The brain's bootstrapping problem and its consequences: Parental provisioning and variation in vertebrate brain sizes

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Abstract

Our understanding of the considerable variation in vertebrate brain size remains incomplete. Large brains are adaptive but brains require unusually high, near-constant energy inputs, and are prioritized energy targets. This trade-off also has understudied developmental consequences: immatures must develop a fully functional brain without already having one. We here propose that energy subsidies through parental provisioning solved this bootstrapping problem, and find strong empirical support. Parental provisioning also improves immature survival and facilitates evolutionary increases in brain size. We call for better integration of costs and benefits of brains, and reevaluation of the cognitive abilities used in comparative tests.

Introduction: expensive brains

The brain has long been recognized as the organ that analyses and integrates the inputs from our senses, regulates our physiology, and generates the motor commands for our movements. In addition, it is responsible for everything between perception and action, i.e., cognition. Relative to body size, brain size is extremely variable across species. Mean brain sizes of ectothermic (fishes, amphibians and reptiles) and endothermic (birds and mammals) vertebrates differ by approximately an order of magnitude, but there is also remarkable variation within each of the five major vertebrate lineages (Figure 1). In addition, brains have tended to become larger over evolutionary time [1,2]. Understanding this enormous variation and these evolutionary trends in relative brain size is a major task for comparative biology and, given our own remarkably enlarged brains, for evolutionary anthropology as well.

Brain size is generally positively correlated with the amount of sensory information (e.g., electrosensing in mormyroid fishes: [3]; stereoscopic vision in primates: [4,5]) or the level of motor control (e.g., number of legs in lizards: [6]; manipulation complexity in primates: [7]), suggesting that these enhanced sensorimotor functions alone may explain brain size changes without reference to greater cognitive abilities [8]. Nonetheless, comparative studies also show a clear link between relative brain size and more narrowly defined cognitive abilities, such as greater capacity for independent or social learning [9–12], and thus greater domain-general intelligence [13,14] and executive functions, such as self-control [15,16]. Even more convincing evidence for an effect of brain size on narrow-sense cognition would be intraspecific correlations between brain size and domain-general intelligence, because sensorimotor capacities do not vary systematically within species. Indeed, in humans, brain size explains a modest, but robust proportion of variation in intelligence [17,18], a result now replicated in chimpanzees [19] and chestnut-headed thrushes [20].

Obviously, one would expect these three sets of abilities (i.e., sensory information gathering, cognitive processing, and motor control) to have coevolved. For instance, perfect information without sophisticated cognitive processing and advanced abilities to act upon the world would not be adaptive. Brain size should therefore predict behavioral performance in fitness-enhancing activities. Indeed, larger-brained species are capable of extractive foraging [21], and tend to be more innovative in the foraging domain (primates: [22]; birds: [23]). They are also better at avoiding predators (mammals: [24]; birds: [25]) and more likely to survive when introduced into novel areas by humans (mammals: [26]; birds: [27]; reptiles and amphibians: [28]). When operating long enough, these effects could induce correlated evolution between brain size and maximum lifespan. In fact, comparative studies have confirmed this correlation for mammals [29,30], birds [31,32], and frogs [33], though not for reptiles [34]. A more indirect, but presumably evolutionarily important consequence of improved survival is that larger-brained species have more stable populations (primates: [35]; birds: [36]), and hence a reduced risk of local extinction [37].

All these findings indicate that increasing brain size should be adaptive under most conditions, as also suggested by the trend toward brain size increase over evolutionary time [1]. One might therefore expect that, once controlled for body size differences, brain sizes would be approximately the same across lineages. But this is not the case: major differences between closely related lineages exist, as between marsupials and placental mammals [38] or between prosimian and anthropoid primates [39], as do differences between more distantly related lineages with similar cognitive demands, such as between social carnivores and anthropoid primates [40]. These differences imply that some brain-size related costs prevent the evolution of similar brain sizes in particular lineages, even if the overall evolutionary trend is up. Thus, a comprehensive explanation for the variation in brain size requires that we incorporate the fitness costs of increased brain (cf. [41]).

The core idea underlying the expensive brain hypothesis [30] is that much of the unexplained variation is due to two unusual features of brains: their high energy use per unit weight [42–44], and above all, the fact that energy allocation to the brain cannot not be downregulated during times of starvation (brain sparing: [45,46]. Interruption of this constant energy flow to the brain generally has lasting negative consequences for brain development and cognitive performance [47,48].

These peculiar features mean that the upper bound of brain size could be determined by the organism's ability to sustain the energy turnover needed to grow or maintain the brain in response to cognitive opportunities in the ecological or social environment. Thus, according to the expensive brain hypothesis, brain size should partly or largely depend on how much energy a given species can provide to its brain without significant dips over time. Reduced energy inputs can arise due to tradeoffs with other energetically costly functions, such as digestion [43] or to ecologically imposed limitations on overall energy acquisition, in particular the inability to adequately deal with periods of unavoidable food scarcity. Heldstab et al. [49] recently reviewed the extensive empirical support for this hypothesis. In sum, the expensive brain hypothesis helps to explain why brain size does not always correspond to expectations based on social or ecological demands and opportunities. This conclusion holds even if controlled for taxonomic variation in neuron densities [50,51].

The expensive brain: developmental aspects

With the expensive brain hypothesis' credentials established, we want to focus on a so far largely neglected implication. Immature endothermic vertebrates, with their relatively large brains [1], face a seemingly insurmountable bootstrapping problem (Figure 2) for several reasons.

First, brains are unusual organs in that they must acquire their cognitive and motor functions through learning and therefore perform poorly relative to adult brains before they are fully grown and differentiated. In mammals, brain growth, though not differentiation, is largely completed around weaning [52]. Accordingly, many species tend to reach adult-level ecological skills such as the recognition of the values of specific food items and processing techniques around weaning [53–55], although the most complex skills, including tool use, are reached much later [56]. Among primates, the development of food/object manipulation techniques follow a fixed trajectory of increasing complexity, which also holds phylogenetically. Larger-brained primate species, while reaching more complex techniques as adults, acquire each lower level technique at a later age than smaller-brained species, and thus experience an overall slowdown of skill development [53]. As a result, although harvesting rates of juveniles are often similar to adults for the simpler food, they tend to be lower for complex techniques, such as extractive foraging [57], especially when tool-supported.

Birds differ strongly from mammals in that both brain and body growth are completed very early [58]. Nonetheless, their reproductive activity starts much later in life (potentially years: [59]), suggesting that the time needed for skill learning limits the age at which adulthood is reached. Comparative work found that birds indeed reach adult-level ecological skills around the age at first reproduction, both for feeding [54,60] and for predator recognition [61,62]. Overall, therefore, immatures in most birds and many mammals are ecologically less competent than adults, and some undergo a long phase of learning before reaching adult levels (birds: [63,64]; mammals: [53,54], even after brain growth has been completed.

Second, immature birds and especially mammals are in a phase of high ecological risk for two main reasons. They are less experienced and often smaller, which exposes them to higher risk of predation or disease [57,62]. They are also generally socially subordinate to adults, and thus may be peripheralized, either socially or in terms of habitat quality. They consequently face particularly high mortality risks, especially at higher population densities [65,66]. These two processes together indicate that the bootstrapping problem gets worse as a species' relative brain size increases.

Third, immatures have relatively higher brain maintenance costs than adults, at least in mammals. Not only are juveniles smaller and less experienced, they are also more encephalized than adults because brain growth is completed before somatic growth is [67]. This forces them to allocate a larger proportion of their energy budget on maintaining the brain (see [68] for humans). In addition, they face extra costs. The creation and pruning of numerous synaptic connections mean that differentiating brains are more costly per unit weight than mature brains [44,69]. Finally, in both birds and mammals proper brain development requires play, which is often quite vigorous and therefore energetically expensive. Indeed, species with more post-natal brain growth (and thus larger adult brains) play more [70]. We are not aware of similarly extensive comparisons in birds (but see [71]).

This combination of the high time and energy costs of brain growth and lower rates of energy acquisition needed to sustain this growth due to insufficient ecological skills or social disadvantages constitutes the catch-22 of large-brained species. We propose that an increase in parental provisioning has enabled species to overcome the concomitant bootstrapping problem and subsequently evolve larger brain size. Here we define parental provisioning as the sum of the energetic investment into the young, directly (in eggs, through gestation, lactation or provisioning of food), or indirectly (by carrying or huddling to keep warm).

As explained in Box 1, the parental provisioning hypothesis builds upon, yet greatly extends, the maternal energy hypothesis [72], which was more limited in its scope and initially based on a very different evolutionary logic, and perhaps because of this, failed to become integrated into more recent approaches.

Box1: **The maternal energy hypothesis: the rise, fall and resurrection of an idea**

Martin [72] noted that the allometric scaling relationship with body size among placental mammals has the same exponent for both brain size and basal metabolic rate. This pattern suggested to him that "the resources channeled to the embryo from the mother" acted as a constraint on the brain size of a given species. The lower scaling exponent for brain size in birds and reptiles was attributed to their oviparity, and thus found to be consistent with this maternal energy effect. Initial attempts to test its predictions therefore focused on this allometric scaling. They were not favorable. First, Pagel and Harvey [73] stressed that the slope of the brain-body relationship depends on the taxonomic level at which they were estimated, and is much lower than that of basal metabolic rate at the most relevant level, that of the species. Second, the allometric slope also varies among different lineages within mammals [74], without any indication that this covaries with similar patterns in basal metabolic rates. Finally, the slope is much higher in birds than the hypothesis predicted [75].

More direct tests were also not favorable. The precocial-altricial contrast in birds is inconsistent with this model, because precocial species have smaller relative adult brain size but have much more developed brains at hatching than altricial ones [75]. Likewise, maternal metabolic rate did not predict neonatal brain size or gestation length in a large sample of mammals [76] (but see [77] for a rebuttal).

These negative outcomes reduced the appeal of the hypothesis, and attention soon turned to other predictors of brain size variation, perhaps also because no compelling argument was offered as to why the burden of building an offspring's brain necessarily had to fall on mothers.

Subsequent development of the hypothesis moved away from interspecific scaling relationships. Focusing on placental mammals, Martin [78] suggested that the pattern of correlations among "body size, brain size, basal metabolic rate, and gestation period indicates that the primary link is between maternal metabolic capacity and the developing brain of the offspring." Thus, the hypothesis directly linked gestation length and maternal metabolic rate to neonatal brain size (cf. [79]). Perhaps the emphasis remained on gestation because he [72] had suggested that in primates most brain growth is completed at birth. Although this may be correct for the number of neurons [80], neonatal brains in many species are less than half of adult size (e.g., [52,81]), especially in great apes and humans [82]. Moreover, brain differentiation (including myelination) is usually postnatal and among the most expensive aspects of brain development [44,69]. Thus, a proper test of the maternal energy hypothesis would require the inclusion of postnatal maternal investment in the form of lactation and (where relevant) provisioning.

Martin [78] also argued that the rate of maternal investment acts as a constraint on brain size, which, he suggested, leaves no room for variation in investment that produces adaptive variation in adult brain size. Thus, he argued for a constraint interpretation rather than one invoking an optimum balance between costs and benefits (which would allow selection to adjust rate of investment and thus duration of dependence or litter size). Due to the "primary link between the basal metabolic rate of the mother and the developing brain of her offspring," he argued that any links between a species' brain size and ecology or social organization would be "a secondary consequence", so that "there may be no very tight relationship between relative brain size and specific behavioral capacities." Subsequent research has shown that adaptive explanations are supported for both the links with ecology [83,84] and social organization [85] and with cognitive performance [13,14]. This stance effectively reduced the appeal of the hypothesis.

Martin [77] expanded the hypothesis's scope by including lactation, whereas Martin and Isler [86] also discussed the importance of the overall duration of investment independent of metabolic turnover by the mother, reinforcing the conclusion that "development of the brain is heavily dependent on resources provided by the mother" ([77], p. 54). Unfortunately, these extensions garnered little attention.

Numerous comparative analyses have examined the link between adult or neonate brain size and life-history parameters in various groups, especially mammals (e.g., [29,30,87]; see also [31] for birds). Many studies found that larger-brained species take longer to reach adulthood (see also [81]). Although this points to competition between the growth of the brain and that of the body [88], such competition would arise regardless of maternal inputs and therefore in itself does not confirm the maternal energy hypothesis. However, one of the comparative studies [89] related their findings to the maternal energy hypothesis, when they found that "evolutionary changes in pre- and postnatal brain growth correlate specifically with duration of the relevant phases of maternal investment (gestation and lactation, respectively)" (see also [90]). They coined the developmental cost hypothesis to explain this pattern (which could be read as merely referring to competition between the growth of the brain and the body), rather than directly referring to the maternal energy hypothesis.

All these results suggest that a modified version of the hypothesis may be viable if it considers all phases of maternal investment, including postnatal provisioning and other forms of energetic investment by both mothers and allomothers, and in addition to the rate of energetic investment also includes the duration of investment per individual offspring. Another adjustment should be that it regards the process as an adaptive strategy (and not a constraint) to achieve the species' optimum brain size. Most importantly, however, it must provide a theoretical argument as to why parental investment is so critical to begin with. The parental provisioning hypothesis is meant to provide all of this.

This history also illustrates how a hypothesis that was initially based on totally different premises could, based on empirical results and new theoretical insights, gradually morph into a very different one, with a new conceptual foundation and a modified set of predictions. However, presumably because the associations with the initial label lingered, the modified hypothesis did not catch on.

Evaluating the parental provisioning hypothesis

Provisioning and brain growth rates

The parental provisioning hypothesis is consistent with fundamental brain growth patterns (Figure 3). Across vertebrates, brain growth rates often show a sharp slowdown after a period of rapid growth [2,91,92]. Parental provisioning can explain this pattern. In mammals, the initial period of rapid growth of the brain is generally isometric with that of the body [2,39,91]. In precocial species, born with relatively large brains [52], its growth slows down after birth, whereas in altricial mammals, growth tends to be highest soon after birth. In both precocial and altricial mammals, brain growth is completed by the end of parental provisioning, i.e., weaning [39,52,80], although subsequent differentiation may continue.

In birds, brain growth is completed by the time offspring fledge in altricial species [93,94], and thus entirely paid for by parental provisioning. In both mammals and altricial birds, parental provisioning therefore provides the developing offspring with a neurological endowment that lasts them a lifetime. Precocial birds face more of a bootstrapping problem than altricial ones, because there is little or no post-hatching provisioning. This explains why, they have slower post-hatching brain growth than altricial species, and achieve smaller relative brain size among adults (Figure 3; [75]).

In other vertebrates, parental provisioning is far more limited. In most fishes, provisioning is entirely through eggs [95], and brain growth is high only during the very brief period before reserves in the egg are depleted, and slows down soon after hatching [92]. However, since so much of the brain still needs to be developed, the brain growth trajectory remains steeper than for the endothermic vertebrates, as illustrated in Figure 3, and species with indeterminate growth retain the same slopes throughout life.

The overall pattern is therefore consistent with the prediction that rates of brain growth are steep only during the parental provisioning phase and are reduced thereafter.

Provisioning and brain size: comparative tests

To establish that variation in the intensity and duration of parental provisioning is linked to adult brain size we need comparative tests. To start with birds, precocial and altricial species differ in brain size, with altricial species having larger brains for their body size than precocial species [75]. While long known [96], this difference has never been satisfactorily explained. The parental provisioning hypothesis links it to the amount of provisioning beyond egg size. In a study of 1176 bird species, Griesser et al. [97] confirmed that the duration of provisioning relative to age at fledging strongly affects adult brain size. In addition, their analysis revealed that the socio-cognitive or eco-cognitive variables traditionally used in comparative analyses did not explain much variation once parental provisioning was included, suggesting that these variables arose as byproducts of the general ability to occupy a skill-intensive niche and provision the young (see below).

Around 90% of bird species show biparental provisioning [98], and the modest variation in the number of caretakers does not affect relative brain size [97]. Among mammals, well over 80% of species have uniparental provisioning by the mother [99]. Nonetheless, there is enough variation to permit testing the effect of the number of caretakers by comparing species with maternal care only (the majority) with those with additional direct care by males and non-reproducing helpers. In this case, care is considered to be either provisioning or carrying (which also alleviates the mother's energy burden). Allomaternal care contributes to larger relative brain sizes in the species involved, with the effect of male care being stronger than that of helpers [100], arguably because the male always helps whereas the number of helpers is highly variable. These findings are therefore also fully consistent with the parental provisioning hypothesis. In a recent analysis of marsupial brain size variation, Todorov et al. [101] found that the only variable with explanatory value was litter size, which, given that size at birth and growth rates are rather uniform in this lineage, is consistent with the parental provisioning hypothesis.

Studies of cartilaginous fishes (Chondrichthyes: sharks, rays, skates and sawfish) showed that species with matrotrophy, i.e., where young are supported beyond the yolk inside the egg, show larger relative brain size than those without it, at least for species up to 100 kg [102,103]. Although highly suggestive, the authors consider this support preliminary because the effect does not hold for the largest species.

Post-hatching parental provisioning is virtually absent among the largely ectothermic lineages (fishes, amphibians and reptiles), with a few exceptions [95]. The relatively large brains of the cartilaginous fishes therefore suggests that parental provisioning may also partially account for the major gap in relative brain size between endotherms and most ectotherms (Figure 1). Parental investment among most ectotherms is very much smaller, since their investment stops at egg deposition and their eggs are tiny [104] compared to weanlings in mammals and fledglings in birds. As a result, the great majority of ectothermic young face the full bootstrapping problem on their own, given that the reserves contained in their eggs are quite limited [92,104]. However, tests of the parental provisioning hypothesis for the few radiations in ray-finned fishes (Actinopterygii), amphibians and reptiles with variation in it are urgently needed.

Implications of parental provisioning's effect on brain size

Parental provisioning and immature survival

Given the high energetic costs of brains, especially of relatively large ones, it is hard to imagine brain size not to be under strong selection. A species' brain size should thus be adaptive, but this is not easy to demonstrate. The comparative tests reviewed above show that increased brain size improves adult survival, but also slows down development. However, the resolution of comparative tests is limited when it comes to reproductive rates, which to an unknown extent reflect external conditions such as food, weather, and population densities. Thus, it remains unclear to what extent the reduced reproductive rates in larger-brained birds and mammals can be attributed to brain size. Yet, higher costs of reproduction are likely, given that they make larger neonates and thus have longer interbirth intervals [30]. As a result, this leaves us guessing whether the overall balance of these effects means that brain size changes are adaptive.

Arguably the most important reason for this uncertainty is that there are currently no published comparative analyses on one important component. The greatest fitness cost of increased brain size appears to be the slower maturation, which increases generation time and thus reduces fitness and so the likelihood of positive selection on increased brain size. Even more importantly, this delay should also tend to reduce survival until adulthood. However, it is conceivable that parental provisioning improves survival to the point of countervailing these negative effects on fitness.

Here, we offer a preliminary analysis for primates, using published information on 18 species in 13 genera for which the relevant information from populations in undisturbed natural habitats has been published (Figure 4; for details, see supplementary materials). We find that brain size, as expected, improves first-year survival (Figure 4.a). However, it also improves survival until the age at first reproduction (Figure 4.b), in spite of the longer time needed to reach this point. In fact, a multiple regression (Table 1) shows that survival to age at first reproduction is positively affected by brain size but negatively by body size, which reflects bigger species taking more time to reach adult size, which should, *ceteris paribus*, reduce survival. The behavioral mechanism responsible for this remarkable pattern must be parental provisioning and protection.

This striking increase in immature survival, together with the previously documented increase in adult survival reviewed above, goes a long way to reassure us that brain size is indeed adaptive in a given species' natural habitat. However, future work must test whether this result generalizes beyond primates.

Selection and brain size

The importance of parental provisioning also invites us to rethink how to integrate the various costs and benefits in selection on brain size. One can in principle recognize three sets of cognitive abilities, here defined broadly to also include sensory and motor abilities. A first set of abilities acts to maintain the adult brain (box A in Figure 5) by guaranteeing a stable energy supply to the brain. A second set enables adequate parental provisioning, and so serves to construct the adult brain (box B in Figure 5). The third set of cognitive abilities produces the cognitive performance that is responsible for the successful survival and reproduction of its bearer (box C in Figure 5). Selection will favor an optimum brain size at which fitness is maximized. The size at which this optimum is reached depends on many details of the ecological and social environment, the species' bauplan, and especially on the extent to which these three sets of cognitive skills overlap.

In the worst case, sets A and B show no overlap with set C. In that case, which may arise if particular selective pressures only produce highly domain-specific cognitive modules, selection on enlarged brain size will be very difficult. More likely, however, the variables that enable a species to pay for their brains (A and B) and those that allow it to thrive more generally (C) show a large overlap, with only few, if any, adult social and ecological skills being distinct. A recent analysis of birds [97] found that, once parental provisioning was controlled for, the correlations between brain size and the commonly measured cognitive abilities, such as group size, duration of social bonds or climatic factors, practically disappeared from the model, apart from ecological behavior patterns directly that affect energy balance, such as long-distance migration [105]. This result suggests that the socio- and eco-cognitive skills affecting adult performance and driving parental provisioning are largely similar, perhaps because selection favors domain-general cognitive processes, such as general intelligence and executive functions [16,22]. In addition, it suggests that some of the variables traditionally thought to affect brain size are perhaps not the main selective pressures. They may feature in analyses merely because they are available for many species.

It is clear that more work is needed to identify the critical cognitive skills. Still, one conclusion can safely be drawn. Fundamentally, the brain must pay for itself. Accordingly, if particular cognitive adaptations from sets A and B also directly improve the organism's energy balance and so allow brain size to expand, selection is more likely to favor their emergence. This condition holds as much for adult survival, for instance by avoiding starvation, as for parental provisioning. As a result, eco-cognitive abilities are more likely to favor brain size increases than socio-cognitive ones [49,84,106], although this does not mean that selection on socio-cognitive abilities is impossible. First, as suggested above, whenever some of the ecologically selected cognitive improvements are domain-general, cognition will be improved in the social domain as well. Second, ecological and social cognition interact where the quality of pair bonds affects the quality of parental provisioning (cf. [85]), where the social structure sets the number of tolerant role models and so affects how readily immatures can learn ecological skills, or where adult role models become active participants in the immatures' skill acquisition through teaching [107,108]. Finally, when the socio-cognitive abilities cause disproportionate increases in reproductive success, they may outweigh the reduction in survival due to the uncompensated increased energy costs (although over time the social advantage will often erode due to being frequency-dependent).

The fact that the same cognitive abilities may serve to pay for energetic costs and produce direct fitness benefits raises a methodological problem. Most conventional methods for analyzing comparative data assume a unilateral flow of causality from various variables representing fitness costs or benefits to the trait of interest. In this case, depending on the stage of lineage evolution, brain size will be involved in a number of feedback loops (cf. Figure 5), and thus both respond to and drive the surrounding landscape of eco-social and life-history traits. Modelling evolutionary brain size trajectories that follow such complex patterns requires new methods. These may include models for more robust and accurate estimation of shifts in the rate of change in variables across large phylogenies [109–111]. Likewise, we need causal models, such as structural equation modelling or d-separation path analysis [112], that allow for more accurate placement of variables as causes or effects in multivariate networks of traits.

Promising insights into the evolution of brain sizes will also likely emerge from the ongoing re-evaluation of the importance of variation in comparative analyses: methods focusing both on average patterns as well as the drivers of variance around trends (e.g., heteroscedasticity of brain-body size allometries observed across vertebrate taxa) are now able to incorporate phylogenetic relationships between species [113,114], providing new tools to disentangle the evolutionary history of brain sizes.

Parental provisioning and the potential for encephalization

Interspecific brain-body allometries have long been explained as reflecting one major process [1,115], as artifacts of non-adaptive genetic correlations [116], or even as statistical artifacts [73]. However, none of these explanations is strongly supported [117,118]. Thus, the taxonomic variation in allometric slopes requires a new explanation, couched in terms of variable selective responses by brain, body or both to new challenges. The parental provisioning hypothesis may make a significant contribution to this debate.

Parental provisioning serves to overcome the problem of having to construct a large, expensive brain without already having one (the bootstrapping problem). The logic of the expensive brain therefore suggests that lineages with more parental provisioning may more readily satisfy the preconditions for major evolutionary increases in brain size (encephalization), whereas those with very limited parental provisioning may remain caught in rather low-cognition niches. Marsh's rule, which states that over evolutionary time species tend to become more encephalized (i.e., brains becoming larger relative to body size: [1]), may therefore apply most strongly to lineages with parental provisioning. Where this process is accompanied by enough adaptive variation in body size within a given lineage, this produces steeper slopes of the brain-body relationship (where both are log-transformed) at higher taxonomic levels among extant species, known as the taxon-level effect [117].

One obvious way to test this prediction is to compare the slope of the brain-body allometry in precocial and altricial bird lineages. Fully precocial species do not provision their young beyond the resources provided in the egg, so their young would face the full bootstrapping problem on their own, whereas altricial species provision their young. In precocials, therefore, the bootstrapping problem may moderate selection on increased brain size, whereas those in altricial lineages have the opportunity to response to such selection by increasing their provisioning. As a result, we would expect steeper slopes for the brain-body allometry among altricial birds than among precocial ones.

Earlier results, produced for other purposes, provide a preliminary test. Nealen and Ricklefs [115] estimated the exponents of the brain-body allometry (i.e., the slopes of the log[brain]- log[body] regression) at multiple taxonomic levels. Their results revealed steeper slopes at the level of orders, families and even genera among altricial taxa than among precocial ones. A more recent study [97] replicated this result with a modern phylogeny and a larger sample: a highly significant interaction effect between body weight and development mode on brain size revealed that altricial species have a far steeper slope. To illustrate this effect, Figure 6 shows the slope differences between altricial and precocial bird orders and families (based on ordinary least-squares regression).

An even more promising testing ground may be ectothermic vertebrates, which largely lack any post-hatching parental provisioning, even if some species guard young. Tsuboi et al. [92] reported that (phylogenetically corrected) brain-body allometry slopes at higher taxonomic levels are indeed clearly higher for birds (0.57) and mammals (0.59) than for fishes (0.50 for Actinopterygii and 0.41 for Chondrichthyes) and amphibians (0.46), though not for reptiles (0.56). Tests at lower taxonomic levels have not been done yet. While these will no doubt soon emerge, this preliminary survey supports the proposition that lineages with parental provisioning are more likely to experience strong encephalization, i.e., Marsh's rule.

Conclusion: parental provisioning and brain size

The data reviewed here prove the utility of expanding the expensive brain hypothesis by incorporating the costs of brain development and the ensuing bootstrapping problem for immatures. Comparative work does indeed show a strong effect of parental provisioning on brain size, and thus supports the notion that a species' brain size depends on the parents' ability to pay for the brain development of their young.

The parental provisioning hypothesis argues that brain size is tightly linked to the ability of adults to avoid starvation, predation, and disease through cognitive means as well as their cognitively supported ability to garner the time and energy to provide their young with the energy needed to construct the brains needed for this. This provisioning comes with the essential benefit of improving immature survival (at least in primates). This hypothesis promises to explain a conservable part of the variation in brain size among the five major vertebrate lineages. It also indicates that where extensive parental provisioning did not evolve, the evolutionary potential for greater encephalization is reduced. Accordingly, the appearance of highly encephalized lineages, such as birds and mammals, had to wait until parental provisioning had established itself in their early representatives.

Finally, the hypothesis draws attention to cognitive abilities underlying parental care as a major factor in cognitive evolution, and thus raises the broader question of which cognitive processes are the target of selection. More generally, it suggests that eco-cognitive skills have played a major role, with socio-cognitive benefits perhaps arising mainly as a byproduct of ecological selection on more domain-general cognitive abilities. It even invites the speculation that the evolving brain creates its own cognitive opportunities rather than responding to cognitive demands imposed by the external environment, in a form of niche construction [119], through socially transmitted learned skills as well as physical modifications of the habitat.

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Figure Legends

Figure 1.
Brain size-body size envelopes of the major vertebrate lineages to illustrate both intra-lineage and inter-lineage variation. The long-dashed outlines represent the two endothermic lineages (birds and mammals), the dotted outlines represent fishes, and the solid outlines the two ectothermic tetrapod lineages (amphibians and reptiles). Redrawn after Tsuboi et al. (2018).

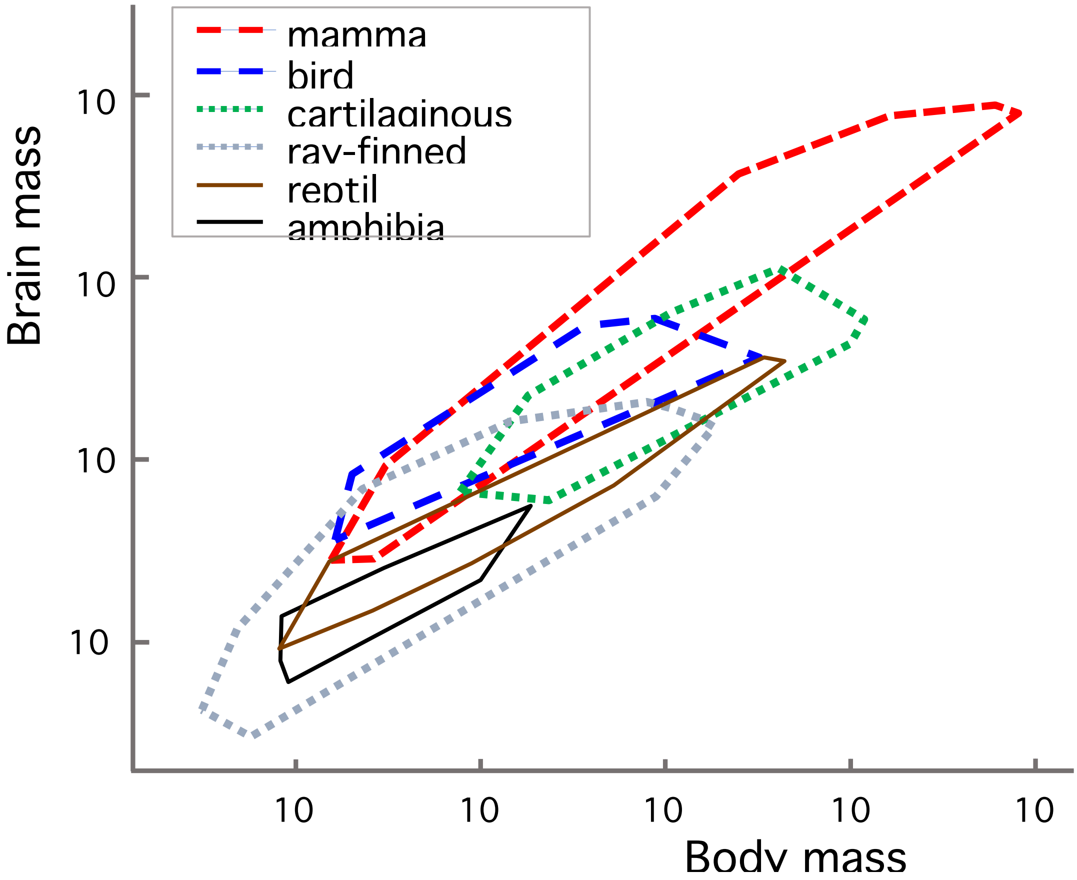

Figure 2.
The bootstrapping problem for developing brains, which without help would likely face a long period of negative energy balance during immaturity. Before it is fully grown and differentiated, the brain does not provide full (adult-level) cognitive benefits (green curve). The costs of growing, differentiating and maintaining the brain rise early and may even exceed adult values due to higher relative brain size of immatures in mammals and costs of brain differentiation, before cognitive benefits, with their corresponding net energetic intake, stabilize at adult level. During adulthood, these benefits outweigh the brain's maintenance costs by a clear margin. Parental provisioning can serve to overcome this bootstrapping problem.

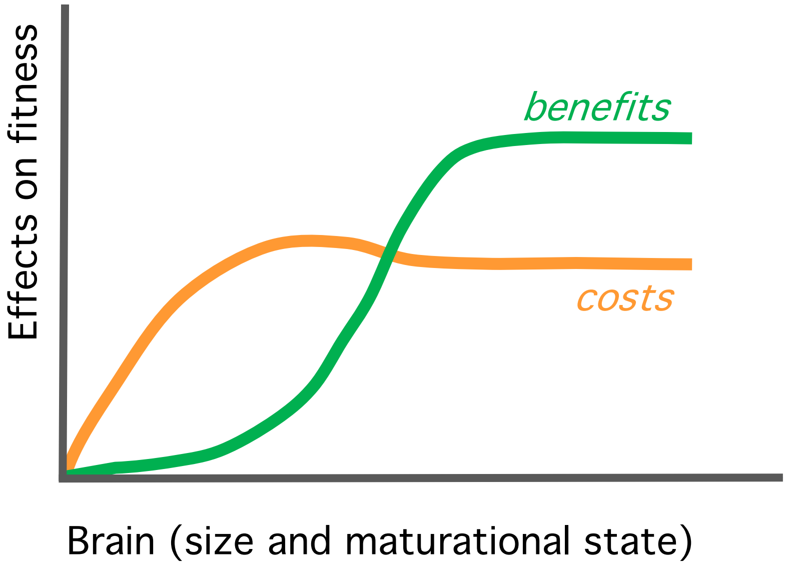

Figure 3.
Schematic depiction of brain growth relative to body growth in different vertebrates as a function of parental provisioning. The first phase (parental provisioning) shows the same, steep slope (virtually isometric: 1.0). After the end of parental provisioning, the slope becomes very low (ca 0.2) in mammals and altricial birds, whereas it become intermediate in precocial birds and ectotherms (ca 0.5) until adulthood is reached, and in most of the latter continues at the same relative rate after that due to indeterminate growth, (*Y-axis not to scale, to clarify slope differences).*

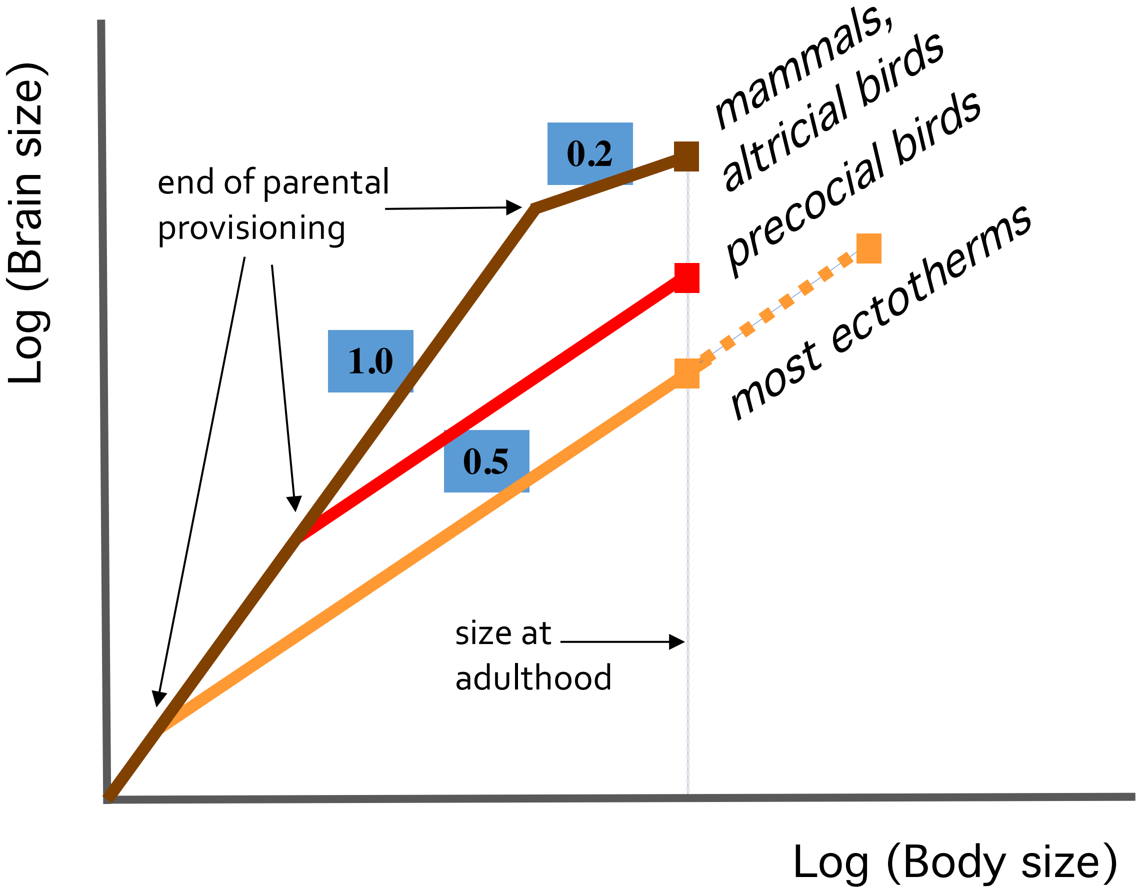

Figure 4.

Survival during first year (a) or until the age at first reproduction (b) as a function of residual (log-transformed) brain size of adult females in a sample of wild primate species with life-table information.

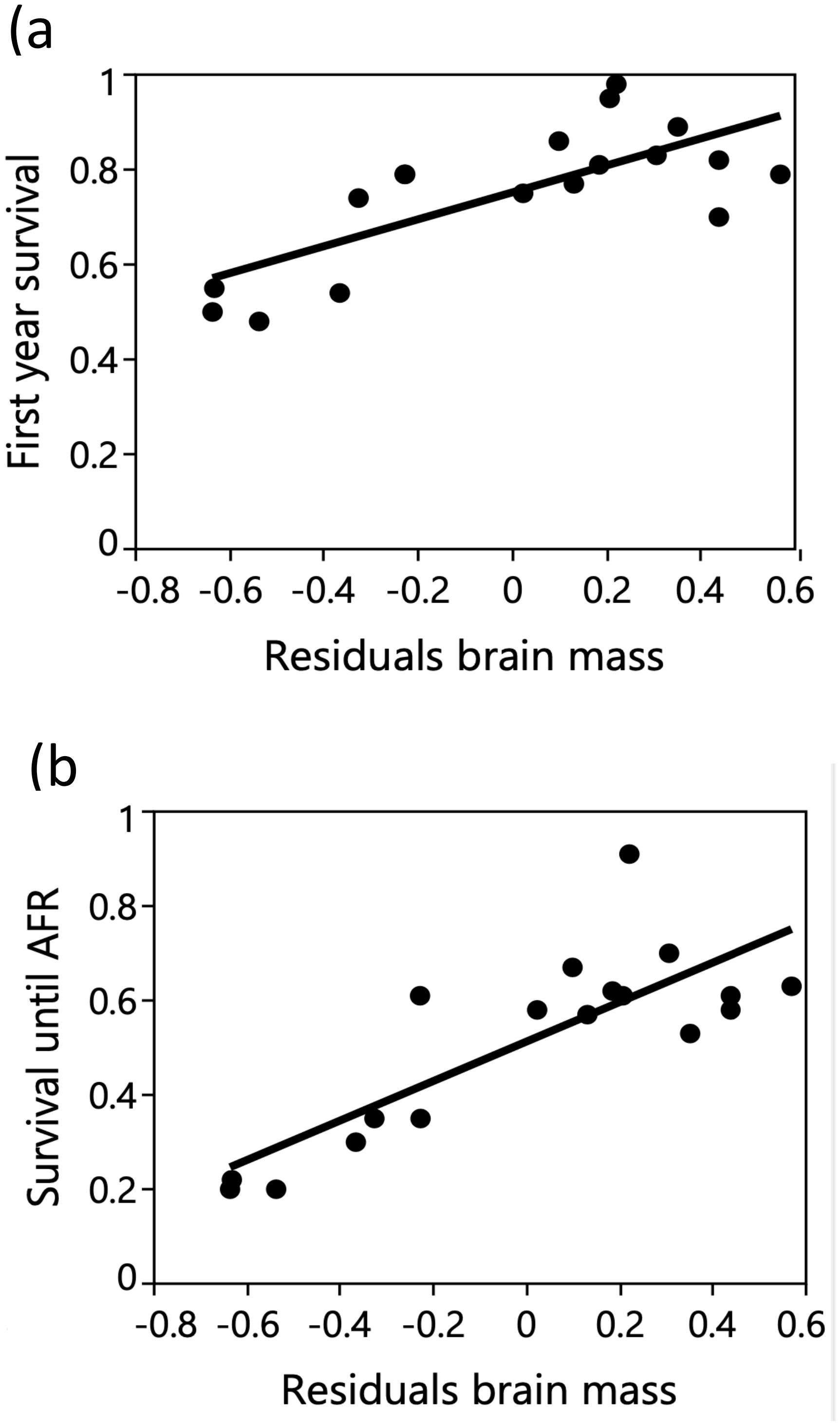

Figure 5.
Natural selection is expected to optimize brain size, by finding the optimum balance between the cognitive abilities (in the broad sense) required to pay for the costs (the maintenance of the adult brain [A] and its construction during development [B]) on the one hand, and the brain-size-dependent cognitive abilities that are translated into fitness (C) on the other. The three sets of cognitive abilities no doubt show high overlap, but their nature remains poorly studied. For birds, set A would presumably contain abilities such as migratory habits, food storing, extractive foraging, and communal roosting; set B abilities like predation avoidance (especially of nest contents), efficient foraging, habitat and nest site selection, flexibility, coordination ability; and set C many of the same abilities, but also avoidance of predation on adults, post-independence skill learning, optimal mate choice, and social skills.

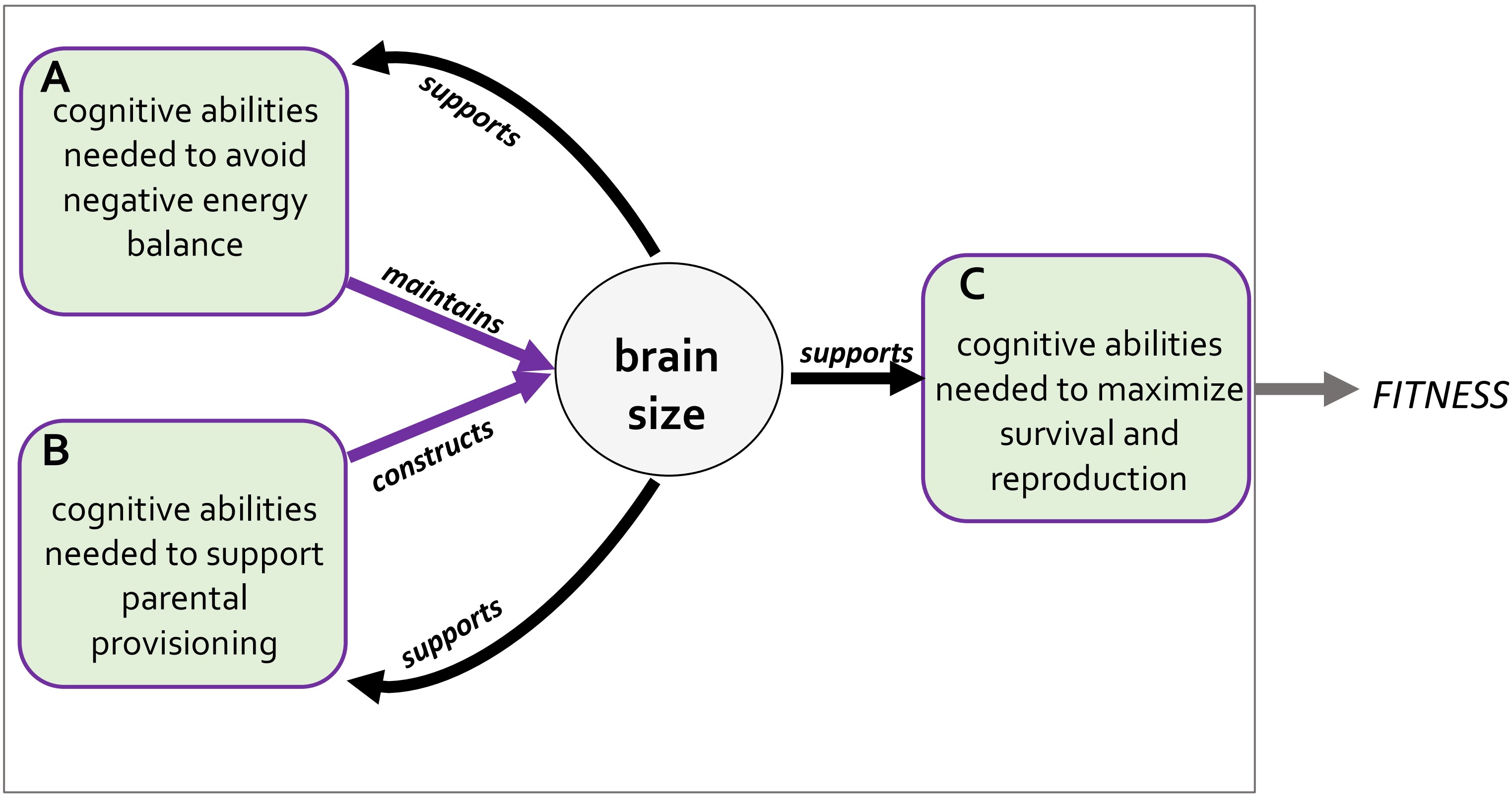

Figure 6.

Slopes of the brain-body allometries of altricial (gray bars) and precocial (white bars) orders and families of birds. Data are taken from Griesser et al. (in review/Bioarxv). Criterion for inclusion > 5 species per order or family. Horizontal bars represent the median, red diamonds the mean, and boxes enclose the central 50% percentile range. The difference at the family level is significant (P<0.05).

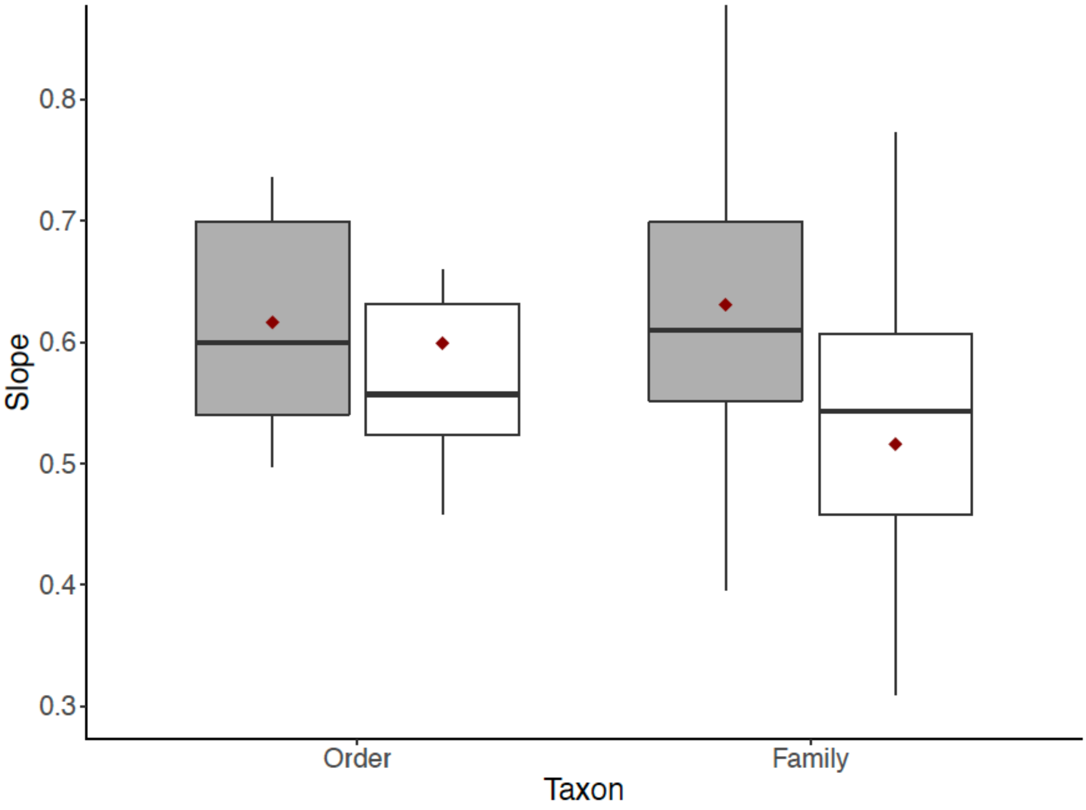

Table 1.

PGLS analysis of survival during 1st year (a) and until age at first reproduction (b) in a set of wild primates with all relevant information. Lambda (which quantifies the magnitude of the phylogenetic signal in the model residuals) is 0 in both cases.

(a) Survival during first year

variable	**estimate**	**s.e.**	**t**	**P**
Intercept	+0.803	0.203	3.95	0.001
Log brain mass (f)	+0.284	0.055	5.21	0.0001
Log body mass (f)	-0.148	0.043	-3.41	0.004

(b) Survival until age at first reproduction

variable	**estimate**	**s.e.**	**t**	**P**
Intercept	+0.534	0.184	2.90	0.011
Log brain mass (f)	+0.418	0.049	8.46	<0.0001
Log body mass (f)	-0.212	0.039	-5.38	<0.0001

Supplementary Materials

Published data on Survival until Age at First Reproduction (AFR) and during first year for 18 different primates species, along with their body mass and brain mass. References are listed below, along with notes on estimates.

Genus	**Species**	**Bo Wt ADF (kg)**	**Br Wt ADF (g)**	**AFR (yr)**	**Surv - AFR**	**Surv-1st yr**	**Source**
Propithecus	*diadema edwardsii*	5.50	38.3	5.5	0.20	0.50	1
Propithecus	*verreauxi*	2.76	26.2	6.0	0.30	0.52	2
Propithecus	*verreauxi*	3.20	26.2	5.0	0.22	0.55	3
Lemur	*catta*	2.20	22.1	3.2	0.20	0.48	4
Alouatta	*seniculus*	5.20	55.4	5.1	0.35	0.79	5
Alouatta	*palliata*	5.35	51.2	4.0	0.35	0.74	6
Cebus	*olivaceus*	2.50	69.0	7.0	0.61	0.82	7
Cebus	*capucinus*	2.30	69.0	6.5	0.63	0.79	8
Cebus	*nigritus*	2.50	64.2	6.4	0.58	0.70	9
Brachyteles	*arachnoides*	8.33	119.4	8.5	0.61	0.95	10
Presbytis	*thomasi*	6.70	57.7	5.4	0.30	0.54	11
Papio	*cynocephalus*	12.80	150.0	5.5	0.57	0.77	12
Cercopithecus	*mitis*	4.20	66.0	7.5	0.67	0.86	13
Macaca	*fascicularis*	3.50	63.2	5.2	0.62	0.81	14
Macaca	*fuscata*	8.03	96.8	6.1	0.58	0.75	15
Hylobates	*lar*	5.40	101.5	10.5	0.53	0.89	16
Pongo	*pygmaeus*	35.50	338.0	14.8	0.91	0.98	17
Gorilla	*beringei*	95.00	433.0	9.5	0.61	0.79	18
Pan	*troglodytes*	34.00	357.0	14.0	0.70	0.83	19

Sources:

1. Pochron et al. 2004
2. Richard et al. 2002 (Beza Mahafaly) (brain size taken from species mean value)
3. Kappeler & Fichtel 2012 (Kirindy) (brain size taken from species mean value)
4. Gould et al. 2003 (survival until AFR estimated)
5. Robinson 1988 (data from Crockett)
6. Fröhlich et al. 1981
7. Robinson 1988 (brain size from Allen & Kay 2012).
8. Bronikowski et al. 2011 (see also Perry et al. 2012).
9. Janson et al. 2012 (body and brain for *Cebus apella* (closest relative, since robust, tufted capuchin; AFR from DiBitetti & Janson 2001)
10. Bronikowski et al. 2011 (AFR from Martins & Strier 2004; brain size from Allen & Kay 2012)
11. Wich et al. 2007 (brain size from *P. melalophos*- geographic sister species)
12. Bronikowski et al. (2011)
13. Bronikowski et al. (2011)
14. van Noordwijk & van Schaik (1999)
15. Takahata et al. (1998) (Yakushima; no survival until AFR for Kinkazan)

16. Reichard & Barelli (2008) & Reichard et al. (2012). Survival to AFR is average of a low and a high estimate: 0.46 given by Reichard & Barelli, and 0.60 based on Reichard et al. 2012).
17. van Noordwijk et al. (2018)
18. Bronikowski et al. 2011
19. Wood et al. (2017) (Ngogo: the site least affected by disease and with no negative population growth) (AFR from Robson et al. 2006)

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