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# Why are there so few smart mammals (but so many smart birds)?

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**The expensive brain hypothesis predicts an interspecific link between relative brain size and life-history pace. Indeed, animals with relatively large brains have reduced rates of growth and reproduction. However, they also have increased total lifespan. Here we show that the reduction in production with increasing brain size is not fully compensated by the increase in lifespan. Consequently, the maximum rate of population increase ( $r_{\max}$ ) is negatively correlated with brain mass. This result is not due to a confounding effect of body size, indicating that the well-known correlation between  $r_{\max}$  and body size is driven by brain size, at least among homeothermic vertebrates. Thus, each lineage faces a ‘grey ceiling’, i.e. a maximum viable brain size, beyond which  $r_{\max}$  is so low that the risk of local or species extinction is very high. We found that the steep decline in  $r_{\max}$  with brain size is absent in taxa with allomaternal offspring provisioning, such as cooperatively breeding mammals and most altricial birds. These taxa thus do not face a lineage-specific grey ceiling, which explains the far greater number of independent origins of large brain size in birds than mammals. We also predict that (absolute and relative) brain size is an important predictor of macroevolutionary extinction patterns.**

**Keywords:** encephalization; life history; speciation; intrinsic rate of increase; cognition

## 1. INTRODUCTION

The ‘expensive brain’ hypothesis proposes that the costs of an increase in brain size must be met by some combination of increasing the total energy turnover or a reduction in energy allocation to another expensive function such as maintenance or production (Isler & Van Schaik submitted). Among these responses, a trade-off with production (growth and reproduction) should be widespread, as its regulation is often responsive to environmental factors and thus easily modified by selection. This hypothesis explains why relatively large-brained mammals and birds often exhibit relatively slow development and maturation times and reduced fertility. However, low production must be compensated by increased reproductive lifespan to retain demographic

viability. Although large-brained animals do indeed exhibit increased adult lifespans (Isler & Van Schaik submitted), the question arises as to whether the increased lifespan can continue to compensate for the delayed maturation and increased interbirth intervals as brain size increases further. One must expect that adult mortality cannot be reduced indefinitely in the face of inevitable accidents and environmental calamities in autonomous animals that are not supported by their conspecifics.

To answer the question whether the prolonging of lifespan can sufficiently compensate for reduced production in relatively large-brained animals, we compare brain size with the maximum rate of population increase ( $r_{\max}$ ), defined in Cole’s (1954) equation as a combination of maximum reproductive lifespan and annual offspring production per female. It is known that  $r_{\max}$ , which reflects a population’s growth rate under optimal conditions, is negatively correlated with body size (Hennemann 1983). Here we ask whether in eutherian mammals this correlation is actually caused by the effect of brain size. An  $r_{\max}$ –brain size trade-off would indicate that there is a maximum viable brain size (‘grey ceiling’) for any given lineage.

If this trade-off is indeed due to the energetic costs of maintaining and producing absolutely or relatively large brains, we predict that the  $r_{\max}$ –brain size trade-off should weaken or even disappear when mothers receive help from conspecifics. Any allomaternal care, be it aimed at the mother or the offspring, and be it by the father or other conspecifics, allows for increased production and perhaps survival, and hence increased expected lifespan. This strong prediction will be tested for cooperatively breeding mammals and for the other class of homeothermic vertebrates, birds.

Birds are oviparous, and young of precocial birds must feed themselves immediately after hatching, so all energy provided by the parents must be put in the egg. Altricial birds have managed to overcome this limitation by evolving extensive provisioning during the hatchling period, which is shared between mothers, fathers and sometimes other conspecifics (81% of all bird species show biparental and 9% cooperative care, Cockburn 2006). In birds, precociality is the ancestral development mode, and altriciality has independently evolved multiple times (Ricklefs & Starck 1998). Consistent with our hypothesis, it has long been known that altricial birds have larger brains on average than precocials (e.g. Portmann 1947). More precisely, we predict that in altricial birds there is no negative relationship between  $r_{\max}$  and brain mass, controlling for body mass effects.

## 2. MATERIAL AND METHODS

We compiled data on fertility rates, age of first reproduction, maximum lifespan, body mass and brain mass of 536 eutherian mammals and 399 avian species from the literature. We obtained  $r_{\max}$  by solving Cole’s (1954) equation numerically. Details of data compilation and the comparative analyses including phylogenetic independent contrasts (IC) are given in the electronic supplementary material. In mammals, species were defined as precocial if the young open their eyes at birth or shortly thereafter. In birds, development modes were altricial, semi-altricial, semi-precocial and precocial (Iwaniuk & Nelson 2003).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2008.0469> or via <http://journals.royalsociety.org>.

One contribution of 10 to a Special Feature on ‘Brain evolution’.

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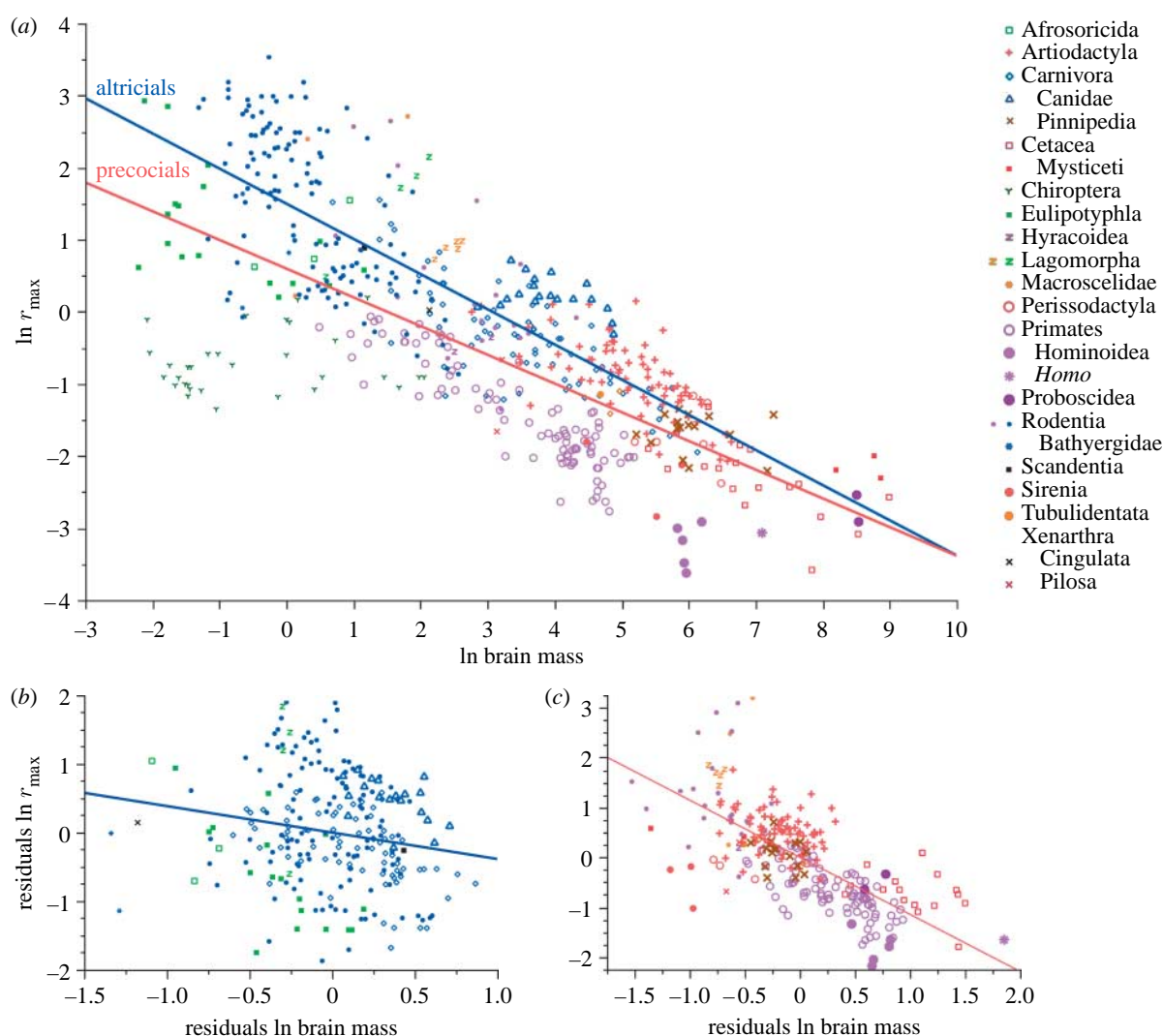


Figure 1. (a) Least-squares regression of  $\ln r_{\max}$  on  $\ln$  brain mass in eutherian mammals ( $n=536$ , *Homo* excluded). The regressions of the residuals of  $\ln r_{\max}$  on the residuals of  $\ln$  brain mass are shown for (b) altricials and (c) precocials separately. Full statistical details are given in the electronic supplementary material.

### 3. RESULTS

In mammals,  $r_{\max}$  is negatively correlated with body mass, as expected. However,  $r_{\max}$  shows a much stronger negative correlation with brain size (figure 1; for bivariate regressions, see the electronic supplementary material), also after controlling for the effect of body mass (table 1; multiple regressions). Indeed, once the effect of brain mass is taken into account, the effect of body mass on  $r_{\max}$  is positive, rather than negative (table 1; in precocials and most of the orders). This relationship is not a statistical artefact that arises because the size of organs is actually a better estimate of body size than body mass itself (Harvey & Krebs 1990), as it is only observed for brain size, but not for other organs (see the electronic supplementary material). In conclusion, consistent with the expensive brain hypothesis, among mammals  $r_{\max}$  is largely driven by brain size, not body size.

Given that these results support the expensive brain hypothesis, we can examine the prediction that species or lineages that increase their brain size without further reducing  $r_{\max}$  must have significant allomaternal inputs. In mammals, this seems likely for members of the family of Canidae, most of which are

biparental or cooperative breeders and which show both relatively large brains and high  $r_{\max}$  (cf. figure 1). Within this family there is no correlation, and if this family is excluded, the negative effect of brain size on  $r_{\max}$  among the remaining carnivores becomes much stronger (table 1).

In birds, we find that  $r_{\max}$  is negatively correlated with brain size only in precocials and semi-precocials, but not in altricials or semi-altricials (figure 2; table 1). In addition, as in mammals, the independent effect of body mass on  $r_{\max}$  is positive rather than negative in precocial and semi-precocial birds (table 1).

In all groups analysed, the correlation between  $r_{\max}$  and brain size is much more driven by fertility rate than reproductive lifespan (table 2).

### 4. DISCUSSION

The observed trade-off between the maximum rate of population increase ( $r_{\max}$ ) and both absolute and relative brain size supports the notion that this trade-off is caused by an energetic constraint, especially since it disappears in lineages where the mother's energetic burden during reproduction is alleviated through helpers. Thus, our results fully support the

Table 1. Multiple least-squares regressions of  $r_{\max}$  in mammals and birds (ln  $r_{\max}$  as dependent variable, ln brain mass and ln body mass as independent variables, *Homo* excluded), for both species-level data (raw) or IC. (Significant effects are shown in *italics*.)

				brain mass		body mass	
	method	<i>n</i>	<i>r</i> <sup>2</sup>	<i>p</i> -value	slope	<i>p</i> -value	slope
<i>mammals</i>							
all species	raw	536	0.596	<0.0001	−0.955	<0.0001	+0.389
	IC	535	0.130	<0.0001	−0.428	0.353	+0.054
altricials	raw	249	0.597	0.005	−0.385	0.439	−0.079
	IC	248	0.116	0.032	−0.357	0.951	−0.006
precocials	raw	256	0.618	<0.0001	−1.157	<0.0001	+0.534
	IC	255	0.162	<0.0001	−0.519	0.068	+0.115
terrestrial Carnivora	raw	98	0.481	0.191	−0.267	0.385	−0.116
	IC	97	0.256	0.0006	−0.649	0.183	+0.154
non-canid Carnivora	raw	79	0.673	<0.0001	−0.893	0.039	+0.264
	IC	78	0.360	<0.0001	−0.976	0.014	+0.325
<i>birds</i>							
all species	raw	388	0.352	<0.0001	−0.433	0.398	+0.042
	IC	387	0.132	0.294	−0.082	0.0007	−0.167
altricials	raw	137	0.532	0.264	+0.115	<0.0001	−0.306
	IC	136	0.123	0.216	−0.168	0.742	−0.032
semi-altricials	raw	77	0.670	0.649	−0.070	<0.0001	+0.362
	IC	76	0.332	0.586	+0.085	<0.0001	−0.443
semi-precocials	raw	42	0.326	0.0002	−1.986	0.0005	+1.201
	IC	41	0.315	0.0007	−1.772	0.002	+1.074
precocials	raw	132	0.259	<0.0001	−0.854	0.0004	+0.368
	IC	131	0.161	0.0002	−0.561	0.158	+0.115

expensive brain hypothesis, which predicts that relatively large brains can evolve only when either energy input increases (Isler & Van Schaik 2006b) or there is an allocation shift from another expensive body function, such as production, or the size of an expensive tissue, such as the digestive tract in primates (Aiello & Wheeler 1995) or the pectoral muscle in birds (Isler & Van Schaik 2006a). To our knowledge, this framework is the only one that accounts for the well-known correlation between life-history patterns and brain size (reviewed in Deaner *et al.* 2003; Barrickman *et al.* 2008), while at the same time incorporating the energetic consequences of lifestyles that are influenced by ecological conditions of habitat and diet.

The  $r_{\max}$ –brain size trade-off indicates that there is a maximum viable brain size for a species (its grey ceiling), beyond which viable populations cannot be sustained. The rate  $r_{\max}$  represents the ability of a species to recover from population crashes due to starvation, disease or other evolutionary disasters, and therefore indexes the risk of local extinction. In species with low  $r_{\max}$ , temporarily high rates of mortality are not easily buffered, so genetically based adaptation to environmental changes is hindered owing to the very limited room for selective mortality. Although it is impossible to pinpoint the exact value of this grey ceiling for any given lineage, it should depend on the stability of the habitat and the species' ability to buffer itself from such fluctuations, and thus its lifestyle. We assume that extant great ape species are very close to the absolute minimum viable  $r_{\max}$ , and thus to the grey ceiling for primates. A similar value may apply to cetaceans, although valid estimates

of maximum lifespan are notoriously difficult to obtain for these animals. In other lineages that are neither arboreal nor oceanic, the threshold may be considerably higher, as they may more often suffer from periodic population crashes.

These analyses demonstrate that at least in the precocial mammals and birds examined here, brain size, rather than body size, drives the value of  $r_{\max}$ , and therefore a species' extinction risk. Thus, we propose that the historical pattern of species extinctions, generally attributed to large body size (Brook & Bowman 2005; but see Pimm *et al.* 1988), is instead at least partly driven by large brain size. Despite substantial benefits of enhanced cognitive abilities (e.g. Sol *et al.* 2007), we therefore predict that during mass extinctions large-brained taxa are especially vulnerable. On a macroevolutionary time scale, homoeothermic vertebrates tend to increase their brain size (but not in reptiles: Jerison 1969). Owing to the  $r_{\max}$ –brain size trade-off, reproductive capacity decreases at the same time, leading taxa to a 'drift' towards ever-lower  $r_{\max}$ . Over evolutionary time, we therefore also predict that lineages will tend to evolve towards a maximum sustainable brain size, and that every clear increase in brain size beyond their grey ceiling is accompanied by a significant change in lifestyle (usually accompanied by the emergence of a new lineage).

But what change of lifestyle would allow the evolution of larger brained lineages? Our results show that, as predicted by the expensive brain hypothesis, allomaternal energy inputs during offspring production are one critically important factor. In lineages in which mothers are helped, such as altricial birds or



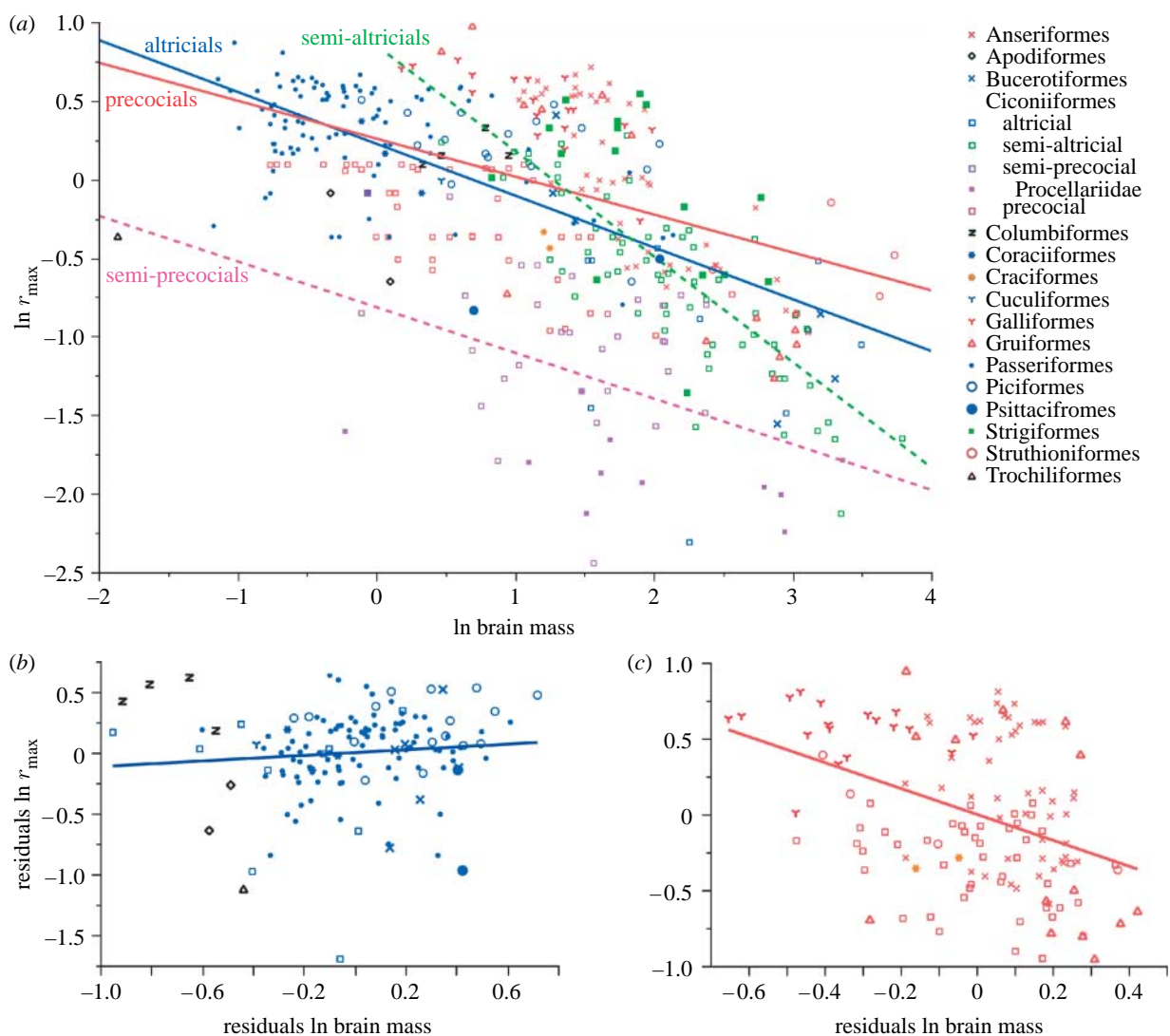


Figure 2. (a) Least-squares regression of  $\ln r_{\max}$  on  $\ln$  brain mass in birds ( $n=389$ ). The regressions of the residuals of  $\ln r_{\max}$  on the residuals of  $\ln$  brain mass are shown for (b) altricials and (c) precocials separately. Full statistical details are given in the electronic supplementary material.

Table 2. Partial correlation coefficients between life-history components of  $r_{\max}$  (maximum reproductive period (MaxRP = max lifespan – age at first reproduction) and fertility) and (a)  $r_{\max}$  or (b) brain mass, partialling out body mass and the other life-history variable. (Partial correlation coefficients ( $r$ ) and their  $p$ -values for species-level data are given; significant values are shown in *italics*.)

		altricials		precocials	
		$r$	$p$ -value	$r$	$p$ -value
(a) $r_{\max}$	mammals				
	maxRP	0.018	0.783	–0.276	< 0.0001
	fertility	0.765	< 0.0001	0.918	< 0.0001
	birds				
(b) brain mass	mammals				
	maxRP	–0.049	0.566	–0.034	0.704
	fertility	0.837	< 0.0001	0.862	< 0.0001
	birds				
(b) brain mass	mammals				
	maxRP	0.281	< 0.0001	0.044	0.482
	fertility	–0.189	0.003	–0.601	< 0.0001
	birds				
(b) brain mass	mammals				
	maxRP	0.068	0.428	0.217	0.015
	fertility	0.120	0.158	–0.239	0.007

canid carnivores, the  $r_{\max}$ –brain size trade-off is not found. This means that allomaternal care enables species to increase their brain size without compromising their demographic viability. More generally, we propose that extensive allomaternal care will allow

brain size, and thus also cognitive abilities, to increase relative to their independently breeding relatives when conditions favour this.

This also explains why there are many lineages of birds that independently evolved relatively large

brains (Nealen & Ricklefs 2001), but only a few in mammals (for phylogenetic analyses, see the electronic supplementary material). For 127 bird families from 23 orders, the upper 10 per cent quantile of brain mass residuals contains 13 families in seven different orders (Bucerotiformes, Psittaciformes, Pici-formes, Strigiformes, Passeriformes and Ciconii-formes), all of which are altricial or semi-altricial. On the other hand, for 109 eutherian mammal families from 18 orders, the upper 15 per cent quantile of brain mass residuals contain 16 families in only two orders (Cetacea and Primates). In the absence of systematic comparisons, we draw attention to one spectacular example, *Homo sapiens* (see Van Schaik & Isler submitted). Humans have evolved allomaternal provisioning of offspring and allocare among adults, especially for the benefit of reproducing females (Hrady 2005), and increased brain size approximately threefold relative to their sister group, the genus *Pan*.

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