Testing hypotheses of brain size variation using Bayesian comparative framework: the case of marsupials

Orlin S. Todorov, Simone P. Blomberg, Karen Sears, Anjali Goswami, Vera Weisbecker

The University of Queensland, School of Biological Sciences

VW: College of Science and Engineering, Flinders University (I get both UQ and Flinders)

# Significance box

This is the most comprehensive study on marsupial brain evolution to date including data on 176 species from Australia, New Guinea and the Americas. We are applying phylogenetically informed imputation techniques and Bayesian statistical methods for the first time in such studies and are confirming previous findings (brain size is constrained by maternal investment; NG marsupials have larger relative brains) and we make several new findings (vulnerability is related to brain size and providing details on the rate of evolution in different marsupial radiations). Additionally, we provide a framework for Bayesian analysis of brain size evolution, incorporating data imputations for the first time.

# Abstract (150 words)

# Introduction

Evolutionary increases of relative brain sizes within mammals are widely considered to be due to selection for relative brain size (Reader & Laland, 2002; Sol, Bacher, Reader, & Lefebvre, 2008), under the assumption that larger brains relate to better cognitive abilities. However, the kind of cognition that is the target of such selection has been a matter of extensive debate and has been researched using a large diversity of variables. Several overarching selection frameworks have been proposed, with three frameworks (social, ecological, cognitive) roughly summarizing different schools of thought about brain size evolution (DeCasien, Williams, & Higham, 2017; Fox, Muthukrishna, & Shultz, 2017; Holekamp & Benson-Amram, 2017; Milton, 1981; Rosati, 2017; Sayol et al., 2016; Todorov, Weisbecker, Gilissen, Zilles, & Sousa, 2019; van Woerden, Willems, van Schaik, & Isler, 2012). The ‘social-brain’ hypothesis suggests that increase in social complexity (such as social or foraging group size and mating system) can select for larger brain sizes, and particularly larger neocortex size (Dunbar, 1998). The ‘ecological brain’ hypothesis focuses on cognitive demands related to ecological factors (diet, home range, predation pressure) (DeCasien et al., 2017; Milton, 1981). Lastly, the cognitive buffer hypothesis is a much more general hypothesis regarding the evolution of brain variation, which does not associate relative size increase with particular behavioural parameters. Rather, it posits that larger brains generally improve fitness and survival, due to advantages related to negotiating novel or unpredictable environments and situations (Daniel Sol, 2009; van Woerden et al., 2012). This buffer function of the brain could result in the generation of positive feedback processes which can even accelerate brain evolution (D. Sol, 2009).

The general picture surrounding the evolution of brain size variation is confounded by several issues mainly related to data collection, choice of relative versus absolute brain size, the choice of correlated behavioural and cognitive variables, scarcity of specimens, and by the statistical approach undertaken (Barton & Montgomery, 2019; Healy & Rowe, 2007; Wartel, Lindenfors, & Lind, 2019). Selection for relatively larger brains is likely antagonized by the high expense of brain growth and maintenance, as there is ample evidence that metabolic, maternal investment and general energetic constrains dampen the evolution of large brain size (Aiello & Wheeler, 1995; Isler & van Schaik, 2009). Among these, reproductive parameters are probably particularly important and act as a constraining factor on brain variation in different clades (Isler & van Schaik, 2006; Isler & van Schaik, 2012; Street, Navarrete, Reader, & Laland, 2017; Tsuboi et al., 2015; V. Weisbecker, Blomberg, Goldizen, Brown, & Fisher, 2015). However, because all selection-based hypotheses generally invoke traits that are tied to reproduction, it is very difficult to dissect energetic reproductive effects from selection (V. Weisbecker & Goswami, 2014). For example, home range and social group sizes are related to mating systems, (Lukas & Clutton-Brock, 2014), social group sizes are related to predation pressure (Hintz & Lonzarich, 2018), which in turn are highly correlated with reproduction and maternal investment (Shuster, 2009); and energy availability for both maternal investment and maintenance is dependent on the ecological factor of diet.

The confoundment of reproductive investment and putative selection agents on brain size increase poses a problem for research into placental mammals, which however attract most research interest because humans and other large-brained mammals belong to it. Placentals have highly varied life histories and reproductive modes which may increase the risk of confounding constraints of reproduction with selection on behavioural and ecological traits (Logan et al., 2018). By contrast, the sister radiation of placentals – the marsupial mammals – have highly homogenous life histories and developmental regimes with a similarly diverse range of behavioural complexities to placentals (Carlisle et al., 2017; V. Weisbecker et al., 2015; V. Weisbecker & Goswami, 2010). Marsupial neonates are born at very early developmental stages after a very short gestation period (12-30 days) and the marsupial brain develops nearly entirely postnatally in all species (Smith, 2006). Marsupials exhibit a diverse array of social and mating systems, diet types, home ranges and cognitive abilities (Todorov, 2019). They are distributed in various habitats with various levels of seasonality (New Guinea, Australia and the Americas). Moreover, aside from the lack of a corpus callosum, marsupial brains do not appear to differ from that of placentals (Ashwell, 2008; Suarez et al., 2018). This unique combination of reproductive homogeneity and ecological, behavioural and social diversity, makes marsupials perfectly suited for testing hypotheses about brain size evolution (Carlisle et al., 2017; V. Weisbecker et al., 2015; V. Weisbecker & Goswami, 2010).

Previous work on marsupial brain size evolution, focusing on the Australasian radiation of marsupials, has yielded surprisingly little support for any of the main hypotheses of behavioural complexity, with a reproductive constraints model, and specifically litter size, representing the best model to explain brain size variation and the only model with significant association between brain size and one of its variables (V. Weisbecker et al., 2015). However, like other studies of brain size evolution, the dataset had multiple missing values, so that model comparisons could only be done one at a time due to constraints of sample size. With a very limited number of species and different species representation for each model the results of that study have been inconclusive. The statistical approach – namely PGLS (Phylogenetic Generalized Least Squares) – is also very sensitive to errors in phylogeny, difficult to use on multiple imputed datasets, and assumes a single mode of evolution throughout the whole tree (Brownian motion) (Mundry, 2014).

In this study, we use a substantially extended dataset (1/3rd larger than previous datasets used) and several novel approaches to provide the most comprehensive test of the main hypothesis of brain evolution. This involves the first use of phylogenetically informed multiple imputations through chained equations of missing data in a brain size studies (Nakagawa & Freckleton, 2008; Resche-Rigon & White, 2018; Rubin, 1987). This has previously been shown to be a better solution to the problem, than omitting missing cases (Fisher, Blomberg, & Owens, 2003). This is followed by testing models using phylogenetically corrected Bayesian generalised linear mixed-effects approach – MCMCglmm – which has fewer assumptions about the distribution of the source data and can test multiple hypothesis on multiple datasets (Hadfield, 2010).

We then firstly ask whether this more comprehensive approach improves on previously tested models of behavioural complexity in marsupials. We also add three additional important hypotheses of brain size evolution, namely whether play behaviour and conservation status (both cognitive buffer-related hypotheses) or hibernation (a brain maintenance-related hypothesis) are associated with brain size variation. To better understand the evolutionary patterns leading to relative brain size variation in marsupials, we compare the evolutionary modes of relative brain size increase in the three landmasses (Australia, New Guinea and the Americas) and test whether evolutionary mode shifts had occurred as a result of invasion in a novel landmass. We also follow up on a previous finding (V. Weisbecker et al., 2015) that New Guinean marsupials appear relatively larger-brained, asking whether New Guinean marsupials follow different mode of brain and body size evolution compared to Australian or American species.

# Results

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | β | SE | Posterior distribution above zero | Mean DIC/ Heritability |
| Developmental  Weaning age  Litter size | 0.03  -0.09 | 0.03  0.05 | 77.5%  **95.88%** | -245 / 0.981 |
| Environmental  Diurnal  Crepuscular  Shelter Safety - intermediate  Shelter Safety - open  Terrestrial  Diet - 2  Diet - 3  Diet - 4  Home Range | 0.03  -0.05  0.03  0.05  -0.05  0.05  -0.07  -0.03  0.01 | 0.08  0.04  0.04  0.07  0.04  0.06  0.07  0.08  0.01 | 67.4%  9.99%  80.89%  76.06%  13.96%  79.89%  14.41%  33.62%  81.21% | -259.5 / 0.981 |
| Social  Group living  Parental care  Mating system  Populations density | 0  -0.02  0.03  0 | 0.05  0.07  0.05  0.01 | 47.68%  34.07%  77.07%  54.85% | -270.7 / 0.982 |
| Metabolic  FMR | 0.04 | 0.08 | 68.95 | -275.5 / 0.982 |
| Hibernation  Torpor | -0.13 | 0.15 | 19.22% | -271.3 / 0.982 |
| Play  Play – 2  Play - 3 | 0.1  0.08 | 0.18  0.17 | 70.37%  69.36% | -248.1 / 0.98 |
| Vulnerability  Status – 2\*  Status – 3\* | 0.02  0.06 | 0.01  0.06 | **96.94%**  84.72% | -278.3 / 0.983 |
| Origin  Origin – 2  Origin - 3 | -0.03  -0.05 | 0.02  0.04 | **4.74%**  12.15% | -282 / 0.984 |

## MCMCglmm models:

### Developmental model

The developmental model included litter size and weaning age as predictors. Weaning age did not show a pronounced effect on brain size, but litter size had a negative effect (95.88% of the posterior distribution below zero, β = -0.086, SE=0.052).

<<Dev mode graph about here>>

### Environmental model

Predictors in this model included activity period, shelter safety, arboreality, diet and home range. We did not find any effect of any of the predictors on brain size.

### Social model

Predictors in this model were group living, parental care, mating system and populations size. None of them had any effect on brain size.

### Metabolic model

The model revealed no effect of field metabolic rate on brain size, including no interaction between body size and metabolic rate.

### Hibernation model

Torpor had no effect on brain size, including no interaction between body size and torpor.

### Play model

Species with larger brain sizes did not exhibit more or more complex play behaviour compared to smaller-brained species. The interaction between body size and play behaviour also did not reveal any effect of brain size.

### Vulnerability model

Vulnerable, endangered, rare, declining or species with very limited habitats were shown to have larger brains within larger bodied marsupials, but smaller brains within small bodied ones (96.94% of the posterior distribution above zero, β = 0.023, SE=0.012 for the interaction between vulnerability and body size).

<<Status graph about here>>

### Origin model

Species from New Guinea were shown to have larger brains within small and average body sized marsupials, compared to Australian or American (4.74% of the posterior distribution above zero, β = -0.031, SE= 0.019).

## Evolutionary models

We show that marsupials in Australia have undergone early burst (EB) of both brain and body size evolution. In contrast, in New Guinea marsupials, we detected EB of evolution of the brain only but Brownian motion (BM) for body size evolution. In America we determined that BM is the best fit for both brain and body size evolution.

|  |  |  |
| --- | --- | --- |
| Origin | Brain | Body |
| Australia | EB | EB |
| New Guinea | EB | BM |
| Americas | BM | BM |

An additional pANCOVA showed that a model including ‘Origin’ as an interaction term was significantly better than a model including marsupials from all origins (F=5.07, P=0.0072 on 4, 2 degrees of freedom), while variance inflation factor (VIF) was <2.

<<ANCOVA graph around here>>>

# Discussion

Given the confounding role of reproduction on studying evolution of brain variation in placentals, we used the relatively reproductively homogenous clade of maruspials as a study group to address most of the current hypotheses on brain evolution. We used the most complete and comprehensive dataset ever employed for mammals, utilised multiple data imputations to avoid problems with missing data, and MCMCglmm as main statistical approach for data analysis. Despite this, we found an intriguing lack of selection-related brain size correlates across the radiation of marsupial mammals. The only unambiguous association of brain size with any variable was with litter size, where the negative correlation with brain size is widely known in marsupials (V. Weisbecker et al., 2015), placentals (Isler & van Schaik, 2009; Navarrete, van Schaik, & Isler, 2011), and beyond mammals (Isler & van Schaik, 2006; Sol et al., 2010). This emphasizes the high importance of reproductive investment into offspring brains, which in placental mammals is augmented by a variety of additional parameters that cause the maternal investiment into the offspring to vary (Barrickman & Lin, 2010; Barton & Capellini, 2011; Isler, 2011; Isler & van Schaik, 2009, 2012; Street et al., 2017; V. Weisbecker et al., 2015; V. Weisbecker & Goswami, 2010). Together with the lack of solid behavioural and ecological correlates, this emphasizes previous suggestions that increases in brain size seem to be associated with different factors in different radiations, which appears to make it all so noisy that an overarching signal is lost (Smaers, Dechmann, Goswami, Soligo, & Safi, 2012; V. Weisbecker et al., 2015). However, our resutls also highlight the extensive potential for many of the correlates found in placentals to be caused by an ultimate cause of maternal (or parental) investment.

Discuss the lack of relationship with FMR as a new measure of MR

Additionally, we were able to confirm that marsupials from New Guinea have the largest brains among marsupials, but this relationship is dependent upon body size – the largest bodied species from both localities do not differ in brain size.

seasonality

predation

hunting pressure - connect to IUCN

Similar to previous studies (Byers, 1999; Iwaniuk, Nelson, & Pellis, 2001), we did not find any clear-cut evidence that play behaviour and its complexity is related to brain size. One explanation can be the scarcity of data, causing our play behaviour data set to contain more than 80% imputed values. This emphasizes the need for more rigorous data collection related to play behaviour, as much needed to addressing this question in a more rigorous matter. Another explanation THIS COULD MEAN

Apart from confirming previous findings, we were able to analyse the relationship between species’ vulnerability and brain size, showing for the first time that larger brained marsupials are more vulnerable to extinction. This effect, again, was dependent on body size (Abelson, 2016; Gonzalez-Voyer, Gonzalez-Suarez, Vila, & Revilla, 2016), where vulnerable, endangered, rare, declining or species with very limited habitats were shown to have larger brains among species with larger body sizes, but smaller brains within species with smaller body sizes. This observation may be due to the fact that large bodied marsupials with larger brains, due to their prosociallity, may fall easier pray to introduced predators in areas with human activity (such as cats and dogs). On the other hand, smaller bodies marsupials with larger brains might be more adaptable to human modified environment due to increase in intelligence and behavioural plasticity, where their small sizes facilitate the ability to avoid predation risks related to human activities and introduced predators(Snell-Rood & Wick, 2013). The interaction we see might also not in fact relate fully to brain size, but rather to the different reproductive mode of big and small brained mammals. E.g. small mammals tend to be k strategists whose survival is aided by their large reproductive output, which combined with an increase in brain size and the concomittant increase in intelligence and behavioural plasticity, might put the in a more favourable position to hedge around exctinction related to human activity.

(Discuss the NG effect in more detail?)

(Discuss the imputations and the MCMCglmm in more detail?)

Conclusion we do later.

# Materials and Methods

All analyses were conducted in R. The code to replicate all analyses, including all data, can be found on LINK TO GITHUB. Packages that were used for the analysis: phytools (Revell, 2012), caper (Orme, 2012), MCMglmm (Hadfield, 2010), mulTree (Guillerme & Healy, 2014), mice (Buuren & Groothuis-Oudshoorn, 2011), phylomice (Blomberg and Drhlik), geiger (Harmon, Weir, Brock, Glor, & Challenger, 2007), RRphylo (Raia et al., 2019). For plotting ggplot2 (Wickham, 2016) and hdrcde (Hyndman, Einbeck, Wand, & Hyndman, 2018) were used.

## Dataset

We use body mass as an estimate for body size, while endocranial volume (ECV) was used as an estimate for brain size. Data on brain volumes were derived from measurements of endocranial volumes (ECV) and were obtained from several different sources (Ashwell, 2008; V. Weisbecker et al., 2015). Most ECV volumes were obtained from Ashwell (2008) which included: 472 skulls from 52 species of Dasyuromorph (carnivorous/insectivorous) marsupials and the marsupial mole, 146 skulls from 14 species of Peramelemorphia (bilbies and bandicoots) and 639 skulls from 116 species of Diprotodontia (koala, wombats, gliders, possums, kangaroos, wallabies, from the collection of the Australian Museum in Sydney. 29 skulls from 16 species of Ameridelphian marsupials from the Museums of Victoria and Queensland. We had added 62 new species of American marsupials to the dataset, whose brain volumes were collected from museum collections using glass beads. This data collection was similar to that employed by Ashwell et al. (2008). Body weight data were taken from (Vera Weisbecker, Ashwell, & Fisher, 2013) but thoroughly updated using latest data from (van Dyck, Gynther, & Baker, 2013). As a result, we collated the largest and most comprehensive dataset on marsupial brain size and body weight to date comprising 176 species.

While endocranial volumes are a reliable proxy for brain size (Jerison, 1973) they do suffer from certain drawbacks. For example, in marsupials, the koala’s (*Phascolarctos cinereus*) endocranial cavity might be exceptionally large compared to the brain contained in it, comprising only around 60% of the total ECV (Taylor, Rühli, Brown, De Miguel, & Henneberg, 2006)*.* Therefore, using ECV without correction in such species might lead to the misleading observation that they have very large brains. To our knowledge, no other species in our dataset has such potential stark discrepancy between ECV and actual brain size.

Moreover, the dataset includes 16 traits chosen so to allow for testing most of the hypothesis about brain variation (See table for traits and sources). The final dataset comprises 176 species of marsupials from all three continents inhabited by the infra-class. Those comprise around 53% of all marsupial species, approximated to be around 330 in total. The full dataset used can be found both as Supplement herein and on Github.

Brain size, body size, origin and activity cycle had no missing values, while the other traits had around 25% missing values on average (see Multiple Imputations section and Supplementary Information for the pattern of the missing data).

For detailed description on rationale for inclusion and sources of the data, see the table with data sources.

## Phylogeny

We included information on phylogenetic non-independence in all our analyses using an ultrametric phylogenetic tree of 175 extant marsupial species (with exception of the extinct Thylacine) obtained from Time Tree. This was deemed appropriate because the tree provided full coverage of all species investigated, using for most taxa the recent marsupial phylogeny of Mitchell et al.

The tree had 12 branches with length of 0 (used as means for resolving polytomies), which due to the requirements of some of the approaches had to be resolved. We did that by adding 0.01% of the median branch length, and then ultrametricized the tree again using extension, with the package phytools (cite the Tail paper).

## Statistical methods

### Multiple imputations

For imputation of missing data, we used the R package phylomice. It is an extension for the package mice, which allows for multiple imputations with the addition of taking the phylogenetic non-independence of the data into account. We use the method of predictive means matching (Demirtas, 2018; Little, 1988), a semi-parametric stochastic regression method in which a small set of candidate values (‘donors’) is found for each missing data point based on multiple regression model, whose predicted regression score is closest to the missing value. The choice of donor is then biased by the phylogenetically closer cases. Because the beta coefficients values in the regression models are chosen at random from the joint posterior distribution, such model introduces considerable stochastic variation, simulated by a Markov chain Monte Carlo procedure.

This imputation method has the advantage that missing data are imputed based on several values observed elsewhere in the set, so they are usually realistic. The pattern of missing values in our dataset is reported in the supplementary material. We have variables with 0 missing values - brain size, body size, origin, diurnality; and such with more than half of the values missing, i.e play (68% or 120 missing), torpor (53% or 94 missing). On average, the dataset contained 25% missing values, which we used as reference for the number of multiple imputations. Check supplement for missing data. Following published recommendations from (White, Royston, & Wood, 2011), the number of datasets we imputed was equal to the percentage of missing data – twenty-five.

We ran the imputations for 500 iterations each, on natural log transformed continuous variables, and raw values of categorical variables (see strip plot of imputations). As predictors, only values with less than 35% missing values were used, which rendered 13 predictors in total. Convergence of the chained equations was assessed visually on the diagnostic plots of mice, using both strip plots and density plots.

All subsequent analysis conducted on variables containing missing values were done on all twenty-five imputed datasets, and final results were pooled from all twenty-five imputations using Rubin’s rule (REF).

### Evolutionary mode variation

To assess the suggestion of Weisbecker et al. (2015) that switches to different land masses may change patterns of marsupial brain evolution, we assessed if differences in evolutionary mode on brain/body mass evolution regimes occurred in Australian, New Guinean, and American marsupials. To investigate if changes in evolutionary mode (i.e. whether Brownian motion or a specific optima-driven mode of evolution occurs) and particularly if the deepest split in the marsupial tree (Ameri- vs. Australidelphia) resulted in different evolutionary patterns, we investigated which mode of evolution best fitted our data - BM vs OU vs EB. Best fitting evolutionary models were assessed using the function fastBM from the geiger package,

### Model assessment

Due to its convenient wrapper functions we used the package mulTree (Guillerme & Healy, 2014) to conduct MCMCglmm (Hadfield, 2015) on each of the 25 imputed datasets. We ran the MCMC for 1 000 042 iterations, with burn in of the first 150 000 iterations, and sampling rate of 250. All priors were set to uniform and uninformative, which assumes that all values of the parameters are equally likely. Each model was run on 2 chains which produced an effective sample size of at least 3000 and all converged successfully (Gelman-Rubin criterion < 1.1). Subsequently, the results from all 50 model runs (25 datasets on 2 chains) were pooled using the Rubin’s rule (REFERENCE). Finally, the fit of all models to explain brain size variation was compared using heritability and DIC.

# Supplementary material

Table with data sources

|  |  |  |  |
| --- | --- | --- | --- |
| Trait | Units | Rationale | Reference |
| Brain | mm3 |  | (Weisbecker et al., 2015) + |
| Body | grams |  | (Birdlife International, 2016; Flannery, 2013; Myers et al., 2006; van Dyck, Gynther, & Baker, 2013; Weisbecker, Ashwell, & Fisher, 2013) |
| Origin | 1 – Australia, 2 – New Guinea, 3 - Americas | Different origins predispose different influence of seasonality, predation pressure, food abundance. | (Flannery, 2013; Myers et al., 2006; van Dyck et al., 2013) |
| Status | 1 - Common, abundant, 2 - Vulnerable, endangered, rare, declining, limited  3 - Extinct | Highly threatened mammals are known to have larger relative brain sizes (Abelson, 2016) | (Birdlife International, 2016; van Dyck et al., 2013) |
| Diurnality | 1- Nocturnal, 2 – Diurnal, 3 - Crepuscular or not fully nocturnal | Nocturnal animals are considered larger brained, but daily activity is related to more complex predator avoidance techniques. | (Flannery, 2013; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Arboreality | 1 - Arboreal or scansorial, 2 - Terrestrial | Arboreal environment is considered more cognitively demanding. | (Flannery, 2013; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Shelter safety | 1 - Protected (burrow/nest in a tree hollow), 2 - Intermediate (tree canopy/hollow log/under rock/nest on the ground or in a soil crack), 3 - Open (under shrubs/in grass/tree shade) | Proxy for predation as selection pressure for larger brains. (Reddon, Chouinard-Thuly, Leris, & Reader, 2018) | (Flannery, 2013; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Diet | 1 - >50% grass/browse, 2 - Seeds, grass, roots, leaves, fruit, invertebrates, 3 - Nectar, fruit, invertebrates, 4 - >50% invertebrate/vertebrate | Foraging complexity and diet rich in nutrients have been shown to influence brain size | (Flannery, 2013; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Group living | 1 – No, 2 - Yes | Measure of social complexity, which imposes greater interaction and recognition demands | (Flannery, 2013; Myers et al., 2006; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Parental care | 1 – No, 2 - Yes | Parental investment is known to positively influence brain size (Isler & van Schaik, 2012) | (Flannery, 2013; Myers et al., 2006; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Mating system | 1 – Promiscuous, 2 - Complex (polygamous/monogamous) | Complex mating systems require more cognitive complexity and usually result in higher parental investment (Schillaci, 2006) | (Flannery, 2013; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Litter size | Average litter per reproductive episode | Constraint on maternal investment. | (van Dyck et al., 2013; Weisbecker et al., 2015) |
| Weaning age | Months | Constraint on maternal investment. | (Weisbecker et al., 2015) |
| Home range | Hectares | Larger home ranges usually imply increased cognitive complexity related to orientation (Clutton‐Brock & Harvey, 1980) | (Myers et al., 2006; van Dyck et al., 2013; Weisbecker et al., 2015) |
| Population density | Individuals per hectare | Increased population density is a proxy of increased interaction and social tolerance. | (van Dyck et al., 2013; Weisbecker et al., 2015) |
| FMR | Field metabolic rate | Measure of metabolic turnover in the wild. | (Riek & Bruggeman, 2013) |
| Torpor | 0 – No, 1 – Yes | Torporing has been shown to be costly to the maintenance of large brains (Heldstab, Isler, & van Schaik, 2018) | (Geiser & Körtner, 2010; McNab, 2008; Ruf & Geiser, 2015) |
| Play | 1 – No, 2 – Rudimentary, 3 - Complex | Proxy for cognitive ability. Play has been shown to correlate with larger brains in birds and mammals (Iwaniuk et al., 2001) | (Ashwell, 2008; Iwaniuk et al., 2001) |

Dataset

Imputed datasets

R Code

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