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Relative Pituitary Gland Size Predicts Mammal Life History Variation

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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 & Kamilar, 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).

Modeling the Evolution of Relative Pituitary Size

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 Ornsterin-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 Bininida-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

Examining 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).

295

296 **Modeling the Evolution of Relative Pituitary Size**

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

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

313

314 ## Discussion

315 We provide the first evidence that the size of the pituitary is linked to life history
316 variation, especially growth rates, across a broad sample of mammal species. Our study
317 demonstrates that the known connection between pituitary size and life history variation

318 at the intraspecific level is also found at the interspecific scale across mammals. Our
319 findings that total pituitary gland size and anterior lobe size (accounting for brain and
320 body mass) were positively associated with fetal and postnatal growth rates across a
321 diverse set of mammalian species suggests that this connection represents coevolution
322 through deep evolutionary time. As expected, we found no effect of relative posterior
323 lobe size on life history variation. This further supports our idea that secretion of
324 hormones produced directly and indirectly by the anterior lobe (e.g. GH and IGF-1,
325 respectively) is the major factor driving growth rates.

326 Investigating the ultimate explanations for life history variation has been a major
327 focus of evolutionary biology research (Roff, 1992; Stearns, 1992; Kappeler & Pereira,
328 2003), though integrating proximate mechanisms into a comparative life history
329 framework is relatively rare (but see Lessells, 2008; Swanson & Dantzer, 2014).
330 Whereas body mass is known to vary with life history traits across species (Harvey &
331 Clutton-Brock, 1985; Harvey *et al.*, 1991), others have demonstrated that interspecific
332 variation in life history traits is related to a wide variety of factors, such as total energy
333 budget size (Pontzer & Kamilar, 2009), energy expenditure (Charnov & Berrigan, 1993;
334 Pontzer *et al.*, 2010; Barton & Capellini, 2011), and mortality rate (Promislow & Harvey,
335 1990). Work by Allman and colleagues (1993b) linked various brain structures with
336 primate lifespan, though did not offer a mechanistic explanation for many of the
337 significant relationships.

338 At the proximate level, several studies have found an important connection
339 between hormone signaling and life history. For example, the hypothalamic-pituitary-
340 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.

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612 Figure Legends

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

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

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

623 Figure 4. Plot of phylogenetic residuals from a PGLS regression of anterior lobe pituitary
624 size on brain mass. The mammal Orders with the largest sample sizes are highlighted:
625 Primates, Rodentia, and Chiroptera.

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Table 1. Loadings of original variables on principal component axes.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Body mass	0.367	0.227	0.055	0.362	-0.175	0.064	-0.155	-0.051	0.669	0.414
Brain mass	0.315	-0.276	-0.412	-0.256	-0.441	0.319	0.247	0.462	0.100	-0.097
Fetal growth rate	0.374	0.194	-0.036	-0.239	0.116	-0.095	0.595	-0.538	0.163	-0.268
Postnatal growth rate	0.329	0.302	-0.068	-0.299	0.092	-0.707	-0.138	0.410	-0.070	0.073
Gestation length	0.336	-0.226	0.180	-0.325	0.657	0.364	-0.303	0.106	0.164	-0.058
Neonate body mass	0.382	0.217	0.099	0.054	-0.011	0.299	0.131	-0.051	-0.646	0.517
Litter size	-0.147	0.402	-0.808	0.015	0.270	0.182	-0.206	-0.124	-0.013	0.017
Weaning age	0.215	-0.432	-0.256	0.631	0.384	-0.246	0.266	0.129	-0.090	-0.011
Weaning body mass	0.353	0.276	0.115	0.360	-0.176	0.131	-0.320	0.040	-0.200	-0.681
Maximum longevity	0.258	-0.470	-0.220	-0.140	-0.264	-0.228	-0.466	-0.529	-0.137	0.085
Eigenvalues	2.409	1.486	0.863	0.729	0.508	0.446	0.350	0.284	0.215	0.072

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Table 2. Multimodel selection using AICc to predict fetal growth rates in mammals.

Predictors	**AICc**	**Delta AICc**
Total pituitary + Body mass + brain mass	*36.703*	*0.000*
Anterior lobe + Body mass + brain mass	*36.902*	*0.199*
Total pituitary + Body mass	*37.612*	*0.908*
Anterior lobe + Body mass	*37.678*	*0.975*
Body mass	47.008	10.304
Posterior lobe + Body mass	48.008	11.305
Body mass + brain mass	49.040	12.336
Posterior lobe + Body mass + brain mass	50.145	13.442
Brain mass	81.213	44.510

Best models are in italics

Models within 2 AICc values of the best model are considered equally good

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Table 3. Best phylogenetic generalized linear models predicting fetal growth rate across mammal species based on AICc values. See Table 2 for AICc values.

Variable	**Estimate**	**Std Error**	**t value**	**p value**
(Intercept)	-2.235	0.304		
Total pituitary volume	0.531	0.136	3.909	<0.001
Body mass	0.389	0.098	3.994	<0.001
Brain mass	-0.241	0.136	-1.768	0.08
Model r^2 = 0.746, p value <0.001, lambda = 0.967, df = 4,119				
Variable	**Estimate**	**Std Error**	**t value**	**p value**
(Intercept)	-2.221	0.307		
Anterior lobe volume	0.445	0.113	3.917	<0.001
Body mass	0.438	0.092	4.786	<0.001
Brain mass	-0.236	0.134	-1.756	0.082
Model r^2 = 0.745, p value <0.001, lambda = 0.970, df = 4,119				
Variable	**Estimate**	**Std. Error**	**t value**	**p value**
(Intercept)	-2.112	0.296		
Total pituitary volume	0.412	0.120	3.437	<0.001
Body mass	0.315	0.089	3.538	<0.001
Model r^2 = 0.742, p value <0.001, lambda = 0.960, df = 3,120				
Variable	**Estimate**	**Std. Error**	**t value**	**p value**
(Intercept)	-2.102	0.298		
Anterior lobe volume	0.348	0.101	3.432	<0.001
Body mass	0.354	0.079	4.487	<0.001
Model r^2 = 0.741, p value <0.001, lambda = 0.961, df = 3,120				

All variables were $\log_{10}$ transformed prior to analysis

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Table 4. Multimodel selection using AICc to predict postnatal growth rates in mammals.

Predictors	**AICc**	**Delta AICc**
Anterior lobe + Body mass	*79.046*	*0.000*
Anterior lobe + Body mass + brain mass	*80.105*	*1.059*
Total pituitary + Body mass	*80.777*	*1.731*
Body mass	82.019	2.973
Total pituitary + Body mass + brain mass	82.238	3.191
Posterior lobe + Body mass	83.418	4.372
Body mass + brain mass	83.809	4.763
Posterior lobe + Body mass + brain mass	85.607	6.561
Brain mass	88.347	9.301

Best models are in italics

Models within 2 AICc values of the best model are considered equally good

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Table 5 Best phylogenetic generalized linear models predicting postnatal growth rate across mammal species based on AICc values. See Table 4 for AICc values.

Variable	**Estimate**	**Std Error**	**t value**	**p value**
(Intercept)	-0.232	0.423	-0.549	0.585
Anterior lobe volume	0.395	0.174	2.268	0.026
Body mass	0.250	0.136	1.842	0.070
Model r^2 = 0.584, p value <0.001, lambda = 0.890, df = 3,73				
Variable	**Estimate**	**Std. Error**	**t value**	**p value**
(Intercept)	-0.372	0.425		
Anterior lobe volume	0.551	0.218	2.531	0.014
Body mass	0.351	0.158	2.217	0.030
Brain mass	-0.313	0.249	-1.260	0.212
Model r2 = 0.604, p value <0.001, lambda = 0.848, df = 4,72				
Variable	**Estimate**	**Std. Error**	**t value**	**p value**
(Intercept)	-0.375	0.414	-0.905	0.368
Total pituitary	0.363	0.198	1.836	0.070
Body mass	0.282	0.147	1.916	0.059
Model r^2 = 0.575, p value <0.001, lambda = 0.888, df = 3,73				

All variables were $\log_{10}$ transformed prior to analysis

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Table 6. Results from trait evolution models explaining variation in pituitary size across mammals.

	Brownian Motion			Ornstein-Uhlenbeck				Early Burst			
Variable	σ^2	log-lk	AICc	σ^2	α	log-lk	AICc	σ^2	*r*	log-lk	AICc
Relative pituitary size[1]	0.001	33.98	-63.89	**0.002**	**0.025**	**49.93**	**-93.73**	0.001	0.000	33.98	-61.83
Relative pituitary size[2]	0.001	23.64	-43.23	**0.002**	**0.017**	**38.61**	**-71.09**	0.001	0.000	23.64	-41.16
Relative anterior lobe size[1]	0.002	3.10	-2.15	**0.003**	**0.026**	**20.85**	**-35.57**	0.002	0.000	3.10	-0.08
Relative anterior lobe size[2]	0.002	1.71	0.63	**0.002**	**0.014**	**13.31**	**-20.49**	0.002	0.000	1.71	2.69

[1] Based on the phylogenetic residuals from a PGLS model using body mass as a predictor

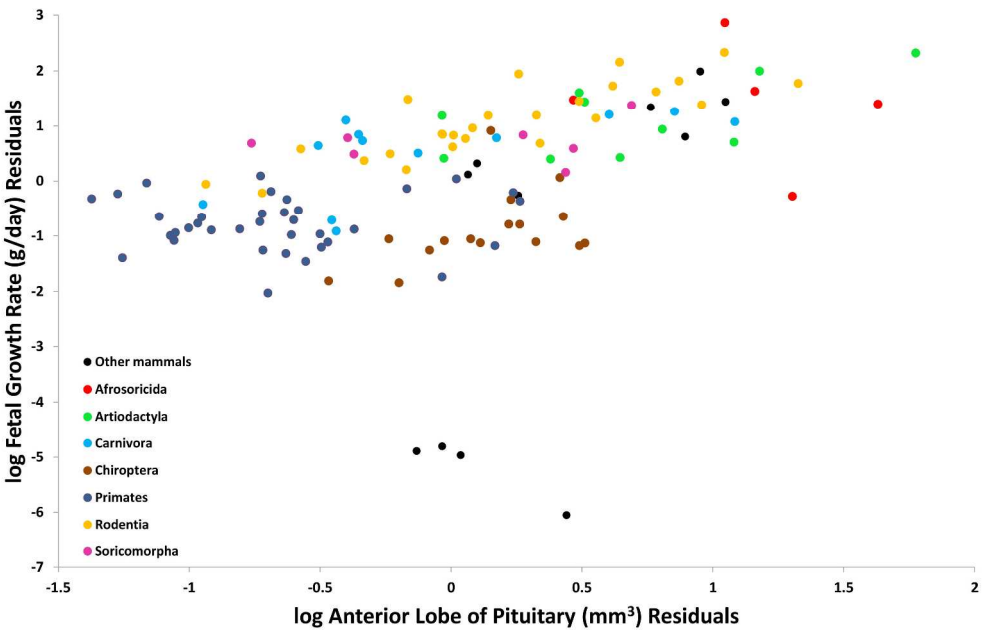
[2] Based on the phylogenetic residuals from a PGLS model using brain mass as a predictor

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

σ^2 = Brownian motion parameter (net rate of evolution)

α = OU parameter (constraint)

r = EB parameter (change in evolutionary rate through time)



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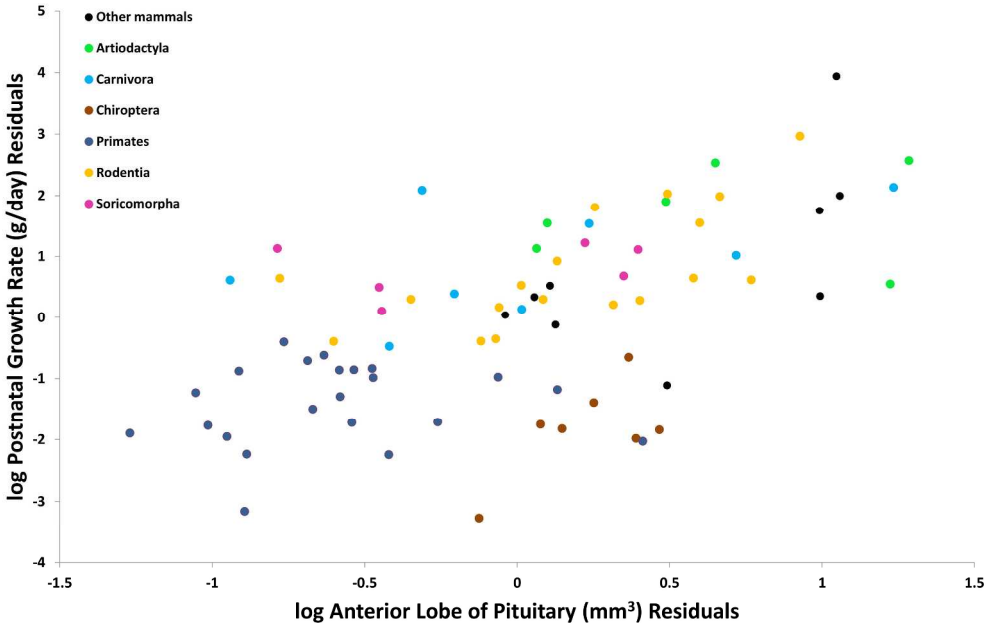

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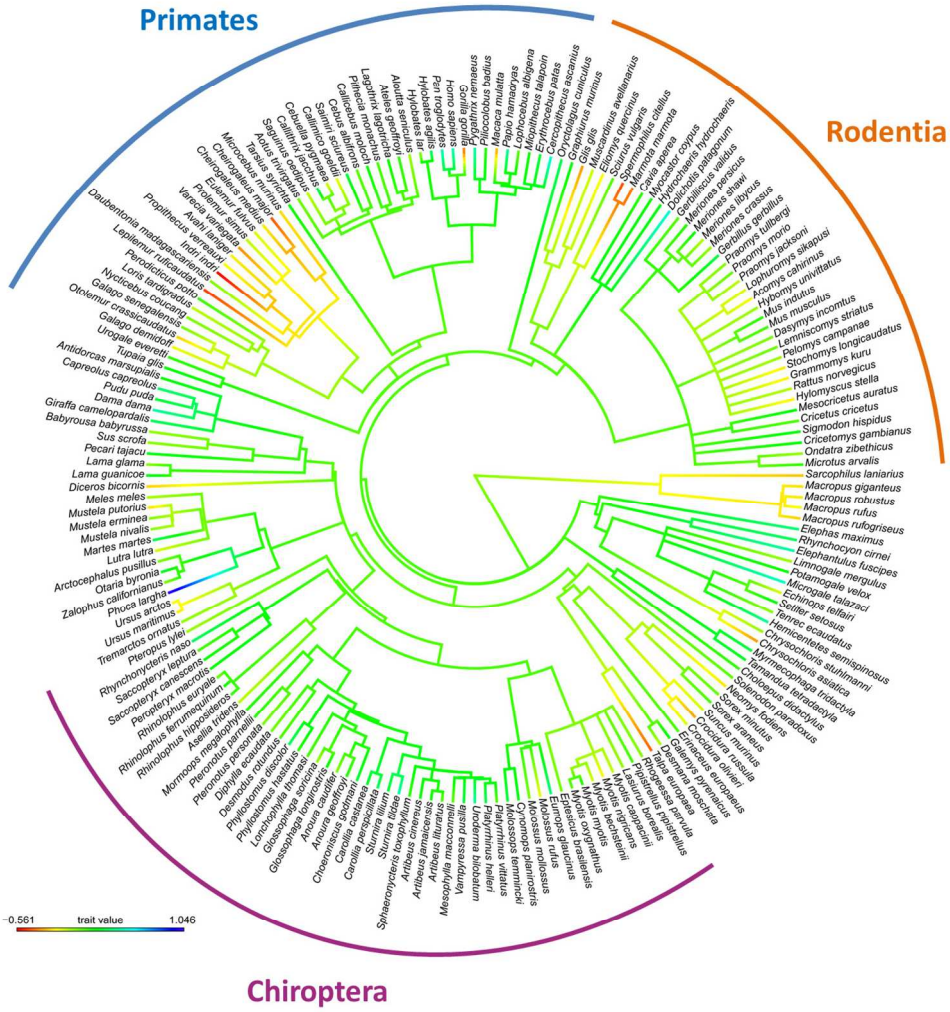

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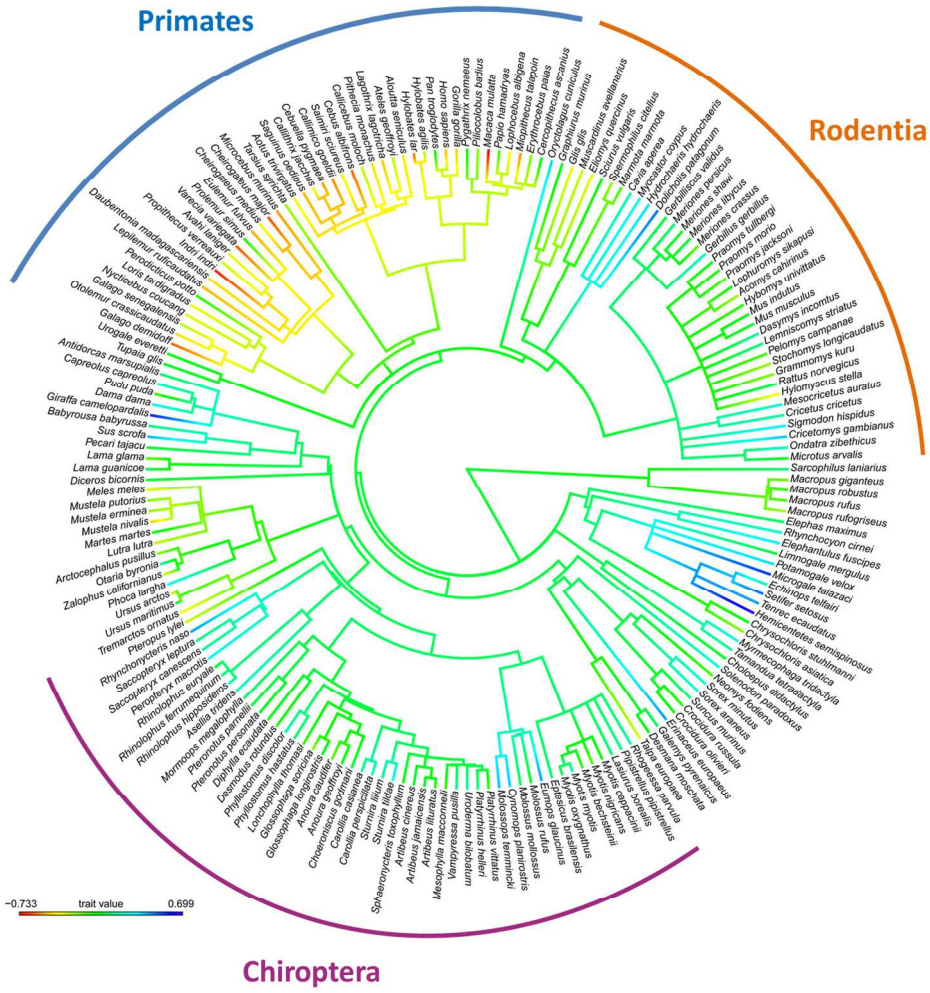

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Species	Order	BodyMass(g)	BrainMass(g)	AntLobeVol(mm3)
Acomys_cahirinus	Rodentia	39	0.91	0.372
Aloutta_seniculus	Primates	3560	46.8	13.466
Anoura_caudifer	Chiroptera	10.4	0.44	0.209
Anoura_geoffroyi	Chiroptera	15.1	0.55	0.379
Antidorcas_marsupialis	Artiodactyla	35750	134.25	120.103
Aotus_trivirgatus	Primates	830	17.1	5.499
Arctocephalus_pusillus	Carnivora	85000	327	146.597
Artibeus_jamaicensis	Chiroptera	39.3	1.09	0.844
Artibeus_lituratus	Chiroptera	44.9	1.26	0.707
Ateles_geoffroyi	Primates	9400	106.4	40.028
Babyrousa_babyrussa	Artiodactyla	78000	127	130.444
Callicebus_moloch	Primates	670	17.65	6.688
Callimico_goeldii	Primates	480	11	2.384
Callithrix_jacchus	Primates	100	7.8	2.416
Capreolus_capreolus	Artiodactyla	20000	97	119.031
Carollia_perspicillata	Chiroptera	16.6	0.51	0.639
Cavia_aperea	Rodentia	735	5.57	6.304
Cebuella_pygmaea	Primates	140	4.5	1.015
Cebus_albifrons	Primates	3100	79.8	15.423
Cercopithecus_ascanius	Primates	2800	59.2	42.327
Cheirogaleus_major	Primates	450	6.8	1.2235
Cheirogaleus_medius	Primates	177	3.14	1.0215
Choloepus_didactylus	Pilosa	3550	25.25	19.395
Cricetomys_gambianus	Rodentia	780	4.48	7.697
Cricetus_cricetus_	Rodentia	325	2.74	3.035
Crocidura_russula	Soricomorpha	11	0.19	0.1046
Dama_dama	Artiodactyla	112500	348.5	520.343
Dasymys_incomtus	Rodentia	120	1.18	1.287
Daubentonia_madagascariensis	Primates	2800	45.15	12.622
Desmodus_rotundus	Chiroptera	34.9	1.02	0.603
Diceros_bicornis	Artiodactyla	1000000	638	508.5
Dolichotis_patagonum	Rodentia	4200	25	55.95
Echinops_telfairi	Afrosoricida	87.5	0.62	0.7355
Elephas_maximus	Proboscidea	2500000	4635	4311.05
Erinaceus_europaeus	Erinaceomorpha	860	3.35	6.415
Erythrocebus_patas	Primates	6700	97.1	44.883
Eulemur_fulvus	Primates	1400	23.3	5.5665
Galago_demidoff	Primates	81	3.38	0.6458
Galago_senegalensis	Primates	186	4.8	1.8085
Giraffa_camelopardalis	Artiodactyla	950000	655	1885.4
Glis_glis	Rodentia	141	2.07	0.659
Gorilla_gorilla	Primates	220000	450	120.029
Graphiurus_murinus	Rodentia	23	0.88	0.646
Hemicentetes_semispinosus	Afrosoricida	110	0.83	3.095
Homo_sapiens	Primates	55000	1250	321.509
Hybomys_univittatus	Rodentia	46	1	0.572

Hydrochaeris_hydrochaeris	Rodentia	26350	67	106.596
Hylobates_lar	Primates	5930	101.9	20.416
Hylomyscus_stella	Rodentia	19	0.71	0.205
Lagothrix_lagotricha	Primates	4010	91.33	24.163
Lama_glama	Artiodactyla	67000	245	122.515
Lasiurus_borealis	Chiroptera	7.8	0.17	0.159
Lemniscomys_striatus	Rodentia	83	1.02	1.033
Lophocebus_albigena	Primates	9250	110.5	33.521
Lophuromys_sikapusi	Rodentia	79	1.04	0.681
Loris_tardigradus	Primates	322	6.6	2.111
Lutra_lutra	Carnivora	8400	54.5	20.676
Macaca_mulatta	Primates	7000	85.4	11.936
Macropus_giganteus	Diprotodontia	18200	58	28.745
Macropus_robustus	Diprotodontia	20000	53.5	31.504
Macropus_rufus	Diprotodontia	16000	54	29.639
Marmota_marmota	Rodentia	1900	7.17	3.898
Martes_martes	Carnivora	1286.5	21	15.003
Meles_meles	Carnivora	6250	57	19.4
Meriones_crassus	Rodentia	150	2.85	1.385
Meriones_libycus	Rodentia	162	1.62	1.309
Meriones_persicus	Rodentia	130	1.89	1.818
Meriones_shawi	Rodentia	121	2.62	1.937
Mesocricetus_auratus	Rodentia	93	1.23	1.626
Microcebus_murinus	Primates	54	1.78	0.407
Microgale_talazaci	Afrosoricida	50.4	0.79	2.13
Microtus_arvalis	Rodentia	34	0.93	0.653
Miopithecus_talapoin	Primates	1000	39.7	8.715
Molossus_mollossus	Chiroptera	15	0.33	0.285
Mus_musculus	Rodentia	21.3	0.55	0.435
Muscardinus_avellanarius	Rodentia	21	0.76	0.271
Mustela_erminea	Carnivora	227	4.6	1.953
Mustela_nivalis	Carnivora	66.5	2.97	0.778
Mustela_putorius	Carnivora	1388	9.67	4.342
Myocastor_coypus	Rodentia	3700	16.89	24.55
Myotis_myotis	Chiroptera	20	0.42	0.484
Myrmecophaga_tridactyla	Pilosa	20000	76	103.277
Neomys_fodiens	Soricomorpha	15.2	0.32	0.1667
Nycticebus_coucang	Primates	600	12.5	4.12
Ondatra_zibethicus	Rodentia	1200	4.95	6.174
Oryctolagus_cuniculus	Lagomorpha	1340	9.5	15.518
Otaria_byronia	Carnivora	187500	430	505.284
Otolemur_crassicaudatus	Primates	850	10.3	2.88
Pan_troglodytes	Primates	43500	420	273.86
Papio_anubis	Primates	12000	201	100.449
Papio_hamadryas	Primates	6500	114	63.111
Pecari_tajacu	Artiodactyla	17000	102	81.417
Perodicticus_potto	Primates	1150	14	8.3265

Phoca_largha	Carnivora	25000	455	670.581
Phyllostomus_discolor	Chiroptera	40.1	1.08	1.267
Phyllostomus_hastatus	Chiroptera	99.9	1.6	1.46
Pipistrellus_pipistrellus	Chiroptera	4.5	0.14	0.143
Praomys_jacksoni	Rodentia	46	0.96	0.503
Praomys_morio	Rodentia	36.5	0.95	0.58
Praomys_tullbergi	Rodentia	34	0.69	0.492
Propithecus_verreauxi	Primates	3480	26.7	9.5835
Pudu_puda	Artiodactyla	4000	56	30.842
Pygathrix_nemaeus	Primates	4000	69	45.606
Rattus_norvegicus	Rodentia	273	2.15	1.918
Rhinolophus_euryale	Chiroptera	18.8	0.47	0.346
Rhinolophus_ferrumequinum	Chiroptera	18	0.52	0.487
Rhinolophus_hipposideros	Chiroptera	5	0.13	0.163
Saguinus_oedipus	Primates	347.5	9.26	2.255
Saimiri_sciureus	Primates	630	24.8	8.012
Sarcophilus_laniarius	Dasyuromorphia	7000	13.6	13.043
Sciurus_vulgaris_	Rodentia	319	4.51	2.99
Setifer_setosus	Afrosoricida	248	1.51	3.393
Sigmodon_hispidus	Rodentia	136	1.43	2.21
Solenodon_paradoxus	Soricomorpha	900	4.67	6.1195
Sorex_araneus	Soricomorpha	10.3	0.2	0.254
Sorex_minutus	Soricomorpha	5.3	0.11	0.1406
Sturnira_lilium	Chiroptera	18.2	0.59	0.608
Suncus_murinus	Soricomorpha	35.5	0.38	0.383
Sus_scrofa	Artiodactyla	107400	96.4	171.556
Talpa_europaea	Soricomorpha	76	1.02	0.3432
Tarsius_syrichta	Primates	87.5	3.63	1.4765
Tenrec_ecaudatus	Afrosoricida	832	2.57	4.987
Tupaia_glis	Scandentia	150	3.15	2.344
Uroderma_bilobatum	Chiroptera	13.9	0.62	0.707
Urogale_everetti	Scandentia	275	4.28	3.0215
Ursus_arctos	Carnivora	101000	347.33	111.68
Ursus_maritimus	Carnivora	130000	126	124.224
Varecia_variegata	Primates	3000	31.5	5.7725
Zalophus_californianus	Carnivora	75000	395	139.623

PitVol(mm3)	PostLobeVol(mm3)	FetalGrowthRate(g/d)	PostnatalGrowthRate(g/d)	Gestation(d)
1.496	0.072	0.346	1.184	38.54
28.968	14.985	2.194		189.9
0.408	0.109	0.020		107.97
0.624	0.143	0.039	0.051	125.14
152.917	29.199	22.665		169.49
10.404	4.401	0.766	2.218	133.47
190.094	37.633	16.062	43.101	357.99
1.255	0.314	0.076		138.7
1.076	0.295	0.084		106.45
82.403	36.632	1.900	3.776	226.37
166.144	32.095	7.904		156.5
9.466	2.419	0.458		164
5.526	2.724	0.344	1.097	153.99
3.427	0.663	0.445	2.649	144
165.747	31.077	11.037		196
0.804	0.121	0.043	0.206	114.6
8.635	1.264	2.025	8.632	61.7
2.55	1.378	0.208	1.181	134.44
30.848	10.234	1.480	2.562	158.29
55.308	10.069	2.523		148.5
3.356	1.748	0.584		70
2.1945	0.74	0.484		61.79
30.478	10.652	1.350		269.63
9.109	0.911	2.243		31.45
3.738	0.493	1.725	23.779	19.5
0.2069	0.0857	0.111	0.863	29
629.974	59.053	20.428	67.680	230
1.613	0.23		2.670	
23.682	8.587	0.739	7.220	166.48
0.918	0.22	0.033		209.35
644	135.5	75.069	672.050	466.24
62.385	5.07	10.342		97.97
1.49	0.6055	0.658		62.54
5032.87	721.82	215.559		634.49
10.09	3.19	1.950	25.457	36.98
65.357	15.289	3.755	7.539	167.2
10.1425	4.093	0.683		120.83
1.547	0.0843	0.115		111
4.431	2.437	0.136	1.772	126.98
2020.9	105.1	156.542		455.25
1.124	0.454		5.148	28.19
168.052	47.616	8.563	19.249	257
0.869	0.22	0.436		23.99
4.146	0.8175	0.741		53.07
369.356	44.916	11.584	8.014	274.78
0.699	0.106	0.337		30

134.677	23.026	34.731		150.73
28.852	7.927	1.892	0.871	212.91
0.286	0.063	0.155		29.49
34.3	8.091	1.971		223.99
184.486	30.517	26.259	151.860	342.74
0.28	0.079	0.159	0.127	84.21
1.393	0.144	0.415	2.306	25.15
55.913	16.81	2.757	7.974	182.64
0.959	0.154		1.275	
3.6865	1.349	0.095	1.100	165.99
31.751	9.365	8.913		64.27
29.989	16.111	2.867	2.801	166.07
36.543	7.524	0.023	15.902	36.56
45.12	13.493	0.020	12.952	34.59
42.657	11.97	0.024	20.599	33.99
7.28	2.913	3.378		35.22
22.523	6.423	3.418	41.861	30.63
29.172	8.416	5.775		48.6
2.16	0.309	0.598		23.5
1.697	0.111	0.935	5.981	25.43
2.46	0.352	1.039		28
2.721	0.258	1.024	4.115	24.8
1.964	0.201	1.334	9.700	15.49
0.642	0.2015	0.158		60.34
2.6215	0.339	0.134		60.74
0.923	0.172	0.459	2.106	21
14.157	4.793	1.100	1.340	164.38
0.451	0.11	0.032		107.97
0.676	0.078	0.300	2.304	19.6
0.474	0.173	0.138		24.97
3.213	0.916	0.229	2.541	66.35
1.403	0.389	0.278	6.021	36.49
6.421	1.541	1.942		41.49
30.168	3.003	8.330	156.096	131.86
0.935	0.361	0.123	0.611	73
139.349	26.786	8.208	25.012	182.74
0.3225	0.0962	0.212	1.680	21.38
9.3165	4.38	0.296	2.902	191.09
7.289	0.657	5.170	30.988	27.86
21.564	3.22	6.730	34.259	30.45
639.965	94.693	41.149		311.55
8.072	4.6495	0.405	4.148	131.04
301.458	25.475	7.915	5.626	231.49
151.723	45.927	5.346	4.559	178.96
108.386	42.456	4.994	6.687	180
119.519	27.584	6.660	137.178	144.88
12.668	3.39	0.210		193

818.65	106.011	35.348	377.423	288.95
1.45	0.134	0.067		107.97
2.557	0.71	0.128	0.587	123.39
0.207	0.042	0.040	0.107	44
0.656	0.099		2.447	35.49
0.683	0.068	0.244		35.99
0.682	0.13	0.380	1.070	23.9
16.771	5.8155	0.699		149.77
45.611	12.937	4.531	46.420	210
63.608	17.399	1.060		182.88
2.471	0.379	2.398	16.750	21.74
0.508	0.111	0.042		92.54
0.649	0.098	0.061		91.24
0.241	0.058	0.028		75.51
5.112	2.543	0.468	2.439	166.49
15.245	5.551	0.655	1.750	164.09
21.523	8.276	0.003	2.367	21
4.135	0.953	1.046		38
5.3527	1.637	1.389		57.63
2.543	0.255	1.330	4.127	27
10.445	3.766	2.278		64.8
0.3117	0.0402	0.128	2.431	21.5
0.1817	0.0234	0.056	1.159	23.81
0.768	0.124	0.048		107.97
0.6165	0.15	0.251	3.791	30.19
248.633	58.082	31.694	261.476	115.2
0.488	0.192	0.414	5.777	30.41
2.662	1.05	0.145		177.99
8.507	2.721	6.796	155.045	60.24
4.626	1.994	0.608	5.662	45.99
0.961	0.175		0.199	130.88
5.7665	2.09	0.608		55.49
159.32	34.567	4.922	312.986	227.56
186.132	39.629	17.213	63.347	64.66
14.1765	7.3005	1.974		102.5
180.6	30.6	25.574	61.224	349.99

NeonateBodyMass(g)	LitterSize	WeaningAge(d)	WeaningBodyMass(g)	MaxLongevity(y)
5.49	2.43	14	12.31	5.9
293.42	1.42	370.04		25
2.14	0.99			
4.99	0.99	62.5	8.24	10
3841.48	1	57.45		19.8
96.49	1.06	76.21	255.99	31
5750	1	356.3	21106.96	32.1
10.57	1			19.2
8.9	1		33.79	
425.85	1.01	816.35	3478.06	47.1
715	1.73	212.91		22.9
74.4	1.01	58.85		26.2
50.5	1.05	66.53	120.02	22.2
27.74	2.31	60.24	96.82	22.8
1208.55	1.79	79.75		17.5
4.89	1	35.63	12.24	17
58.38	2.14	20.86	142.52	6
14.5	1.93	90.73	70	18.6
231.92	1.01	270.32	917.69	40.4
371	1.01	146.54		31.2
18.08	2.26	47.14		
14.65	2.04	60.65		23.2
364	1	52.61		36.8
22.68	3.11	34.54		8.4
4.71	7.14	24.85	87.47	3.6
0.8	4.04	23.82	5.89	4
4698.44	1	177.63	16720.38	21.1
	2.67	30	30	
121.79	1.01	197.7	1535	23.3
6.94	1	253.01		29.2
34999.99	1	583.09	426865.48	49
578.96	1.75	76.28		14.4
7.49	5.49	31.18		19
97000	1.41	218.26		65.5
15.54	4.64	40	235	11.7
621.67	1.01	211.79	2202.46	28.3
74.99	1.1	134.64		35.5
9.89	1.29	43.47		13.4
11.5	1.5	93.93	122.47	17.1
55244.9	1.29	212.91		
	5.17	27.84	27.72	
2095.89	1.05	920.35	18967.67	55.4
3.49	3			6.9
7.39	5.32	21.5		
3182.96	1	725.86	8999.99	122.5
4.4	2.3			

1500	3.49	109.75		15.1
398.86	1.01	725.86	1025.02	56
1.47	3.11			
437.09	1.01	312.66		32
8999.99	1	131.7	29000	28.9
4.29	3.12	38	5.84	
2.25	4.64	27.28	15.81	4.8
498.58	1.01	211.71	2170	36
7.8	3	13.67	13.61	
11	1.44	167.49	139	19.3
284.99	2.01	100.8		18.2
471.47	1.01	304.16	1314.91	40
0.84	1	510.82	8124.03	25
0.7	1	366.19	4743.41	22
0.81	1	359.99	7416.19	25
29.74	4	49.18		17.4
30	3.49	54.19	679.99	18.2
90.24	3.11	91.3		18.6
3.34	4.21	30.24		5.6
5.24	4.54	30.18	45	5.2
4.99	5.83	19		6
4.35	5.84	29.31	25	
2.35	8.79	18.65	22.93	3.9
4.78	2	40.45		18.2
3.64	2.23	29.38		5.8
1.93	4.99	17.18	9.18	4.8
179.04	1.01	178.98	416.46	27.7
3.49	0.99	60.45		
1.06	5.54	21.5	10	4
0.8	4.3	37.61		5.3
2.25	6.74	60.93	25.22	12.5
2	5.07	36.74	45.63	9.1
9.5	8.48	54.39		11.1
205.7	5.34	52.83	1750	8.5
6	1.5	41.99	23.1	37.1
1500	1	79.96	3499.99	31
0.71	6.39	35.34	10	3.1
50.47	1.12	181.21	520	25.8
21.99	6.55	27.84	153.7	
39.11	5.24	26.3	211.06	
12819.99	1	363.96		29
46.57	1.14	124.62	499.99	22.7
1745.02	1.05	1260.81	8499.99	59.4
947.31	1.01	596.6	3640.26	37.5
890	1.01	363.96	3299.79	37.5
618.53	1.56	47.25	4773.44	31.5
37.16	1.09	149.15		26.8

10213.75	1	30.74	21815.73	47.6
7.29	0.99			9
15.94	0.99	72.82	59.09	18
1.28	1.37	33.44	3.89	16.6
	3.67	30	20	
2.68	3.28	30.77		
2.7	3.36	24.5	10.5	5.2
102.65	1.02	177.83		31
780	1.22	54.75	2863.2	18.3
191.94	1.01			26
5.8	8.99	25.37	53.07	3.8
3.89	1	105.72		
5.64	0.98	45.87		30.5
2.1	1	33.2		29.4
41	1.9	49.85	105	26.2
107.5	1	177.41	418	30.2
0.02	2.88	243.33	200	13
8.83	4.5	64.51		14.8
24.7	3.24	25.22		14.1
6.6	5.44	15.29	18.2	5.2
89.99	1.64	74.71		12.1
0.42	6.56	21.43	8.36	3.2
0.22	6.04	23.5	4.73	
5.25	0.99			12
2.44	3.1	19.16	25.87	3.2
807.77	4.52	97.88	6469.99	27
3.24	3.89	32.49	51.49	
25.6	1.01	82.49		16
24.24	16.89	21.87	225	8.7
12.6	2.22	34.27	100	12.4
	0.99	40.58	8.14	
19.97	1.69	30.24		11.5
499.99	2.24	182.5	26000	40
670.48	1.66	205.17	8500	43.8
93.69	2.16	90.73		37
6347.89	1.41	319.01	20199.75	35.7