Relative Pituitary Gland Size Predicts Mammal Life History Variation

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Relative Pituitary Gland Size Predicts Mammal Life History Variation

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Running title: Pituitary Gland Size and Mammal Life History
Abstract

At the proximate level, hormones are known to play a critical role in influencing the life history of mammals, including humans. The pituitary gland is directly responsible for producing several hormones, including those related to growth and reproduction. Although we have a basic understanding of how hormones affect life history characteristics, we still have little knowledge of this relationship in an evolutionary context. We used data from 129 mammal species representing 14 orders to investigate the relationship between pituitary gland size and life history variation. Because pituitary gland size should be related to hormone production and action, we predicted that species with relatively large pituitaries should be associated with fast life histories, especially increased fetal and postnatal growth rates. Phylogenetic analyses revealed that total pituitary size and the size of the anterior lobe of the pituitary significantly predicted a life history axis that was correlated with several traits including body mass, and fetal and postnatal growth rates. Additional models directly examining the association between relative pituitary size and growth rates produced concordant results. We also found that relative pituitary size variation across mammals was best explained by an Ornstein-Uhlenbeck model of evolution, suggesting an important role of stabilizing selection. Our results support the idea that the size of the pituitary is linked to life history variation through evolutionary time. This pattern is likely due to mediating hormone levels but additional work is needed. We suggest that future investigations incorporating endocrine gland size may be critical for understanding life history evolution.

Keywords: brain evolution, growth factor, phylogenetic comparative methods, proximate mechanisms, macroevolution, primates, ungulates, bats
Introduction

Life history traits vary noticeably across and within species and are influenced by a variety of ultimate and proximate factors (Calder, 1984; Austad & Fischer, 1991; Charnov, 1991; Stearns, 1992; Hawkes et al., 1998; Ricklefs & Wikelski, 2002; Gaillard et al., 2003; Kamilar et al., 2010; Kamilar & Cooper, 2013). From an ultimate perspective, comparative analyses have yielded important insights into the evolutionary variables that underlie life history variation. For instance, environmental conditions related to temperature and food abundance can impact species growth rates and the timing of reproduction (Western, 1979; Promislow & Harvey, 1990; Martin, 1995; Gillooly et al., 2002). Other researchers argue that mortality rates should impact life history variation (Brown & Sibly, 2006). In particular, species experiencing high mortality rates (e.g. due to high predation) are associated with an earlier age of first reproduction, shorter lifespans, and/or increased growth rate (Wilkinson & South, 2002).

At the proximate level, a variety of hormones are known to play a critical role in influencing the behavior and life history of mammals, including humans (Bribiescas, 2001; Holzenberger et al., 2003; Dantzer & Swanson, 2012). Most of this research is focused on single species studies, demonstrating important connections between hormone signaling and biological variation across and within age/sex classes. Burnham et al. (2003) showed that human males in committed, romantic relationships exhibited 21% lower testosterone levels compared to other men. Males with lower testosterone levels are not more successful in attracting mates. Rather, longitudinal research has demonstrated that men with higher testosterone levels were more likely to be partnered
4.5 years later, but that those who became partnered fathers experienced significant declines in testosterone levels (Gettler et al., 2011).

Hormones are produced from multiple glands in the body. The pituitary gland is directly responsible for producing several hormones, including those related to growth and reproduction. For example, the anterior pituitary produces growth hormone (GH), thyroid stimulating hormone, and prolactin, and the posterior pituitary produces oxytocin and vasopressin (Melmed, 2011). In addition, some of these hormones, such as GH, target organs in the body and result in the subsequent production of additional hormones. In one pathway, the pituitary secretes GH, which targets the liver, stimulating the production of insulin-like growth factor 1 (IGF-1). Hormone signaling pathways are highly conserved, and are central to correlated responses in growth, reproduction, and survival. For example, the insulin/IGF pathway facilitates increased growth and reproduction in early life, and reduced signaling in part due to changes in gene expression, and increases lifespan in species as diverse as worms, flies, mice, and dogs (Kenyon, 2010).

In addition, evidence from experimental studies has supported the idea that the pituitary gland has a significant effect on animal life history. For example, experimental research in mice has shown that genetic mutations inhibiting the normal development of the anterior pituitary result in a substantial increase in longevity, most likely due to a reduction in GH and IGF-1 production (Flurkey et al., 2001; Bartke, 2005). Additionally, data from humans suggest that pituitary disorders, including tumors, can result in over-secretion of GH and lead to increased growth rates (Ayuk et al., 2004; Vierimaa et al., 2006). The relationship between pituitary size and mammal growth and life history is not
limited to genetically altered or pathological individuals. In fact, research from wild mammal populations has demonstrated that changes in the size and cell composition of the pituitary within species are related to variation in growth rates and female reproductive season and cycle stage (Richardson, 1979; Nelson & Inao, 1982). All of these studies demonstrate that the size of the pituitary is related to levels of hormone production, and that variation in pituitary-related hormone production affects growth, reproduction, and lifespan.

Hormone levels and life history traits are likely interrelated in mammal species, based on recent interspecific studies. Buffenstein and Pinto (2009) noted that several hormones, including thyroxine, GH, and IGF-1 are secreted at lower levels in naturally long-lived rodents and bats. A recent study by Swanson and Dantzer (2014) using a phylogenetic comparative approach demonstrated that several life history characteristics, including maximum lifespan and neonate mass, were significantly related to interspecific differences in IGF-1 plasma concentrations across 41 mammal species. Both of these comparative studies suggest that evolutionary shifts in baseline hormone levels can alter life history traits.

Although we have a basic understanding of how hormones affect life history characteristics, we still have little knowledge of this relationship in an evolutionary context. Using a phylogenetic approach to understand how proximate mechanisms influence life history traits can provide important insights into evolutionary physiology and biology (Braendle et al., 2011; Williams, 2012). Therefore, we used a broad comparative dataset to investigate the relationship between relative pituitary gland size and several mammal life history traits. We are particularly interested in fetal and
postnatal growth rates because these traits are likely to be most affected by the production and action of relatively well-known hormones (e.g. GH and IGF-1). We predicted that species with relatively large pituitaries should be associated with increased fetal and postnatal growth rates. In addition, since the hormones related to these traits are produced by the pituitary's anterior lobe, we predicted that the size of the anterior lobe should be an even stronger predictor of growth. We expected to find a similar relationship between relative pituitary size and other life history traits that are known correlates of species growth rates, including maximum longevity and gestation.

Finally, we followed recent studies of trait evolution (Cooper & Purvis, 2010; Harmon et al., 2010) by testing three evolutionary models that may explain the diversity of mammal relative pituitary size: a random walk model (modeled as Brownian motion process), a random walk model with a single stationary peak (modeled as an Ornstein-Uhlenbeck process), and an early burst model where traits diversify rapidly early in the clade’s history, and trait evolution slows as time progresses (modeled as a Brownian motion process with an evolutionary rate change parameter).

Materials and methods

Data collection

We collected data from a total of 129 mammal species, which represented 14 orders (see Online Appendix A). In particular, five orders represent most of the species in our dataset: Primates (37 species), Rodentia (30 species), Chiroptera (17 species), Carnivora (12 species), and Artiodactyla, (10 species). We obtained pituitary size (post mortem volume) information for all species from the most comprehensive dataset
published to date (Bauchot & Legait, 1978). Bauchot and Legait (1978) included the
total size of the pituitary as well as the size of the anterior, intermediate, and posterior
lobes. In addition, Bauchot and Legait (1978) reported body and brain mass data (in
grams) for each species. We excluded data from domesticated species because
domestication has been suggested to influence the relative size of the pituitary
(Oboussier, 1940). Nearly all the data were obtained from adults, but the sexes were
not specified. Having a mixed sex sample represent species likely increased the
variation in the dataset and resulted in increased type II error in our analyses. We did
not examine the influence of the intermediate lobe on life history traits as this part of the
pituitary is highly variable and poorly studied across mammals (Bauchot & Legait,
1978).

We gathered data for ten life history traits: body mass, brain mass, gestation
length, neonate body mass, litter size, weaning age, weaning body mass, maximum
longevity, fetal growth rate, and postnatal growth rate. We chose these traits because
most of them have been used in recent studies of vertebrate life history evolution
(Catlett et al., 2010; Swanson & Dantzer, 2014). We followed previous studies by
calculating fetal growth rate as litter mass divided by gestation length (Lindenfors, 2002;
Tecot et al., 2012), and postnatal growth rate as litter mass at weaning minus litter mass
at birth, divided by age at weaning (Mitani & Watts, 1997). We obtained these data from
the PanTHERIA database (Jones et al., 2009). This database has been extensively
used in comparative studies examining the evolution of mammalian traits (Pontzer &
Kamilar, 2009; Kamilar et al., 2010; Cooper et al., 2011; Safi et al., 2011; Venditti et al.,
2011). Maximum longevity values were also based on data presented in another widely
used life history database, AnAge (Tacutu et al., 2013). Unfortunately, data associated with all the life history traits were not available for all species with pituitary size data. Therefore, we used different analytical approaches that included different subsets of species (see Appendix S1 for the data associated with each species).

Data analyses

Examining Life History Variation in Multivariate Space

First, we performed a principal components analysis (PCA) that included all 10 traits to examine life history diversity in multivariate space. This analysis included 69 species from our total dataset. We used the `prcomp` function in R (R_Development_Core_Team, 2014) and set the scale and center arguments to TRUE. These functions transform the variables to have unit variance and be zero centered before the analysis is run. We considered using a phylogenetic PCA (Revell, 2009) but the goal of the analysis was to quantify variation in the dataset as opposed to quantifying multivariate distances among taxa since they diverged (Revell, 2009; and Revell, Pers Comm). Therefore, a typical PCA is most appropriate.

Examining the Relationship between Pituitary Size and Life History Traits

We used phylogenetic generalized linear models (PGLS) with Pagel's lambda (Pagel, 1999; Freckleton et al., 2002; Nunn, 2011) to examine the relationship between pituitary size and multivariate space in life history traits. In each model, the optimal value of lambda was found using a likelihood approach. Total pituitary size and anterior lobe size were used as single predictors in separate PGLS models. Similarly, principal
components with eigenvalues greater than one were used as single dependent variables in separate models. This arrangement yielded four total models.

We used a second set of PGLS models to more directly examine the relationship between relative pituitary size and mammal growth rates. In addition, this approach allowed us to use a larger sample size than the PCA analysis because not all life history traits were required for each taxon. Each growth rate was used as a dependent variable in separate analyses and we conducted three analyses for each trait. Each analysis contained one of our variables of interest: total pituitary size, anterior lobe size, or posterior lobe size. We used the size of the pituitary’s posterior lobe as an “analytical control”, expecting no significant effect on life history variation because the posterior lobe, which is functionally associated with the hypothalamus, secretes oxytocin (OT) and arginine vasopressin (AVP) and not growth hormones. In addition, these hormones are actually synthesized by the hypothalamus and simply stored in the posterior lobe of the pituitary. Although prior research has shown that AVP influences social behavior, which in theory could influence life history traits such as growth rates and maximum longevity (though Kamilar et al., 2010 did not find a positive relationship between sociality and longevity in mammals), neuropeptide receptors have a stronger connection to behavior, not the hormone levels themselves (Insel, 2010). In addition, much of our knowledge of AVP and social behavior comes from studies examining a small number of rodent species (Winslow et al., 1993; Wang et al., 1996), and generalizing these findings to most mammal species is problematic (Insel, 2010). Considering these factors, we predicted that posterior lobe size would have little or no effect on growth rates. We also included brain mass and body mass as covariates in each model.
because these traits are known to be related to life history traits (Calder, 1984; Allman et al., 1993a; Allman et al., 1993b; Wilkinson & South, 2002; Leigh, 2004; Barton, 2006; Pontzer & Kamilad, 2009). In addition, pituitary gland size increases with body and brain size (Bauchot & Legait, 1978).

All data were log$_{10}$ transformed prior to analysis. We examined Q-Q plots, the distribution of phylogenetic residuals, and fitted value vs. residual value plots for each model to be confident that our data met the assumptions of our statistical tests. If we discovered outliers, then we re-ran the model with the outlier data points removed. All PGLS models were conducted with the caper package (Orme et al., 2014) for R (R_Development_Core_Team, 2014) and utilized the mammal supertree presented in Bininda-Emonds et al. (Bininda-Emonds et al., 2007; Bininda-Emonds et al., 2008).

Finally, we used a multi-model selection procedure to better understand the relative importance of the predictor variables and covariates in the second set of PGLS models. We examined several null models, which contained one or both covariates (body mass and/or brain mass). Additional models included one or both covariates along with each measure of pituitary size: total pituitary size, anterior lobe size, and posterior lobe size. We used Akaike Information Criterion corrected for small sample size (AICc) to judge model fit (Burnham & Anderson, 2002). We considered the model with the lowest AICc value as the best model and additional models within 2 AICc values of the best model as equally good (Burnham & Anderson, 2002).
We calculated relative total pituitary size and anterior lobe size from four sets of phylogenetic residuals that were subsequently used in our evolutionary modeling analyses. These residuals were produced from four PGLS models regressing the pituitary variable onto body mass or brain mass using log_{10} transformed data: total pituitary size ~ body mass, total pituitary size ~ brain mass, anterior lobe size ~ body mass, and anterior lobe size ~ brain mass. We used the fitContinuous function in the geiger package (Harmon et al., 2008) for R (R_Development_Core_Team, 2014) to test the three models of trait evolution. For each type of phylogenetic residual, we tested three models of evolution. We set the model argument to BM to model evolution via Brownian motion, OU to model Ornstein-Uhlenbeck evolution, and EB to model an early burst pattern of evolution. We judged the model fit based on AICc values (Burnham & Anderson, 2002). The best model exhibited the lowest value and other models within 2 AICc values of the best model were treated as equally good (Burnham & Anderson, 2002). All models used the mammal supertree presented in Bininda-Emonds et al (Bininda-Emonds et al., 2007; Bininda-Emonds et al., 2008). Polytomies were randomly resolved to a series of dichotomies with branch lengths of zero using the multi2di function in ape (Paradis et al., 2004).

Results
Examine Life History Variation in Multivariate Space

Our PCA of life history traits yielded two principal components (PC) with eigenvalues greater than 1 (eigenvalue of PC1 = 2.41 and PC2 = 1.49). Seven of the 10
variables exhibited similar loading values (between 0.310 and 0.383) and were positively related to PC1: body mass, brain mass, fetal growth rate, postnatal growth rate, gestation length, neonate mass, and weaning body mass (Table 1). Three life history variables heavily loaded on PC2, but in different directions: litter size (+), weaning age (-), and maximum longevity (-).

**Examining the Relationship between Pituitary Size and Life History Traits**

Based on our first set of PGLS models, total pituitary size was positively and significantly related to PC1 (estimate = 1.72, \( P<0.001, df=1,67 \)). Therefore, larger pituitaries were associated with increased values in the seven life history traits that loaded most heavily on PC1 (e.g. body mass, brain mass, fetal and postnatal growth rates). In contrast, total pituitary size was negatively related to PC2 and this relationship only approached statistical significance (estimate = -0.343, \( P=0.07, df=1,67 \)). The models examining the size of the anterior lobe of the pituitary produced similar results to those using total pituitary size.

Our second set of PGLS models, examining the relationship between pituitary size and mammal growth rates produced consistent results. We found that pituitary gland size was significantly related to fetal and postnatal growth rates in mammals, while accounting for body and brain mass. Based on AICc values, four equally good models predicted mammal fetal growth rates (Table 2). Two models contained total pituitary size and one or two covariates (brain and/or body mass), and two models contained anterior lobe size and one or two covariates. When we examined these models in more detail, the pituitary size variables were always positive and significant.
predictors of fetal growth rate ($P<0.001$) (Table 3). In addition, our null models, which
used only one or two covariates, produced poor models (Table 2). Similarly, the models
including posterior lobe size poorly explained fetal growth rates. The four marsupial
species in our dataset were outliers, exhibiting very low fetal growth rates for their
relative anterior pituitary size. Removing these species from the analyses produced
nearly identical results. We present a visual approximation between the anterior lobe
size and fetal growth rates in Fig. 1.

Our models predicting mammal postnatal growth rates produced concordant
results. Based on AICc values, we found three equally good models explaining
postnatal growth rates (Table 4). One model contained total pituitary size and body
mass. The other two models contained anterior lobe size and either body mass or body
mass and brain mass. Anterior lobe size was positively and significantly ($P<0.05$)
related to mammal postnatal growth rate in each model (Table 5). For the model
containing total pituitary size, this variable was positively associated with postnatal
growth rates at the $P=0.07$ level. Importantly, our null models poorly explained variation
in postnatal growth rates (Table 4). Poorly fitting models were also produced when
posterior lobe size was used as a predictor. We present a visual approximation between
the anterior lobe size and postnatal growth rates in Fig. 2.

We should note that the sample sizes varied between the fetal and postnatal
growth rate analyses because not all species contained data for both variables. More
importantly, the proportion of species from different orders is similar for the fetal and
postnatal growth rates analyses (but the latter analyses have a smaller total sample
size).
Modeling the Evolution of Relative Pituitary Size

We found that an Ornstein-Uhlenbeck model of trait evolution best explains relative total pituitary size and anterior lobe size (Table 6 and Figs. 3 and 4). These results are consistent, regardless of whether the pituitary is scaled to body mass or brain mass. Based on AICc values, both the Brownian motion and early burst models of evolution were much less likely to adequately explain pituitary size diversity.

Examining relative anterior lobe size on the mammal phylogeny reveals some interesting patterns. Accounting for body mass, relatively small anterior lobes are distributed throughout the mammal tree, but especially exhibited by many strepsirrhine primates (Fig. 3), *Spermophilus* and *Marmota* rodents, and marsupials. In contrast, *Phoca largha*, the spotted seal, clearly has the relatively largest anterior lobe. Some of these relative sizes differ when brain mass is accounted for, as opposed to body mass. In this case, primates exhibit the smallest relative anterior lobe sizes; this includes both strepsirrhine and haplorrhine species (Fig. 4). Relatively large anterior lobes are distributed throughout the mammal tree, but are especially exhibited by the tenrecs and caviid rodents. The relative total pituitary size exhibited similar patterns so is not displayed here.

Discussion

We provide the first evidence that the size of the pituitary is linked to life history variation, especially growth rates, across a broad sample of mammal species. Our study demonstrates that the known connection between pituitary size and life history variation
at the intraspecific level is also found at the interspecific scale across mammals. Our findings that total pituitary gland size and anterior lobe size (accounting for brain and body mass) were positively associated with fetal and postnatal growth rates across a diverse set of mammalian species suggests that this connection represents coevolution through deep evolutionary time. As expected, we found no effect of relative posterior lobe size on life history variation. This further supports our idea that secretion of hormones produced directly and indirectly by the anterior lobe (e.g. GH and IGF-1, respectively) is the major factor driving growth rates.

Investigating the ultimate explanations for life history variation has been a major focus of evolutionary biology research (Roff, 1992; Stearns, 1992; Kappeler & Pereira, 2003), though integrating proximate mechanisms into a comparative life history framework is relatively rare (but see Lessells, 2008; Swanson & Dantzer, 2014). Whereas body mass is known to vary with life history traits across species (Harvey & Clutton-Brock, 1985; Harvey et al., 1991), others have demonstrated that interspecific variation in life history traits is related to a wide variety of factors, such as total energy budget size (Pontzer & Kamilar, 2009), energy expenditure (Charnov & Berrigan, 1993; Pontzer et al., 2010; Barton & Capellini, 2011), and mortality rate (Promislow & Harvey, 1990). Work by Allman and colleagues (1993b) linked various brain structures with primate lifespan, though did not offer a mechanistic explanation for many of the significant relationships.

At the proximate level, several studies have found an important connection between hormone signaling and life history. For example, the hypothalamic-pituitary-adrenal axis, or stress hormone axis, plays a role in early life history transitions (Crespi
et al., 2013) and the hypothalamic-pituitary-gonadal axis helps mediate trade-offs between mating and parenting effort (Wingfield et al., 1990; Maney, 2008). Various hormones are known to mediate the relationship between the anterior pituitary and growth (Melmed, 2011). For example, relatively large pituitaries produce more GH and stimulate the production of IGF-1 in the liver (Ayuk et al., 2004; Vierimaa et al., 2006), resulting in increased growth rates (Kenyon, 2010). In addition to levels of hormone secretion, a host of other factors can influence hormone action, such as genetics, the number and affinity of receptors, and binding proteins (Romero, 2004). While further research is necessary to confirm the mechanism(s) responsible for the positive relationships between pituitary gland size and growth across mammal species, we suggest that interspecific variation in relative anterior pituitary gland size reflects hormone production and likely action (i.e., growth).

Although our study focused on broad patterns across distantly related mammal species, we did include data from humans. Although humans have relatively large brains for their body size (Barton, 2006), humans are not unusual compared to other mammals in the relationship between relative pituitary size and growth rates. Humans are not an outlier in any of our analyses, which is notable considering their very slow development, coupled with earlier weaning and relatively fast reproduction (Ellison, 2001). In other words, in terms of explaining growth rates, the size of the human pituitary is expected for a mammal of their brain and body size. Interestingly, a recent study by Barton and Venditti (2013) found that another component of the human brain, the frontal lobe, is not unusually large when compared to other mammals.
An Ornstein-Uhlenbeck model best explains relative pituitary size diversity among mammals. This model supports the idea that pituitary size evolution is constrained. The typical mechanism invoked to explain this constraint is stabilizing selection (Cooper & Purvis, 2010; Harmon et al., 2010). It may not be too surprising that an endocrine gland responsible for producing several hormones related to essential physiological processes exhibits a relatively slow rate of evolution. Our finding for pituitary gland size contrasts findings from a recent paper by Cooper and Purvis (Cooper & Purvis, 2010) that modeled the evolution of mammal body mass. They found that an early burst model best explained body mass variation, with this trait evolving quickly in the early history of mammals and then slowing through time. The fact that different models of evolution best explain mammal body mass and pituitary size suggests that these traits have evolved independently to some extent.

In summary, our study demonstrates the importance of examining biological traits that are often investigated at the proximate level, in a broader evolutionary context (Braendle et al., 2011; Crespi et al., 2013). By using a phylogenetic comparative approach to explore some of the complex relationships between hormones and life history traits, our findings lead us to suggest that pituitary size has evolved in concert with life history characteristics, especially fetal and postnatal growth rates. At this point, we cannot be certain of the direction of causality in this relationship. It is possible that selection on pituitary size is a byproduct of selection on life history traits. For example, pituitary size may be affected by selection on growth rates or reproductive cyclicity in response to ecological or social pressures. In addition, it is interesting to note that the relationship between pituitary-related hormone levels and other life history axes, such
as those related to maximum longevity, is less clear. For instance, at the intraspecific
level, over-secretion and inhibition of hormones of pituitary origin are associated with
reduced and increased longevity, respectively (Flurkey et al., 2001; Ayuk et al., 2004;
Bartke, 2005; Vierimaa et al., 2006). However, a comparative study conducted by Stuart
and Page (2010) that found no relationship between maximum lifespan and IGF-1 levels
across 36 mammal species. Interestingly, recent work by Swanson and Dantzer (in
press) did find a significant negative relationship between IGF-1 levels and a life history
principal component that is heavily loaded by maximum longevity.

Future work should benefit from advances in laboratory methods and the
reduced cost of laboratory work that can provide a wealth of new information regarding
the hormone characteristics of a wide range of mammals. The increased availability of
hormone related data for numerous species should spur new research into the
comparative evolution of these traits. In addition, quantitative analyses incorporating
data from other endocrine glands (e.g. hypothalamus, thymus, thyroid) may provide a
more complete picture of the hormone synthesis pathways in an evolutionary context.
Finally, complementary genetic and epigenetic data on variation in hormone signaling,
behavior, and life history are required to better understand the complex interactions
between proximate mechanisms and resultant biological characteristics (Kenyon, 2010;
Holekamp et al., 2013). We demonstrate that associated data related to endocrine
gland size may be critical for fully understanding life history evolution.
Acknowledgments

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Cambridge.


Figure Legends

Figure 1. Plot of anterior lobe of the pituitary residuals (accounting for brain mass) versus fetal growth rate residuals (accounting for brain mass) across mammals. Different mammal clades are highlighted. Note that the four marsupial species in the dataset exhibit the lowest fetal growth rate values. Data are in log$_{10}$ space.

Figure 2. Plot of anterior lobe of the pituitary residuals (accounting for brain mass) versus postnatal growth rate residuals (accounting for brain mass) across mammals. Different mammal clades are highlighted. Data are in log$_{10}$ space.

Figure 3. Plot of phylogenetic residuals from a PGLS regression of anterior lobe pituitary size on body mass. The mammal Orders with the largest sample sizes are highlighted: Primates, Rodentia, and Chiroptera.

Figure 4. Plot of phylogenetic residuals from a PGLS regression of anterior lobe pituitary size on brain mass. The mammal Orders with the largest sample sizes are highlighted: Primates, Rodentia, and Chiroptera.
Table 1. Loadings of original variables on principal component axes.

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<td>-0.808</td>
<td>0.015</td>
<td>0.270</td>
<td>0.182</td>
<td>-0.206</td>
<td>-0.124</td>
<td>-0.013</td>
<td>0.017</td>
</tr>
<tr>
<td>Weaning age</td>
<td>0.215</td>
<td>-0.432</td>
<td>-0.256</td>
<td>0.631</td>
<td>0.384</td>
<td>-0.246</td>
<td>0.266</td>
<td>0.129</td>
<td>-0.090</td>
<td>-0.011</td>
</tr>
<tr>
<td>Weaning body mass</td>
<td>0.353</td>
<td>0.276</td>
<td>0.115</td>
<td>0.360</td>
<td>-0.176</td>
<td>0.131</td>
<td>-0.320</td>
<td>0.040</td>
<td>-0.200</td>
<td>-0.681</td>
</tr>
<tr>
<td>Maximum longevity</td>
<td>0.258</td>
<td>-0.470</td>
<td>-0.220</td>
<td>-0.140</td>
<td>-0.264</td>
<td>-0.228</td>
<td>-0.466</td>
<td>-0.529</td>
<td>-0.137</td>
<td>0.085</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>2.409</td>
<td>1.486</td>
<td>0.863</td>
<td>0.729</td>
<td>0.508</td>
<td>0.446</td>
<td>0.350</td>
<td>0.284</td>
<td>0.215</td>
<td>0.072</td>
</tr>
</tbody>
</table>
Table 2. Multimodel selection using AICc to predict fetal growth rates in mammals.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>AICc</th>
<th>Delta AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total pituitary + Body mass + brain mass</td>
<td>36.703</td>
<td>0.000</td>
</tr>
<tr>
<td>Anterior lobe + Body mass + brain mass</td>
<td>36.902</td>
<td>0.199</td>
</tr>
<tr>
<td>Total pituitary + Body mass</td>
<td>37.612</td>
<td>0.908</td>
</tr>
<tr>
<td>Anterior lobe + Body mass</td>
<td>37.678</td>
<td>0.975</td>
</tr>
<tr>
<td>Body mass</td>
<td>47.008</td>
<td>10.304</td>
</tr>
<tr>
<td>Posterior lobe + Body mass</td>
<td>48.008</td>
<td>11.305</td>
</tr>
<tr>
<td>Body mass + brain mass</td>
<td>49.040</td>
<td>12.336</td>
</tr>
<tr>
<td>Posterior lobe + Body mass + brain mass</td>
<td>50.145</td>
<td>13.442</td>
</tr>
<tr>
<td>Brain mass</td>
<td>81.213</td>
<td>44.510</td>
</tr>
</tbody>
</table>

Best models are in italics
Models within 2 AICc values of the best model are considered equally good
Table 3. Best phylogenetic generalized linear models predicting fetal growth rate across mammal species based on AICc values. See Table 2 for AICc values.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.235</td>
<td>0.304</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total pituitary volume</td>
<td>0.531</td>
<td>0.136</td>
<td>3.909</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.389</td>
<td>0.098</td>
<td>3.994</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brain mass</td>
<td>-0.241</td>
<td>0.136</td>
<td>-1.768</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.746$, $p$ value $<$0.001, lambda = 0.967, df = 4,119

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.221</td>
<td>0.307</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior lobe volume</td>
<td>0.445</td>
<td>0.113</td>
<td>3.917</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.438</td>
<td>0.092</td>
<td>4.786</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brain mass</td>
<td>-0.236</td>
<td>0.134</td>
<td>-1.756</td>
<td>0.082</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.745$, $p$ value $<$0.001, lambda = 0.970, df = 4,119

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.112</td>
<td>0.296</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total pituitary volume</td>
<td>0.412</td>
<td>0.120</td>
<td>3.437</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.315</td>
<td>0.089</td>
<td>3.538</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.742$, $p$ value $<$0.001, lambda = 0.960, df = 3,120

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.102</td>
<td>0.298</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior lobe volume</td>
<td>0.348</td>
<td>0.101</td>
<td>3.432</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.354</td>
<td>0.079</td>
<td>4.487</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.741$, $p$ value $<$0.001, lambda = 0.961, df = 3,120

All variables were log$_{10}$ transformed prior to analysis.
Table 4. Multimodel selection using AICc to predict postnatal growth rates in mammals.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>AICc</th>
<th>Delta AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior lobe + Body mass</td>
<td>79.046</td>
<td>0.000</td>
</tr>
<tr>
<td>Anterior lobe + Body mass + brain mass</td>
<td>80.105</td>
<td>1.059</td>
</tr>
<tr>
<td>Total pituitary + Body mass</td>
<td>80.777</td>
<td>1.731</td>
</tr>
<tr>
<td>Body mass</td>
<td>82.019</td>
<td>2.973</td>
</tr>
<tr>
<td>Total pituitary + Body mass + brain mass</td>
<td>82.238</td>
<td>3.191</td>
</tr>
<tr>
<td>Posterior lobe + Body mass</td>
<td>83.418</td>
<td>4.372</td>
</tr>
<tr>
<td>Body mass + brain mass</td>
<td>83.809</td>
<td>4.763</td>
</tr>
<tr>
<td>Posterior lobe + Body mass + brain mass</td>
<td>85.607</td>
<td>6.561</td>
</tr>
<tr>
<td>Brain mass</td>
<td>88.347</td>
<td>9.301</td>
</tr>
</tbody>
</table>

Best models are in italics

Models within 2 AICc values of the best model are considered equally good
Table 5 Best phylogenetic generalized linear models predicting postnatal growth rate across mammal species based on AICc values. See Table 4 for AICc values.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.232</td>
<td>0.423</td>
<td>-0.549</td>
<td>0.585</td>
</tr>
<tr>
<td>Anterior lobe volume</td>
<td>0.395</td>
<td>0.174</td>
<td>2.268</td>
<td>0.026</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.250</td>
<td>0.136</td>
<td>1.842</td>
<td>0.070</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.584$, p value $<0.001$, lambda = 0.890, df = 3,73

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.372</td>
<td>0.425</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior lobe volume</td>
<td>0.551</td>
<td>0.218</td>
<td>2.531</td>
<td>0.014</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.351</td>
<td>0.158</td>
<td>2.217</td>
<td>0.030</td>
</tr>
<tr>
<td>Brain mass</td>
<td>-0.313</td>
<td>0.249</td>
<td>-1.260</td>
<td>0.212</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.604$, p value $<0.001$, lambda = 0.848, df = 4,72

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.375</td>
<td>0.414</td>
<td>-0.905</td>
<td>0.368</td>
</tr>
<tr>
<td>Total pituitary</td>
<td>0.363</td>
<td>0.198</td>
<td>1.836</td>
<td>0.070</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.282</td>
<td>0.147</td>
<td>1.916</td>
<td>0.059</td>
</tr>
</tbody>
</table>

Model $r^2 = 0.575$, p value $<0.001$, lambda = 0.888, df = 3,73

All variables were log_{10} transformed prior to analysis.
Table 6. Results from trait evolution models explaining variation in pituitary size across mammals.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Brownian Motion</th>
<th>Ornstein-Uhlenbeck</th>
<th>Early Burst</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>σ²</td>
<td>log-lk</td>
<td>AICc</td>
</tr>
<tr>
<td>Relative pituitary size¹</td>
<td>0.001</td>
<td>33.98</td>
<td>-63.89</td>
</tr>
<tr>
<td>Relative pituitary size²</td>
<td>0.001</td>
<td>23.64</td>
<td>-43.23</td>
</tr>
<tr>
<td>Relative anterior lobe size¹</td>
<td>0.002</td>
<td>3.10</td>
<td>-2.15</td>
</tr>
<tr>
<td>Relative anterior lobe size²</td>
<td>0.002</td>
<td>1.71</td>
<td>0.63</td>
</tr>
</tbody>
</table>

¹ Based on the phylogenetic residuals from a PGLS model using body mass as a predictor
² Based on the phylogenetic residuals from a PGLS model using brain mass as a predictor

Three models of evolution were tested for each variable, with values in bold font indicating the best model

σ² = Brownian motion parameter (net rate of evolution)
α = OU parameter (constraint)
r = EB parameter (change in evolutionary rate through time)
<table>
<thead>
<tr>
<th>Species</th>
<th>Order</th>
<th>BodyMass(g)</th>
<th>BrainMass(g)</th>
<th>AntLobeVol(mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acomys_cahirinus</td>
<td>Rodentia</td>
<td>39</td>
<td>0.91</td>
<td>0.372</td>
</tr>
<tr>
<td>Alouatta_seniculus</td>
<td>Primates</td>
<td>3560</td>
<td>46.8</td>
<td>13.466</td>
</tr>
<tr>
<td>Anoura_caudifer</td>
<td>Chiroptera</td>
<td>10.4</td>
<td>0.44</td>
<td>0.209</td>
</tr>
<tr>
<td>Anoura_geoffroyi</td>
<td>Chiroptera</td>
<td>15.1</td>
<td>0.55</td>
<td>0.379</td>
</tr>
<tr>
<td>Antidorcas_marsupialis</td>
<td>Artiodactyla</td>
<td>35750</td>
<td>134.25</td>
<td>120.103</td>
</tr>
<tr>
<td>Aotus_trivirgatus</td>
<td>Primates</td>
<td>830</td>
<td>17.1</td>
<td>5.499</td>
</tr>
<tr>
<td>Arctocephalus_pusillus</td>
<td>Carnivora</td>
<td>85000</td>
<td>327</td>
<td>146.597</td>
</tr>
<tr>
<td>Artibeus_jamaicensis</td>
<td>Chiroptera</td>
<td>39.3</td>
<td>1.09</td>
<td>0.844</td>
</tr>
<tr>
<td>Artibeus_lituratus</td>
<td>Chiroptera</td>
<td>44.9</td>
<td>1.26</td>
<td>0.707</td>
</tr>
<tr>
<td>Ateles_geoffroyi</td>
<td>Primates</td>
<td>9400</td>
<td>106.4</td>
<td>40.028</td>
</tr>
<tr>
<td>Babyrousa_babyrussa</td>
<td>Artiodactyla</td>
<td>78000</td>
<td>127</td>
<td>130.444</td>
</tr>
<tr>
<td>Callicebus_moloch</td>
<td>Primates</td>
<td>670</td>
<td>17.65</td>
<td>6.688</td>
</tr>
<tr>
<td>Callimico_goeldii</td>
<td>Primates</td>
<td>480</td>
<td>11</td>
<td>2.384</td>
</tr>
<tr>
<td>Callithrix_jacchus</td>
<td>Primates</td>
<td>100</td>
<td>7.8</td>
<td>2.416</td>
</tr>
<tr>
<td>Capreolus_capreolus</td>
<td>Artiodactyla</td>
<td>20000</td>
<td>97</td>
<td>119.031</td>
</tr>
<tr>
<td>Carollia_perspicillata</td>
<td>Chiroptera</td>
<td>16.6</td>
<td>0.51</td>
<td>0.639</td>
</tr>
<tr>
<td>Cavia_aperea</td>
<td>Rodentia</td>
<td>735</td>
<td>5.57</td>
<td>6.304</td>
</tr>
<tr>
<td>Cebuella_pygmaea</td>
<td>Primates</td>
<td>140</td>
<td>4.5</td>
<td>1.015</td>
</tr>
<tr>
<td>Cebus_albifrons</td>
<td>Primates</td>
<td>3100</td>
<td>79.8</td>
<td>15.423</td>
</tr>
<tr>
<td>Cercopithecus_ascanius</td>
<td>Primates</td>
<td>2800</td>
<td>59.2</td>
<td>42.327</td>
</tr>
<tr>
<td>Cheirogaleus_major</td>
<td>Primates</td>
<td>450</td>
<td>6.8</td>
<td>1.2235</td>
</tr>
<tr>
<td>Cheirogaleus_medius</td>
<td>Primates</td>
<td>177</td>
<td>3.14</td>
<td>1.0215</td>
</tr>
<tr>
<td>Choloepus_didactylus</td>
<td>Pilosa</td>
<td>3550</td>
<td>25.25</td>
<td>19.395</td>
</tr>
<tr>
<td>Cricetomys_gambianus</td>
<td>Rodentia</td>
<td>780</td>
<td>4.48</td>
<td>7.697</td>
</tr>
<tr>
<td>Cricetus_cricetus</td>
<td>Rodentia</td>
<td>325</td>
<td>2.74</td>
<td>3.035</td>
</tr>
<tr>
<td>Crocidura_russula</td>
<td>Soricomorpha</td>
<td>11</td>
<td>0.19</td>
<td>0.1046</td>
</tr>
<tr>
<td>Dama_dama</td>
<td>Artiodactyla</td>
<td>112500</td>
<td>348.5</td>
<td>520.343</td>
</tr>
<tr>
<td>Dasymys_incomts</td>
<td>Rodentia</td>
<td>120</td>
<td>1.18</td>
<td>1.287</td>
</tr>
<tr>
<td>Daubentonia_madagascariensis</td>
<td>Primates</td>
<td>2800</td>
<td>45.15</td>
<td>12.622</td>
</tr>
<tr>
<td>Desmodus_rotundus</td>
<td>Chiroptera</td>
<td>34.9</td>
<td>1.02</td>
<td>0.603</td>
</tr>
<tr>
<td>Diceros_bicornis</td>
<td>Artiodactyla</td>
<td>1000000</td>
<td>638</td>
<td>508.5</td>
</tr>
<tr>
<td>Dolichotis_patagonum</td>
<td>Rodentia</td>
<td>4200</td>
<td>25</td>
<td>55.95</td>
</tr>
<tr>
<td>Echinops_telfair</td>
<td>Afroscricida</td>
<td>87.5</td>
<td>0.62</td>
<td>0.7355</td>
</tr>
<tr>
<td>Elephas_maximus</td>
<td>Proboscidea</td>
<td>25000000</td>
<td>4635</td>
<td>4311.05</td>
</tr>
<tr>
<td>Erinaceus_europaeus</td>
<td>Erinaceomorpha</td>
<td>860</td>
<td>3.35</td>
<td>6.415</td>
</tr>
<tr>
<td>Erythrocebus_patas</td>
<td>Primates</td>
<td>6700</td>
<td>97.1</td>
<td>44.883</td>
</tr>
<tr>
<td>Eulemur_fulvus</td>
<td>Primates</td>
<td>1400</td>
<td>23.3</td>
<td>5.5665</td>
</tr>
<tr>
<td>Galago_demidoff</td>
<td>Primates</td>
<td>81</td>
<td>3.38</td>
<td>0.6458</td>
</tr>
<tr>
<td>Galago_senegalensis</td>
<td>Primates</td>
<td>186</td>
<td>4.8</td>
<td>1.8085</td>
</tr>
<tr>
<td>Giraffa_camelopardalis</td>
<td>Artiodactyla</td>
<td>950000</td>
<td>655</td>
<td>1885.4</td>
</tr>
<tr>
<td>Glis_glis</td>
<td>Rodentia</td>
<td>141</td>
<td>2.07</td>
<td>0.659</td>
</tr>
<tr>
<td>Gorilla_gorilla</td>
<td>Primates</td>
<td>220000</td>
<td>450</td>
<td>120.029</td>
</tr>
<tr>
<td>Graphiurus_murinus</td>
<td>Rodentia</td>
<td>23</td>
<td>0.88</td>
<td>0.646</td>
</tr>
<tr>
<td>Hemicentetes_semispinosus</td>
<td>Afroscricida</td>
<td>110</td>
<td>0.83</td>
<td>3.095</td>
</tr>
<tr>
<td>Homo_sapiens</td>
<td>Primates</td>
<td>55000</td>
<td>1250</td>
<td>321.509</td>
</tr>
<tr>
<td>Hybomys_univittatus</td>
<td>Rodentia</td>
<td>46</td>
<td>1</td>
<td>0.572</td>
</tr>
<tr>
<td>Species</td>
<td>Class</td>
<td>Weight (kg)</td>
<td>Length (mm)</td>
<td>Group</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>-----------</td>
<td>-------------</td>
<td>-------------</td>
<td>-----------</td>
</tr>
<tr>
<td>Hydrochaeris_hydrochaeris</td>
<td>Rodentia</td>
<td>26350</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>Hylobates_lar</td>
<td>Primates</td>
<td>5930</td>
<td>101.9</td>
<td></td>
</tr>
<tr>
<td>Hylophoicus_stella</td>
<td>Rodentia</td>
<td>19</td>
<td>0.71</td>
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