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

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# Abstract (150 words)

# Introduction

Compared to other vertebrates, mammals have impressively large brains relative to body size (“relative brain size” herein), which confers advanced cognitive abilities to the class compared to the ancestral vertebrate condition (Jerison, 1973). It is assumed that this brain size increase is mostly the result of selection for the increase in relative brain size (Healy & Rowe, 2007). Similarly, 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). However, the source of this selection pressure is unclear: several selection-focused hypotheses have been put forward in an attempt to explain the increase in relative brain size and its subsequent fitness benefits in variety of cognitively demanding tasks. Among the more widely debated hypotheses, the ‘social-brain’ hypothesis suggests that increases 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). On the other hand, the ‘ecological brain’ hypothesis proposes that increase in cognitive demands related to ecological factors (diet, home range, predation pressure) can select for increase in relative brain size (DeCasien, Williams, & Higham, 2017; Milton, 1981) . There exists also a more holistic hypothesis regarding the evolution of brain variation which do not associate relative size increase with particular behavioural parameters. This ‘cognitive-buffer’ hypothesis claims that larger brains generally improve fitness and survival, due to advantages related to tackling novel and unpredictable environments and situations (Daniel Sol, 2009; van Woerden, Willems, van Schaik, & Isler, 2012). Additionally, it has been proposed that the buffer function of the brain could result in the generation of positive feedback processes which can even accelerate brain evolution(D. Sol, 2009).

It is widely recognized that processes of selection for relatively larger brains are antagonized by the high expense of brain growth and maintenance, as larger brains are known to be metabolically costly. Studies of brain size constraints under this ‘expensive tissue’ hypothesis (or more specifically the ‘expensive brain’ hypothesis’) have revealed indications of metabolic, maternal investment and general energetic constrains on the evolution of large brain size (Aiello & Wheeler, 1995; Isler & van Schaik, 2009).

Even though the two approaches to studying brain variation have many times been applied separately, a conclusive picture about the evolutionary processes shaping brain size can only be drawn by simultaneously investigating both the effects of selection pressures and the limitations imposed by developmental constraints (Logan et al., 2018; V. Weisbecker, Blomberg, Goldizen, Brown, & Fisher, 2015). At the same time, many previous studies focus solely on rejecting or confirming only one of the many hypotheses. The same applies to studies focusing only on constraints or selection, as many times such processes interact with each other. For example, home range is related to mating systems (Lukas & Clutton-Brock, 2014), social group sizes are related to predation pressure (Hintz & Lonzarich, 2018), maternal investment is dependent on mating systems (Shuster, 2009) and energetic availability is dependent on diet.

A drawback of most studies on brain size evolution is their almost exclusive focus on placental mammals. Placentals include the largest-brained mammals (such as cetaceans or canid carnivorans), but also have highly varied life histories and reproductive modes that increase the risk of confounding constraining traits of reproduction with selecting traits of behaviour (Logan et al., 2018). This makes the sister radiation of placentals – the Marsupial mammals – an attractive alternative of study. Marsupial mammals combine strikingly homogenous life histories and developmental regimes with a similarly diverse range of behavioural complexities as placentals (Carlisle et al., 2017; V. Weisbecker et al., 2015; V. Weisbecker & Goswami, 2010). Moreover, marsupials are a discrete, phylogenetically well-resolved, monophyletic radiation diverging from placentals around 130-160 mya (Luo, Yuan, Meng, & Ji, 2011). Their altricial neonates are born after very short gestation periods (12-30 days) and most receive little to no maternal investment. Moreover, marsupials exhibit a diverse array of social and mating systems, diet types, home ranges, cognitive abilities (Todorov, 2019). They are distributed in various habitats with various levels of seasonality (New Guinea, Australia and the Americas). This unique combination of reproductive homogeneity and ecological, behavioural and social diversity, makes marsupials perfectly suited for testing hypothesis about brain size evolution (Carlisle et al., 2017).

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 maternal constraints model and specifically litter size, representing the best model to explain brain size variation (V. Weisbecker et al., 2015). In addition, there was an unexpected highly significant effect of geological location, with New Guinean marsupials shown to be significantly larger-brained than their Australian relatives. However, the species in the dataset were nearly exclusively Australasian. In addition, like most other studies of brain size evolution, the coverage of data for the explanatory variables was low, so that model comparisons could only be done one at a time. With very limited amount of species and different species representation for each model the results of that study might have been inconclusive. The statistical approach – namely PGLS – is also very sensitive to errors in phylogeny, has many assumptions about the data and assumes single mode of evolution throughout the whole tree (Brownian motion) (Mundry, 2014).

In this study, we incorporate a new dataset of 62 South American marsupial species into existing data, thus increasing the number of marsupial brain sizes data by a third. Most of the body weight data has been updated with latest information from(van Dyck, Gynther, & Baker, 2013), and many other trait data had been updated with new or updated information. We then address the common limitation of incomplete data coverage by using for the first time phylogenetically adjusted multiple data imputation technique on a comparative dataset (Rubin, 1987). Such an approach unprecedentedly improves the statistical power of the study as technically, we do not have to deal with missing data at all.

We then apply a phylogenetically corrected Bayesian comparative analysis method – MCMCglmm – which has less assumptions about the distribution of the source data and can test multiple hypothesis on multiple datasets (Hadfield, 2010).

Dealing with missing data has been a pervasive issue in comparative studies. The most common solution to the problem has been to omit cases with missing values, which often results in losing whole cases only because of one or two missing values. A proposed and tested approach is multiple data imputation (Nakagawa & Freckleton, 2008; Resche-Rigon & White, 2018; Rubin, 1987) which has previously been shown to be a better solution to the problem, than omitting missing cases (Fisher, Blomberg, & Owens, 2003).

We then firstly ask whether this more comprehensive approach improves on previously tested models of behavioural complexity in marsupials; we then go on to test three additional important hypotheses of brain size evolution, namely whether play behaviour, hibernation and conservation status are associated with brain size increases. 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 and test whether evolutionary rate shifts had occurred as a result of invasion in a novel landmass. We test whether New Guinean marsupials had increased rate of evolution compared to Australian or American species, which might explain why this latest marsupial radiation has the largest relative brain size.

# Significance box

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 contributing with 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.

# Results

|  |  |  |  |
| --- | --- | --- | --- |
| Model | β | SE | Posterior distribution above or below zero |
| Developmental  Weaning age  Litter size | -0.086 | 0.052 | -95.88% |
| Environmental  Activity  Shelter safety  Terrestriality  Diet  Home range |  |  |  |
| Social  Group living  Parental care  Mating system  Populations size |  |  |  |
| Metabolic  FMR |  |  |  |
| Hibernation  Torpor |  |  |  |
| Play |  |  |  |
| Vulnerability | -0.14 | 0.081 | -96.08 |
| Origin | 0.31 | 0.12 | +99.42% |

## 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).

### 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 slightly smaller brains (96.08 of the posterior distribution below zero, β = -0.14, SE=0.081), but the interaction with body size yields to a postive relationship (96.94% of the posterior distribution above zero, β = 0.023, SE=0.012).

### Origin model

Species from New Guinea were shown to have larger brains (99.42% of the posterior distribution above zero, β = 0.31, SE=0.12), but the interaction with body size was positive (95.26% of the posterior distribution below 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 |

1. **Evolutionary models of BM, OU, EB**

**Prediction:** Later invasions into new ecospaces have involved bursts of variation as the clade adapts.

**Rationale:** We would expect this for Australia because of the invasion from Gondwana and for NG because of the invasion from Australia; We would not expect this because crown marsupials have been in S. Am. Since the isthmus of panama formed.

**Result:**

In Australia we have EB for body and brain

In Ng we have EB for brain but BM for body

In America we have BM for both brain and body

**Conclusion:** Prediction supported – VW: in Ng we have significantly greater relative brain size and there seems to have been a jump in brain size that body mass for some reason has not participated in. The polarity of this is interesting – it really is the brain that jumps, not body mass. Why??? Seasonality? Human hunting pressure? Competition with placentals? Cognitive buffer?

An additional pANCOVA showed that a model including ‘Origin’ as an interaction term was significantly better than a model including maruspials from all origins (F=5.07, P=0.0072 on 4, 2 degrees of freedom), while variance inflation factor (VIF) was <2.   
  
<figure 1 around here – report slopes and intercepts for the 3 origins>

## Rate shifts

RRphylo report here (Figures)

## Ancestral state estimation

Report ANC here

# Discussion

In this comprehensive study of brain size evolution, we find an intriguing lack of selection-related brain size correlates across the radiation of marsupial mammals. However, our use of RRphylo/SURFACE suggests that this very common issue in brain size evolution studies may arise because there is no one single correlate of brain size. Rather, 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).

Our models included the most comprehensive dataset of marsupials to date, including species from all geographic regions, along with updated body mass and trait data. In order to tackle uncertainty due to missing data we used phylogenetic imputations and Bayesian comparative analysis method – MCMCglmm, which allowed us to run the analysis on several imputed datasets.

Nevertheless, these new and more rigorous analyses confirmed previous findings, namely, that the only major determinant of brain size evolution in marsupials is their developmental mode, and more specifically litter size is inversely related to relative brain size (V. Weisbecker et al., 2015). Additionally, we were able to confirm that marsupials from New Guinea do have the largest brains among marsupials, and this relationship is dependent upon body size – the largest bodied species from both localities do not differ in brain size. 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.

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 (I need to graph this too) (Abelson, 2016; Gonzalez-Voyer, Gonzalez-Suarez, Vila, & Revilla, 2016)

Why in marsupials

Seasonality/predation cognitive buffer -> BM/RRphylo – in NG

The interaction we see might not actually relate 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. This might make them less threatened but will have the side effect of relatively smaller brains because larger litters are associated with smaller brain sizes.

reveals solid support for the two hypotheses that posit an energetic constraint on mammalian brain size, while adding the subclass of Marsupialia to the considerable number of placental clades for which no connections between social complexity and relative brain size are apparent [Walker et al., 2006; Healy and Rowe, 2007; Finarelli, 2009b; Shultz and Dunbar, 2010b]. Specifically, the maternal investment constraint model has far more support than the environmental interaction and social brain models. In addition, the constraint-based variables of litter size and NG origins (as well as possibly latitudinal distribution, which was close to the significance cutoff) are the only unambiguous associates of marsupial brain size. The significantly larger brains of NG marsupials in particular provide good support for the notion that low seasonality represents ‘nutrition safety’ for the brain [van Woerden et al., 2010, 2012]. It is possible that this effect is amplified by the better soils of NG, which might contribute to better food availability overall [Flannery, 1994; Ashwell, 2008]. However, this needs further research, since many NG ecosystems – particularly rainforest communities – are on fairly poor soil.

1. Discuss the framework and elaborate on advantages and some drawbacks ( i.e. the case of a lot of missing data)
   1. Imputation as a useful tool and extending the phylo-part of MICE
   2. MCMC as better (more flexible) compared to pgls
   3. Pooling
2. ANC and further explorations after incorporating fossil data
3. Discuss convergence and the further directions using this method in brain evolution studies (maybe shape too?)
4. Red line about ECV vs brain
5. Whinge about more data in B(F)MR and cog ability (play, etc)
6. Discuss all models and stress on the new ones. Discuss differences and similarities with previous attempts in the field and propose further work (maybe suggest neuronal morphology, numbers, and density gradients?)

IN THE END WRITE SOMETHING LIKE

Despite the hugely improved sophistication of data, completeness through imputation, and modelling, the only model that explains relative brain size best is maternal constraints and specifically litter size. This could be because marsupials actually can’t change brain size for some reason, and that matches with their lower variation around the regression line compared to placentals. But also, reproductive parameters are tightly linked with a plethora of behavioural and ecological traits in the other models – for example, mating and home range blabla. Marsupials with their low level of reproductive confoundment may therefore indicate that a majority of correlations found in placentals have their ultimate cause in reproductive traits. For example, LITERTURE primate social systems/group size…

# 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 provided by (REF). Body weight data were taken from (Vera Weisbecker, Ashwell, & Fisher, 2013) but thoroughly updated using latest data from (van Dyck et al., 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 is 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 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 evolution (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 we 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 (e.g. Tail paper ref ;-)).

## 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. Following an established rule of thumb (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.

### Ancestral state estimation

For ancestral states, we used the package phytools and the function fast anc. We estimated ancestral traits on absolute brain size, and on the phylogenetically corrected residuals from the regression with body size. In the absence of fossils, this method has limited power of inference but provides a good overview over where changes in relative brain size are to be expected.

### Evolutionary mode variation and regime changes

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) or regime changes are related to any of our models, we looked at where differences in evolutionary rate change occur within our phylogenetic tree and whether there was a coincidence of a model parameter (e.g. origin) and changes in mode of evolution. Similarly, to particularly investigate 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 fastBM from the geiger package,

Rate shifts

We evaluated the appearance of rate shifts within the three different land masses DESCRIBE IN DETAIL

### 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.Ppooling function 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). For variables X, Y, Z, it is possible that the relationship between body mass and brain volume change with changes in the explanatory variable in question (i.e. an interaction exists with body mass). We therefore initially computed the model with an interaction term; when this was not significant the model was ran without an interaction term. Finally, the fit of all models to explain brain size was compared using heritability and BIC.

# 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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