTERESTS

The authors declare no competing interests.

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