

## Research



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# Phylogenetic signal in primate behaviour, ecology and life history

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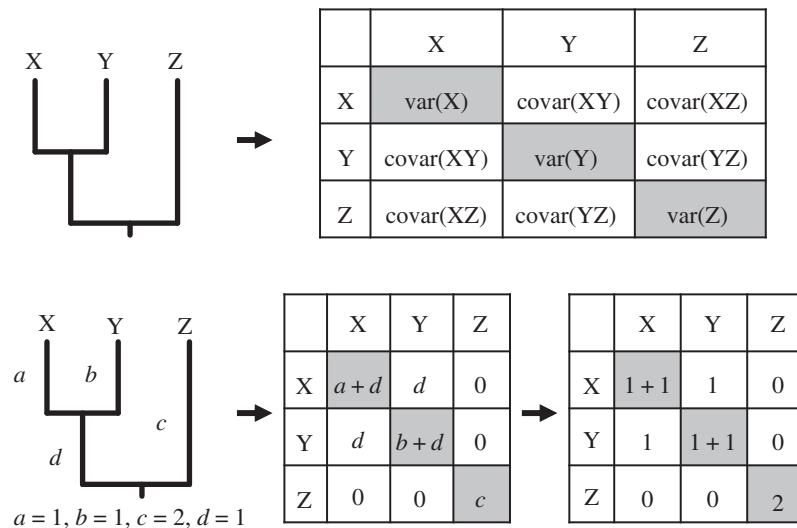
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Examining biological diversity in an explicitly evolutionary context has been the subject of research for several decades, yet relatively recent advances in analytical techniques and the increasing availability of species-level phylogenies, have enabled scientists to ask new questions. One such approach is to quantify phylogenetic signal to determine how trait variation is correlated with the phylogenetic relatedness of species. When phylogenetic signal is high, closely related species exhibit similar traits, and this biological similarity decreases as the evolutionary distance between species increases. Here, we first review the concept of phylogenetic signal and suggest how to measure and interpret phylogenetic signal in species traits. Second, we quantified phylogenetic signal in primates for 31 variables, including body mass, brain size, life-history, sexual selection, social organization, diet, activity budget, ranging patterns and climatic variables. We found that phylogenetic signal varies extensively across and even within trait categories. The highest values are exhibited by brain size and body mass, moderate values are found in the degree of territoriality and canine size dimorphism, while low values are displayed by most of the remaining variables. Our results have important implications for the evolution of behaviour and ecology in primates and other vertebrates.

## 1. Introduction

Closely related species tend to exhibit similarities in a range of traits, including morphological, behavioural, life-history and ecological characteristics, because they inherited them from their common ancestors [1]. These similarities form one of the most fundamental patterns in evolutionary biology. Species' traits that are more similar in close relatives than distant relatives are often said to show high phylogenetic signal. Conversely, species' traits that are more similar in distant relatives than close relatives (e.g. in convergent evolution), or are randomly distributed across a phylogeny, are said to show low phylogenetic signal. Much research has focused on quantifying these differences in phylogenetic signal among species and traits [2–5]. However, there is still disagreement about the ubiquitous nature of phylogenetic signal in biological traits, especially in behaviour and ecology. For instance, some authors argue that closely related species will always occupy similar, although not necessarily identical, environments [6]. Others suggest that strong phylogenetic signal should be the *a priori* expectation when examining ecological variation in a phylogenetic context [7–9]. Still others stress that strong phylogenetic signal in behavioural and ecological traits occurs in some clades for some traits, but not in others [10]. Consequently, it is still important to ask whether behavioural and ecological traits always exhibit phylogenetic signal, especially when compared with other biological characteristics. Unfortunately, owing to confusions in terminology and interpretation, phylogenetic signal still remains a misunderstood concept, especially in evolutionary anthropology. Therefore, in this study, we first briefly review the term phylogenetic signal, describe how it can be measured, mechanisms that may underlie the pattern and potential pitfalls in its estimation. We end by exploring phylogenetic signal in a range



**Figure 1.** Example of a phylogenetic variance–covariance matrix.

of primate morphological, behavioural, life-history, ecological and climatic niche variables.

## 2. What is phylogenetic signal?

Phylogenetic signal can be defined as the tendency for related species to resemble each other, more than they resemble species drawn at random from a phylogenetic tree [4,11]. More simply, phylogenetic signal is the pattern we observe when close relatives are more similar than distant relatives [1]. Species' traits can show high or low phylogenetic signal; where phylogenetic signal is high, closely related species exhibit similar trait values and trait similarity decreases as phylogenetic distance increases [10]. Conversely, a trait that exhibits weak phylogenetic signal may vary randomly across a phylogeny or show numerous cases where distantly related species converge on a similar trait value, while closely related species exhibit notably different trait values [12]. Note that previous authors have referred to phylogenetic signal using different terms, including phylogenetic effects, phylogenetic constraints and phylogenetic inertia. These terms are inconsistently defined, and thus mean different things to different people (see [11] for a review). We therefore follow other authors in recommending that these terms are avoided [10,11,13].

## 3. How is phylogenetic signal measured?

Several methods have been developed for measuring phylogenetic signal, including both autocorrelation methods and methods that use an explicit model of trait evolution. For recent detailed comparisons of the strengths and weaknesses of different measures of phylogenetic signal, see Münkemüller *et al.* [5] and Hardy & Pavoine [14]. Here, we focus on the two most commonly used metrics to date: Blomberg's  $K$  [4] and Pagel's  $\lambda$  [2,15,16]. These metrics are for continuous characters only (some methods exist for discrete characters [17] but these are beyond the scope of this study and not yet widely used). Both  $K$  and  $\lambda$  use an explicit model of trait evolution, namely the constant–variance or Brownian motion model [18,19]. It is important to note that phylogenies with arbitrary branch lengths (e.g. all branch lengths equal) are not appropriate for estimating phylogenetic signal using  $K$  or  $\lambda$ .

Under Brownian motion, the magnitude and direction of trait change through time is independent of the current state of the trait and has an expected mean change of zero. Therefore, a trait changes gradually through time. In this scenario, the expected covariance between species' trait values at the tips of the phylogeny is exactly proportional to the shared history of the species involved, i.e. the sum of their shared branch lengths. In addition, the expected variance of a trait value for a given species is proportional to total length of the tree, i.e. the summed branch length from the root to the tip for that species [19]. All of this means that a phylogeny can be represented as an  $n \times n$  phylogenetic variance–covariance matrix, where  $n$  is the number of species in the phylogeny. The off-diagonals of the matrix represent the covariances between species pairs, i.e. the sum of their shared branch lengths. The diagonals of the matrix represent the species variances, i.e. the total length of the tree (figure 1). We return to phylogenetic variance–covariance matrices below.

The Brownian motion model may not be a very realistic representation of the evolutionary process. However, trait evolution by random walk is not as unlikely as it first appears; it is the expectation under both genetic drift and natural selection where there are many, constantly changing selection pressures, or where traits randomly evolve from one adaptive peak to another. Both of these scenarios seem reasonable over long time periods given that environments (and hence selection pressures) are constantly fluctuating. In addition, using the Brownian motion model greatly simplifies the math needed to fit evolutionary models, allowing for a more tractable interpretation of results. Note that trait variation across a phylogeny may also be described by other models of evolution [13,20–23], though Brownian motion has been the best studied to date.

### (a) Blomberg's $K$

Blomberg's  $K$  measures phylogenetic signal by quantifying the amount of observed trait variance relative to the trait variance expected under Brownian motion [4]. More precisely,  $K$  is the ratio of two mean squared errors (MSEs).  $MSE_0$ , the mean squared error of the tip data in relation to the phylogenetic mean of the data, is divided by  $MSE$ , the mean squared error extracted from a generalized least-squares (GLS) model

that uses the phylogenetic variance–covariance matrix in its error structure. If trait similarities are effectively predicted by the phylogeny, MSE will be small so the ratio of  $MSE_0$  to MSE (and  $K$ ) will be large. Conversely, if trait similarities are not predicted by the phylogeny, MSE will be large so the ratio of  $MSE_0$  to MSE (and  $K$ ) will be small. Finally, to make values of  $K$  comparable among different phylogenies, the observed  $MSE_0$  to MSE ratio is standardized by the expected mean squared error ratio under Brownian motion.

$K$  varies continuously from zero (the null expectation), indicating that there is no phylogenetic signal in the trait (i.e. that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives), to infinity. Where  $K = 1$  indicates that there is strong phylogenetic signal and the trait has evolved according to the Brownian motion model of evolution, while  $K > 1$  indicates that close relatives are more similar than expected under a Brownian motion model of trait evolution. We can test whether  $K$  is significantly different from zero (i.e. no phylogenetic signal) by randomizing the trait data across the phylogeny and calculating the number of times the randomized trait data gives a higher value of  $K$  than our observed value. This number can then be divided by the total number of randomizations to get a  $p$ -value.

### (b) Pagel's $\lambda$

Pagel's  $\lambda$  is a quantitative measure of phylogenetic dependence introduced by Pagel [15,16] and varies continuously from zero (the null expectation) to unity.  $\lambda = 0$  indicates that there is no phylogenetic signal in the trait, i.e. that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives. Where  $\lambda = 1$  indicates that there is strong phylogenetic signal, and the trait has evolved according to the Brownian motion model of evolution. Intermediate values of  $\lambda$  indicate that although there is phylogenetic signal in the trait, it has evolved according to a process other than pure Brownian motion [2,15,16]. Note that although most implementations of the method constrain  $\lambda$  to be less than or equal to unity,  $\lambda$  can also be greater than unity, indicating that close relatives are more similar than expected under a Brownian motion model of trait evolution. The upper bound of  $\lambda$ , however, is restricted because covariances cannot exceed variances in a phylogenetic variance–covariance matrix [2] (figure 1).

To estimate Pagel's  $\lambda$ , a maximum-likelihood approach is used to find the value of  $\lambda$  that best explains trait variation among species at the tips of the phylogeny. In practice, the  $\lambda$  parameter transforms the off-diagonal values, or the covariances between pairs of species, of the phylogenetic variance–covariance matrix. As described above (and in figure 1), under Brownian motion these off-diagonal/covariance values are equal to the sum of the shared branch lengths of the species. In terms of the phylogeny, these off-diagonals represent the internal branches of the tree. Thus, when  $\lambda = 1$ , the internal branch lengths stay the same, so the tree topology also stays the same. When  $\lambda < 1$ , these internal branches get shorter altering the tree topology, and when  $\lambda = 0$ , the internal branch lengths will also be equal to zero resulting in a star phylogeny (see the electronic supplementary material, S1). Because  $\lambda$  is estimated using maximum likelihood, we can test if  $\lambda$  is significantly different from

zero (i.e. no phylogenetic signal) or unity (i.e. the Brownian expectation) using likelihood ratio tests comparing a model with the observed maximum-likelihood value of  $\lambda$  to a model with a fixed  $\lambda$  of zero or unity.

Note that  $\lambda$  is not just a measure of phylogenetic signal, it is also often used to transform the branch lengths of a phylogeny for use in other analyses, for example, to account for phylogenetic non-independence in a variety of statistical tests, including regression [2], principal components analysis [24],  $t$ -tests [25] and discriminant function analysis [26].

### (c) Estimating Blomberg's $K$ and Pagel's $\lambda$ using R.

Both Blomberg's  $K$  and Pagel's  $\lambda$  are easy to estimate using R [27].  $K$  can be estimated using the function `phylosignal` (or `Kcalc`) in `picante` [28].  $\lambda$  can be estimated using the function `fitContinuous` in `GEIGER` [29] or `pgls` (by fitting the model: `trait~1`) in `caper` [30]. Both  $K$  and  $\lambda$  can also be estimated using the function `phylosig` in `phytools` [31]. Examples are available on the AnthroTree website (<http://www.anthrotree.info>; [13]).

## 4. How is phylogenetic signal interpreted?

Although people will often refer to 'high' or 'low' phylogenetic signal, the exact definition of high and low varies among studies. For example, low phylogenetic signal can refer to  $K$  and  $\lambda$  values from zero to any value less than unity; high phylogenetic signal can refer to  $K$  and  $\lambda$  values from significantly greater than zero to infinity. Regardless of how high and low phylogenetic signal are defined, it is common to see the pattern of phylogenetic signal being used to provide information about evolutionary processes. Low phylogenetic signal is often interpreted as evolutionary lability [4] or high rates of trait evolution leading to large differences among close relatives. Adaptive radiations are expected to be characterized by low phylogenetic signal in ecological niche traits because in adaptive radiations close relatives rapidly diversify to fill new niches. Other kinds of divergent selection or convergent evolution may also result in a pattern where close relatives are, on average, less similar than distant relatives. High phylogenetic signal, i.e.  $K$  and  $\lambda = 1$ , is expected under genetic drift or neutral evolution, because these processes should approximate a Brownian motion model of evolution (i.e. gradual, random, non-directional trait change through time; [19]). High phylogenetic signal is also often interpreted as evolutionary or phylogenetic conservatism [10]. Phylogenetic conservatism may be the result of stabilizing selection, pleiotropy, high levels of gene flow, limited genetic variation, low rates of evolution, physiological constraints or various biotic interactions (e.g. competition) restricting the evolution of new phenotypes [11,32–34]. Note, however, that the point at which phylogenetic signal is considered high enough to be phylogenetic conservatism varies among authors (e.g.  $K$  or  $\lambda > 1$ , [10];  $K$  or  $\lambda = 1$ , [35];  $0 \leq K$  or  $\lambda \leq 1$ , [32]).

Unfortunately, interpreting phylogenetic signal is not as simple as it appears. Using simulations, Revell *et al.* [18] found that different evolutionary processes can produce similar  $K$ -values, especially when  $K$  is low. They also found no relationship between  $K$  and evolutionary rate under constant-rate genetic drift, their simplest evolutionary model. Although  $K$  or  $\lambda = 1$  is usually interpreted as the result of

neutral genetic drift, Hansen *et al.* [36] noted that this process is identical to one in which traits were evolving to an optimum which itself evolved according to a Brownian process (i.e. the Ornstein–Uhlenbeck model of evolution). This pattern could also arise during natural selection that randomly fluctuates, or where selective pressures themselves exhibit strong phylogenetic signal, thus producing strong phylogenetic signal in the trait(s) on which these selection pressures are acting. Finally, some evolutionary processes can also increase phylogenetic signal relative to the Brownian motion expectation; for example, genetic drift occurring at different rates across the tree results in  $K > 1$  [18].

Phylogenetic signal is also context (i.e. data and phylogeny) dependent and can be influenced by scale, convergent evolution, taxonomic inflation and cryptic species [10]. Because of this, using  $K$  or  $\lambda$  (or any other measure of phylogenetic signal) to infer evolutionary processes or rates must be performed with consideration of the traits involved, the hypotheses to be tested and any available external information [35]. Note that this only applies to studies whose aim is to quantify and report measures of phylogenetic signal. For analyses that use  $K$  or  $\lambda$  to account for phylogenetic non-independence in statistical tests, the evolutionary process underlying the phylogenetic signal is irrelevant.

There may be certain situations where interpreting the processes producing patterns of trait variation are less challenging. For instance, we would expect relatively weak phylogenetic signal in the ecological traits of species in adaptive radiations because closely related species have diversified into different niches so will exhibit distinct biological characteristics. In addition, examining the amount of phylogenetic signal in possible selective forces (e.g. climate/habitat characteristics) may help us to interpret phylogenetic signal in other traits. For instance, if the temperature conditions species experience drive variation in body size, strong phylogenetic signal in body mass may be the result of strong phylogenetic signal in temperature variables. However, if we estimate phylogenetic signal for the temperature niche space of species and find that it is low, then this suggests that correlation with temperature is not likely to explain the strong phylogenetic signal in body mass. A similar approach was used to examine the relative importance of phylogeny and environmental factors for explaining the behavioural diversity of *Eulemur* populations [37].

## 5. Problems, misconceptions and other considerations with phylogenetic signal

Earlier we discussed some issues in using the pattern of phylogenetic signal to infer an evolutionary process. However, there are several other common problems and misconceptions associated with phylogenetic signal. We will briefly outline some of these below.

One issue involves the sample size of the trait under investigation. Irrespective of tree shape,  $K$  has good power (greater than 80%) to detect significant phylogenetic signal when sample sizes are greater than 20 [4]. For  $\lambda$ , power is good only for sample sizes greater than 30 [2]. This difference is partially due to significance in  $\lambda$  being determined by likelihood ratio tests, which can give notably imprecise  $p$ -values at low sample sizes. Like any statistic, when sample sizes are large, even small  $K$  and  $\lambda$  values will yield statistically significant  $p$ -values; thus as the number of species increases, the

ability to detect significant levels of phylogenetic signal increases. Consequently, it is important to think about statistical significance versus biological significance when sample sizes are extremely high or low. For large sample sizes, it may be more useful to focus on the actual measure of phylogenetic signal rather than placing too much emphasis on the significance or non-significance of  $p$ -values. Similarly for small sample sizes, finding  $K$  and  $\lambda$  of zero should not be taken to mean that there is no phylogenetic signal in the variable, or to justify the use of non-phylogenetic statistical analyses (see below). Instead, we would advise performing such analyses with several sets of branch lengths (i.e. in phylogenetic generalized least-squares models (PGLSs), we would advise comparing models with  $\lambda = 1$  to those with the maximum-likelihood estimate of  $\lambda$  and/or  $\lambda = 0$ ).

Another problem involves error in both the phylogeny and the measurement of the trait under investigation. Although errors in tree topology obviously affect measures of phylogenetic signal, simulations show that polytomies and missing branch length information, by far the most common problems in phylogenetic trees, have negligible effects on estimates of  $K$  or  $\lambda$  [5]. In terms of measurement error, Blomberg *et al.* [4] noted that  $K$  is sensitive to measurement error and suggested that it may obscure significant phylogenetic signal. Recently, Hardy & Pavoine [14] confirmed this using simulations to show that measurement error substantially decreases the power of  $K$  to detect significant phylogenetic signal and also biases values of  $K$  downwards. This bias was stronger in trees with many short branches near the tips [14]. Measurement error may be particularly problematic in comparative studies, where data are generally species averages and the raw data come from multiple sources.

Another issue to consider is the phylogenetic/taxonomic scale of the analysis. Measures of phylogenetic signal in any biological trait may vary at different phylogenetic/taxonomic scales. Therefore, a trait may exhibit high levels of phylogenetic signal at one level, e.g. at the level of genera, yet this pattern may break down at higher or lower levels of analysis. In addition, measuring phylogenetic signal does not account for variation within species. For instance, body mass is phylogenetically conserved across primates, yet we know that body mass varies within species geographically [38–42]. Within-species variation in behaviour and ecology is also well documented in many species, both in a geographical context, as well as between sexes [37,43–48].

One final common misconception about phylogenetic signal involves analyses that correct for the phylogenetic non-independence of species. In analyses using multiple species, species are not independent data points because they share characteristics with their close relatives owing to common ancestry [1]. This violates the assumptions of many statistical models; thus phylogenetic comparative methods are used to account for this statistical problem. Some authors argue that unless the variables in the analysis show significant phylogenetic signal, standard non-phylogenetic methods should be employed [49]. However, it is important to note that this refers to phylogenetic signal in the residuals of an analysis, not of the raw variables themselves [50]. Thus, a  $K$  or  $\lambda$  of zero for variable  $X$  does not necessarily mean that the regression of variable  $Y$  on variable  $X$  should be performed non-phylogenetically, unless the residuals from the regression also have no significant phylogenetic signal. Also note that a

PGLS with a  $\lambda = 0$  is exactly the same as a non-phylogenetic GLS model.

## 6. Phylogenetic signal in primate traits

Several researchers have examined primate behaviour and ecology in a phylogenetic perspective, although formally testing for phylogenetic signal using current methods has been rare. One of the first quantitative studies of primate behaviour in an explicitly phylogenetic context was conducted by DiFiore & Rendall [51] using social system traits of most primate genera. They found that Old World monkey behaviour was phylogenetically conserved, even though these species occupy a wide variety of habitats and a strong link between habitat variability and behaviour was expected. Additional studies focused on ecological niche space. For example, Fleagle & Reed [52] found a significant correlation between the ecological similarity and phylogenetic relatedness of primates within each continent. A more taxonomically narrow study found that closely related populations of *Eulemur* exhibited similar social organization characteristics independent of local habitat conditions [37], perhaps because social organization characteristics are associated with behaviours related to mating, which could be difficult to modify [37]. In contrast, no phylogenetic effect was found for diet, activity budget or ranging in *Eulemur* populations. The importance of phylogeny for explaining primate behavioural and social organization variation was also recently emphasized by Thierry [53]. He argued that there are several cases where the absence of measureable behavioural variation across species (especially across macaque species) can be best explained by the phylogenetic relationships of the species and not ecological factors. Finally, a recently published paper by Kamilar & Muldoon [12] explicitly tested if the climatic niche space of Malagasy primates exhibited significant phylogenetic signal. They found relatively low levels of phylogenetic signal for each climatic niche axis; closely related species often occupied quite different climatic niches while distantly related species often converged on similar climatic niches. This may reflect the fact that Malagasy primates comprise an adaptive radiation and have rapidly diversified to fill a wide variety of niches.

Considering the mixed evidence for the idea that behavioural and ecological traits exhibit significant phylogenetic signal, a more detailed examination of this issue is warranted. To date, there have been only two broad-scale studies of phylogenetic signal in biological traits [2,4]. These studies found that, in a variety of taxa, the traits that exhibited the highest levels of phylogenetic signal were body size and morphology, followed by life-history, physiology and finally behavioural traits. Although the findings of these studies are important, they did have some significant limitations. For mammals in particular, both analyses used comparative datasets that were phylogenetically broad (e.g. across Mammalia, within Carnivora and Primates, etc.), but were fairly limited in terms of the number of species in each dataset (mean = 52). Therefore, in many cases, these datasets may have not sufficiently captured important trait variation. Second, in many ways, the traits examined were quite narrow in scope. For instance, 17 of the 60 traits examined were some measure of body mass/weight. Only four datasets quantified social organization (group size in 75 antelope

species, 28 macropod species, 26 hystricognath rodent species and 15 mole rat species). Similarly, only five of the 60 datasets consisted of life-history traits, and these were only examined in carnivores (52 species), mole rats (15 species) and 'mammals' (26 species). Finally, Freckleton *et al.* [2] did not include any primate-only dataset, and Blomberg *et al.* [4] only examined four primate datasets, three of which were body mass or mass dimorphism and one being testis size.

Therefore, although previous studies provided us with a general picture of phylogenetic signal for many traits, we still have little knowledge about variation in phylogenetic signal across numerous biological traits, especially within a single mammalian order. Here, we address this issue by investigating phylogenetic signal for numerous traits in a taxonomically well-sampled primate dataset. In particular, we address the following questions: (i) What is the strength of phylogenetic signal in primate morphological, behavioural, ecological, life-history and climate niche traits? (ii) Is there variation in phylogenetic signal among and within these trait categories? (iii) What does phylogenetic signal tell us about primate trait evolution?

If the findings of previous studies that formally tested for phylogenetic signal hold true [2,4], then we would expect to find that phylogenetic signal is strongest in morphological traits, followed by life-history variables, and then behaviour. In addition, we predict that the climatic niche space of species should have low phylogenetic signal. This prediction is based on what we know about the macroecology of primate communities, where distantly related primate species are found sympatrically in the same study site (and consequently, climatic environment), especially in Africa and Asia [54,55]. Also, we expect to find variation in phylogenetic signal among traits within biological categories. For instance, the amount of leaves in a species' diet may have relatively high phylogenetic signal compared with other food items because leaves comprise a very limited portion of the diet for small-bodied taxa (i.e. relatively invariable across closely related small species, such as callitrichines, cheirogaleids) and is often a significant component of the diet in primate clades with specialized anatomical traits that are related to leaf processing (e.g. colobines, *Alouatta*). We predict that this dietary specialization will also influence activity budgets. Specialized folivores typically spend a significant amount of time dedicated to resting. Therefore, we expect that resting time will have a stronger phylogenetic signal than other activity budget variables. In contrast to folivory, fruit-eating is not dependent on body mass and/or anatomical specializations, and therefore, the fruit component of a species' diet can be more variable. This should also have ramifications for other aspects of behaviour and ecology.

## 7. Material and methods

J.M.K. collated data for a total of 213 primate species from various databases, published datasets, articles and books (see the electronic supplementary material, S2). The dataset contains 31 variables representing nine trait categories: (i) body mass; (ii) brain size; (iii) life-history; (iv) sexual selection; (v) social organization; (vi) diet; (vii) activity budget; (viii) ranging patterns; and (ix) climatic niche variables (table 1).

Unfortunately, data were not available for all variables for all species. Therefore, the number of species per analysis ranged from 64 to 195. Although our dataset is not exhaustive, it is the

**Table 1.** Variables and trait categories examined in the study. Numbers in parentheses are the number of species with data for that variable.

trait category	variable
body mass	male mass (195), female mass (195)
brain size	mean brain size (170), relative brain size <sup>a</sup> (164)
life history	litter size (166), gestation length (138), weaning age (118), interbirth interval (110), maximum longevity (147)
sexual selection	body mass dimorphism <sup>b</sup> (195), canine size dimorphism (121), relative testis mass <sup>c</sup> (64)
social organization	group size (153), number of adult males (143), number of adult females (145), adult sex ratio (129)
diet	per cent diet from fruit (115), leaves (118), animal matter (93)
activity budget	per cent time feeding (72), resting (70), moving (70), social (77)
ranging patterns	home range size (148), daily travel length (109), territoriality index <sup>d</sup> (104)
climatic niche space <sup>e</sup>	mean rainfall (175), mean temperature (175), actual evapotranspiration (175), potential evapotranspiration (175), latitude (175)

<sup>a</sup>Calculated as the phylogenetic residuals of female brain size regressed on female body mass.

<sup>b</sup>Body mass dimorphism and canine size dimorphism were calculated as the ratio of male : female values.

<sup>c</sup>Calculated as the phylogenetic residuals of testes weight regressed on associated body weights.

<sup>d</sup>Calculated per Mitani & Rodman [56]:  $\text{day range}/(4 \times \text{home range}/\pi)$ .

<sup>e</sup>Climate data are averaged across the geographical range of each species.

most comprehensive to date in terms of the number of species, and number of traits used to examine phylogenetic signal in a single order. We focused our dataset on traits that were readily available for numerous species, were continuously measured and were often used in prior comparative analyses.

We used the *10kTrees* dated phylogeny v. 3 with the associated taxonomy from GenBank [57]. We estimated phylogenetic signal in each trait using Blomberg's  $K$  and Pagel's  $\lambda$  (see §1), with the *picante* [28] and *phytools* packages [31], respectively, in R [58].

## 8. Results and discussion

### (a) Overview

We found statistically significant levels of phylogenetic signal in nearly all 31 variables using both Blomberg's  $K$  and Pagel's  $\lambda$ . Three variables did not exhibit a significant amount of phylogenetic signal as measured by  $K$ , group size ( $n = 153$ ,  $K = 0.063$ ,  $p = 0.433$ ), day range ( $n = 109$ ,  $K = 0.123$ ,  $p = 0.126$ ) and per cent social time ( $n = 77$ ,  $K = 0.116$ ,  $p = 0.083$ ). One variable, potential evapotranspiration, did not exhibit a significant amount of phylogenetic signal using  $\lambda$  ( $n = 175$ ,  $\lambda = 0.129$ ,  $p = 0.072$ ). Because results using  $K$  and

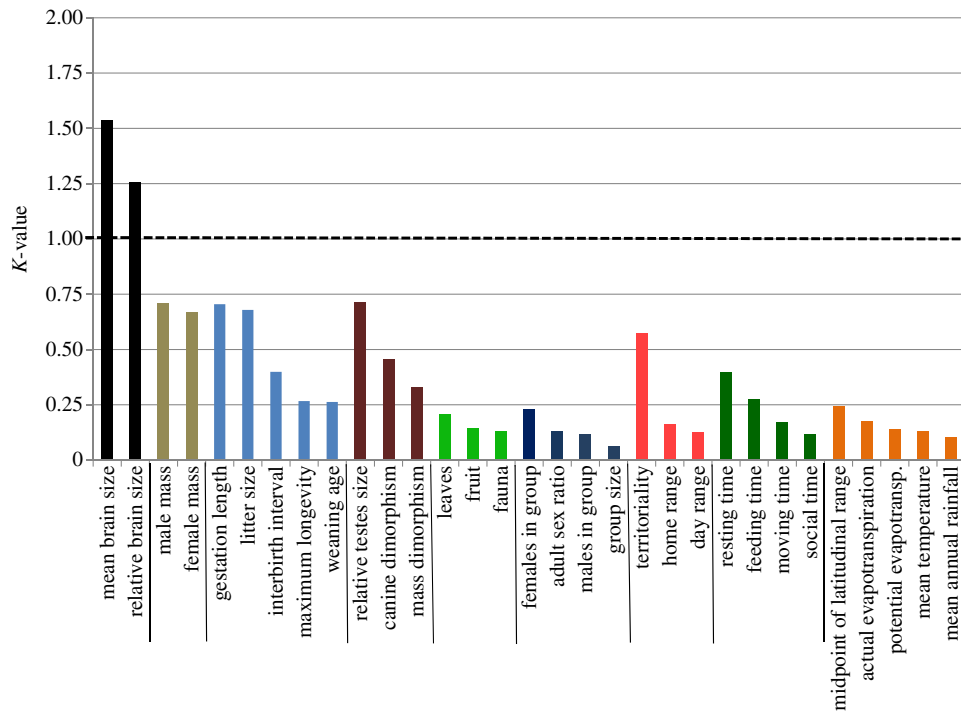
$\lambda$  were very similar, and  $K$  can also inform us about trait variation that is more similar than expected under Brownian motion, we focus on the results using  $K$  (see figure 2 and electronic supplementary material, S3).

Although most traits exhibited statistically significant phylogenetic signal,  $K$  varied widely across, and sometimes within, trait categories. Most traits had a  $K$ -value between zero and unity; only absolute and relative brain size had  $K \geq 1$ , indicating that these traits are phylogenetically conserved (cf. [10,35]). Across trait categories, phylogenetic signal tended to be highest in brain mass and life history, followed by proxies for sexual selection, ranging behaviour and activity budget, with diet, social organization and climatic niche variables consistently exhibiting the weakest phylogenetic signal. These findings are generally concordant with those of previous studies of phylogenetic signal that analysed fewer species and other mammalian clades [2,4]. Yet, our results provide further insights into the macroevolutionary patterns of additional traits.

In addition to differences in phylogenetic signal across trait categories, our results provide important detail about within trait category variation. In fact, there is notable variation in the phylogenetic signal of several variables within trait categories. For instance, within the ranging behaviour category,  $K = 0.572$  for territoriality, but  $K = 0.163$  for home range and 0.123 for day range. Life-history variables also showed a large amount of variation in  $K$ : phylogenetic signal varied from  $K = 0.705$  for gestation length to  $K = 0.263$  for weaning age. This relatively high variability in phylogenetic signal within some trait categories suggests that simply assuming a trait will have low or high phylogenetic signal based on the trait category it falls into (e.g. assuming that a behavioural trait will always have low phylogenetic signal) may obscure interesting and important variation.

### (b) Phylogenetic signal in primate brain size and body mass

Absolute and relative brain size were the only variables that exhibited phylogenetic conservatism, i.e. close relatives had more similar brain sizes than expected under Brownian motion ( $K > 1$ ). This probably reflects the relatively invariable brain sizes within genera, and even within families, of primates. Generally, high phylogenetic signal in morphological traits is attributed to their strong correlation with body mass; however,  $K$ -values for both male and female body mass were lower than for brain size (male mass:  $K = 0.707$ ; female mass:  $K = 0.670$ ). Similarly, a recent study of Malagasy primate body mass found levels of phylogenetic signal that do not differ from the Brownian expectation [38]. Thus, the high phylogenetic signal in brain size cannot be entirely explained by allometry alone. Instead, this probably reflects developmental and energetic constraints on absolute and relative brain size [59]. Interestingly, there is a notable difference between phylogenetic signal in brain size and various behavioural, ecological and life-history traits that are correlated with brain size. Behavioural traits known to correlate with brain size include social system type, level of coalition formation and group size [60]. However, the amount of variation in these variables explained by brain size is generally low (e.g. 5–26% in [60]), so clearly other factors are also involved.



**Figure 2.** Phylogenetic signal in primate traits using  $K$ . We highlighted a  $K$ -value of 1 as that indicates strong phylogenetic signal that perfectly follows Brownian motion, and below this line indicates a departure from strong phylogenetic signal.  $K$ -values greater than 1 indicate traits that are phylogenetically conserved. Different trait categories are separated by vertical lines. (Online version in colour.)

$K$ -values for body mass were higher than all other traits except for brain size and relative brain size. Many previous studies have found very similar body masses among congeneric species (Malagasy primates, [38], e.g. mammals, [61]). In addition, Cooper & Purvis [23] showed that the best model of primate body mass evolution involved rapid body size diversification early in the clade's history followed by reduced rates of evolution towards the present. This is reflected in the significant difference among body size distributions of primate clades from different regions [62] (i.e. among catarrhines, platyrrhines and strepsirrhines), with very little body size variation within more recent groups, especially genera. One explanation for this pattern is that the body size of a primate is a fairly good proxy for the niche space it will occupy [43,63,64]; thus the large body size differences deeper in primate evolutionary history reflect periods of rapid niche diversification as species entered new regions [65], and the relatively conserved body sizes within present-day primate clades may reflect competition for resources among close relatives [23,66,67]. This is supported by evidence from fossil primates which suggests that direct competition between omomyiforms and adapiforms (the two main Palaeogene primate radiations) influenced body mass evolution in omomyiforms [68]. Body sizes may also be limited by various metabolic or resource availability constraints [69].

Other traits related to body mass are often used as proxies of sexual selection. Canine dimorphism, body mass dimorphism and relative testes size all have  $K$ -values of between 0.25 and 0.5, i.e. they have lower phylogenetic signal than body mass itself. In particular, we can see several examples of differences in body mass dimorphism between sister taxa that have diverged relatively recently, e.g. *Alouatta* versus *Ateles*. Female body mass is quite similar across these species, yet body mass dimorphism is greater in *Alouatta* compared with *Ateles*. We see similar shifts in dimorphism when we compare great apes to gibbons, and even when comparing most cercopithecines

to most colobine monkeys. These results imply that sexual selection has been a more important agent of evolutionary change compared with natural selection when examining body mass evolution in the more recent past.

### (c) Phylogenetic signal in primate life-history, ecology, behaviour and climatic niche variables

Other than the traits related to body size and brain size discussed earlier, only three traits had values of  $K > 0.5$ : gestation length, litter size and territoriality. The phylogenetic signal in gestation length and litter size is likely to be partly because of correlations among these life-history variables and body mass, which also has a quite high phylogenetic signal. In addition, the fact that litter size is fairly conserved among primates is unsurprising as most primate species produce only one offspring per litter, with twinning being rare, although there are a few exceptions where multiple offspring per litter are regularly produced, e.g. callitrichines, cheirogaleids and *Varecia* [70,71]. Likewise, territoriality exhibited moderately high phylogenetic signal. Much of this pattern may be due to the callitrichines, as they exhibited nine of the highest 22 territoriality values. Monogamy and cooperative breeding are commonly observed in these species, traits that are often tied to territoriality in mammals [72,73]. This aspect of their behaviour is likely driving the relatively uniform territoriality scores. By contrast, members of a single genus, *Macaca*, exhibited wide variation in scores falling in the first, second and third quartiles of the entire data range.

The remaining traits show moderate to low phylogenetic signal (i.e.  $K < 0.5$ ), although  $K$  is usually greater than zero. Within behavioural traits, including those in the social organization, ranging patterns (excluding territoriality) and activity budget categories, phylogenetic signal was highest in the number of adult females in a group ( $K = 0.230$ ) and lowest

for total group size ( $K = 0.063$ ). In fact, total group size exhibited the lowest  $K$ -value of any trait we examined. This may be because closely related species often occupy different habitats [12,74] and are therefore likely to experience differences in habitat-specific conditions that influence group size, such as predation risk, resource availability, parasite diversity and infanticide risk [75–77]. The low phylogenetic signal in total group size may explain why there is also low phylogenetic signal in time spent being social ( $K = 0.116$ ), as these variables are highly correlated.

Phylogenetic signal in dietary traits was also relatively low, though the degree of folivory exhibits the strongest connection to phylogeny. This may be in part due to the relationship between folivory and body mass, which itself has a high phylogenetic signal. Folivory is more common in larger bodied primates, because large primates cannot obtain enough protein from animal matter alone, and small primates cannot efficiently digest leaves [64]. In addition, several large primate species have specialized morphological traits for processing leaves (especially the colobine monkeys), and thus often consume a large quantity of leaves [78,79]. These specializations may also limit their ability to consume large amounts of other food types, especially ripe fruit in the case of colobine monkeys, reducing levels of frugivory or faunivory in these clades.

Climatic niche variables exhibited some of the most consistently weak phylogenetic signals for primates (mean  $K = 0.158$ ). This is perhaps unsurprising, as we know that distantly related primates are often sympatric; and thus experience similar climatic conditions [55], while close relatives are often allopatric [80]. Previous research has also shown that within species, many primates are ecologically flexible in terms of their geographical distribution and associated climate and habitat conditions [12,55,81]. The low phylogenetic signal in climatic niche variables is advantageous for interpreting the moderate to high phylogenetic signal exhibited by some behavioural and ecological traits, as it suggests that these results are not merely because of strong phylogenetic signal in selective regimes as defined by climate and by proxy habitat variation.

It should be noted that the low levels of phylogenetic signal detected in most of our traits may also reflect methodological issues. As we mentioned in §1,  $K$  is sensitive to measurement errors. Many of our traits represent complex characteristics that are difficult to score, so measurement

error is likely. For example, activity budget data are collected in different ways in different studies, so combining them for one analysis may introduce various biases. In addition, we were using species means for each variable, and this may obscure important intraspecific variation. Finally,  $K$  is also sensitive to errors in the phylogeny, and although we are using the best phylogeny available, errors are still likely, particularly in branch lengths. Despite ‘error’ in these data (either due to measurement error or intraspecific variation), species-level data include important biological information that has been successfully used in comparative analyses for decades [82–86]. In addition, our results demonstrate that error is probably not the major factor responsible for the patterns we recovered. For example, our territoriality index exhibited much higher phylogenetic signal compared with day range or home range, although the former is a product of the latter two variables. Similarly, the percentage of time resting exhibited more than twice the phylogenetic signal of the percentage of time moving, although both variables are likely to have similar amounts of measurement error.

In conclusion, statistically significant levels of phylogenetic signal are common, but not ubiquitous, in a wide variety of primate characteristics, including behaviour and ecology. However, phylogenetic signal is generally lower than the Brownian motion expectation, which may demonstrate a degree of ecological and behavioural plasticity across primates. Although examining primate ecology in a phylogenetic context has become more common in recent years, there are still many questions that have received little attention. Future studies should attempt to integrate evolutionary data into behavioural/ecological models to hopefully obtain a more complete picture of diversity. Understanding phylogenetic signal in our traits of interest may be an excellent first step in this direction.

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## References

- Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*, pp. 248. Oxford, UK: Oxford University Press.
- Freckleton RP, Harvey PH, Pagel M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)
- O’Neill MC, Dobson SD. 2008 The degree and pattern of phylogenetic signal in primate long-bone structure. *J. Hum. Evol.* **54**, 309–322. (doi:10.1016/j.jhevol.2007.08.008)
- Blomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)
- Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffrers K, Thuiller W. 2012 How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3**, 743–756. (doi:10.1111/j.2041-210X.2012.00196.x)
- Wiens JJ, Graham CH. 2005 Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* **36**, 519–539. (doi:10.1146/annurev.ecolsys.36.102803.095431)
- Swenson NG, Enquist BJ, Thompson J, Zimmerman JK. 2007 The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecol. Lett.* **88**, 1770–1780. (doi:10.1890/06-1499.1)
- Johnson MTJ, Stinchcombe JR. 2007 An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* **22**, 250–257. (doi:10.1016/j.tree.2007.01.014)
- Duncan RP, Williams PA. 2002 Darwin’s naturalization hypothesis challenged. *Nature* **417**, 608–609. (doi:10.1038/417608a)
- Losos JB. 2008 Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**, 995–1007. (doi:10.1111/j.1461-0248.2008.01229.x)



11. Blomberg SP, Garland T. 2002 Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.* **15**, 899–910. (doi:10.1046/j.1420-9101.2002.00472.x)
12. Kamilar JM, Muldoon KM. 2010 The climatic niche diversity of Malagasy primates: a phylogenetic approach. *PLoS ONE* **5**, e11073. (doi:10.1371/journal.pone.0011073)
13. Nunn CL. 2011 *The comparative method in evolutionary anthropology and biology*. Chicago, IL: University of Chicago Press.
14. Hardy OJ, Pavoine S. 2012 Assessing phylogenetic signal with measurement error: a comparison of Mantel tests, Blomberg's *et al.*'s *K*, and phylogenetic distograms. *Evolution* **66**, 2614–2621. (doi:10.1111/j.1558-5646.2012.01623.x)
15. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
16. Pagel M. 1997 Inferring evolutionary processes from phylogenies. *Zool. Scripta* **26**, 331–348. (doi:10.1111/j.1463-6409.1997.tb00423.x)
17. Fritz SA, Purvis A. 2010 Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042–1051. (doi:10.1111/j.1523-1739.2010.01455.x)
18. Revell LJ, Harmon LJ, Collar DC. 2008 Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* **57**, 591–601. (doi:10.1080/10635150802302427)
19. Felsenstein J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)
20. Butler MA, King AA. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**, 683–695. (doi:10.1086/426002)
21. Martins EP. 1994 Estimating the rate of phenotypic evolution from comparative data. *Am. Nat.* **144**, 193–209. (doi:10.1086/285670)
22. Webster AJ, Purvis A. 2002 Testing the accuracy of methods for reconstructing ancestral states of continuous characters. *Proc. R. Soc. Lond. B* **269**, 143–149. (doi:10.1098/rspb.2001.1873)
23. Cooper N, Purvis A. 2010 Body size evolution in mammals: complexity in tempo and mode. *Am. Nat.* **175**, 727–738. (doi:10.1086/652466)
24. Revell LJ. 2009 Size-correction and principal components for interspecific comparative studies. *Evolution* **63**, 3258–3268. (doi:10.1111/j.1558-5646.2009.00804.x)
25. Lindenfors P, Revell LJ, Nunn CL. 2010 Sexual dimorphism in primate aerobic capacity: a phylogenetic test. *J. Evol. Biol.* **23**, 1183–1194. (doi:10.1111/j.1420-9101.2010.01983.x)
26. Motani R, Schmitz L. 2011 Phylogenetic versus functional signals in the evolution of form-function relationships in terrestrial vision. *Evolution* **65**, 2245–2257. (doi:10.1111/j.1558-5646.2011.01271.x)
27. R Development Core Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
28. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010 Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464. (doi:10.1093/bioinformatics/btq166)
29. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131. (doi:10.1093/bioinformatics/btm538)
30. Orme CDL, Freckleton RP, Thomas GH, Petzoldt T, Fritz SA, Isaac NJB, Pearse W. 2012 caper: comparative analyses of phylogenetics and evolution in R. *Methods Ecol. Evol.* **3**, 145–151.
31. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
32. Wiens JJ *et al.*. 2010 Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)
33. de Mazancourt C, Johnson E, Barraclough TG. 2008 Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11**, 380–388. (doi:10.1111/j.1461-0248.2008.01152.x)
34. Bradshaw AD. 1991 Genostasis and the limits to evolution. *Phil. Trans. R. Soc. B* **333**, 289–305. (doi:10.1098/rstb.1991.0079)
35. Cooper N, Jetz W, Freckleton RP. 2010 Phylogenetic comparative approaches for studying niche conservatism. *J. Evol. Biol.* **23**, 2529–2539. (doi:10.1111/j.1420-9101.2010.02144.x)
36. Hansen TF, Pienaar J, Orzack SH. 2008 A comparative method for studying adaptation to a randomly evolving environment. *Evolution* **62**, 1965–1977. (doi:10.1111/j.1558-5646.2008.00412.x)
37. Ossi KM, Kamilar JM. 2006 Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behav. Ecol. Sociobiol.* **61**, 53–64. (doi:10.1007/s00265-006-0236-7)
38. Kamilar JM, Muldoon KM, Lehman SM, Herrera JP. 2012 Testing Bergmann's rule and the resource seasonality hypothesis in Malagasy primates using GIS-based climate data. *Am. J. Phys. Anthropol.* **147**, 401–408. (doi:10.1002/ajpa.22002)
39. Lehman SM. 2007 Ecological and phylogenetic correlates to body size in the Indridae. *Int. J. Primatol.* **28**, 183–210. (doi:10.1007/s10764-006-9114-4)
40. Fooden J, Albrecht GH. 1993 Latitudinal and insular variation of skull size in crab-eating macaques (Primates, Cercopithecidae: *Macaca fascicularis*). *Am. J. Phys. Anthropol.* **92**, 521–538. (doi:10.1002/ajpa.1330920409)
41. Frost SR, Marcus LF, Bookstein FL, Reddy DP, Delson E. 2003 Cranial allometry, phylogeography, and systematics of large-bodied papionins (Primates: Cercopithecinae) inferred from geometric morphometric analysis of landmark data. *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **275A**, 1048–1072. (doi:10.1002/ar.a.10112)
42. Baden AL, Brenneman RA, Louis Jr EE. 2008 Morphometrics of wild black-and-white ruffed lemurs [*Varecia variegata*, Kerr 1972]. *Am. J. Primatol.* **70**, 913–926. (doi:10.1002/ajp.20583)
43. Kamilar JM, Pokempner AA. 2008 Does body mass dimorphism increase male–female dietary niche separation? A comparative study of primates. *Behaviour* **145**, 1211–1234. (doi:10.1163/156853908785387601)
44. Kamilar JM. 2006 Geographic variation in savanna baboon (*Papio*) ecology and its taxonomic and evolutionary implications. In *Primate biogeography* (eds SM Lehman, JG Fleagle), pp. 169–200. New York, NY: Springer.
45. Kamilar JM, Marshack JL. 2012 Does geography or ecology best explain 'cultural' variation among chimpanzee communities? *J. Hum. Evol.* **62**, 256–260. (doi:10.1016/j.jhevol.2011.11.008)
46. Panger MA, Perry S, Rose L, Gros-Louis J, Vogel E, Mackinnon KC, Baker M. 2002 Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.* **119**, 52–66. (doi:10.1002/ajpa.10103)
47. Boinski S. 1988 Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behav. Ecol. Sociobiol.* **23**, 177–186. (doi:10.1007/BF00300352)
48. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
49. Losos JB. 2011 Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *Am. Nat.* **177**, 709–727. (doi:10.1086/660020)
50. Revell LJ, Collar DC, Mooers A. 2009 Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution* **63**, 1090–1100. (doi:10.1111/j.1558-5646.2009.00616.x)
51. DiFiore A, Rendall D. 1994 Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc. Natl Acad. Sci. USA* **91**, 9941–9945. (doi:10.1073/pnas.91.21.9941)
52. Fleagle JG, Reed KE. 1999 Phylogenetic and temporal perspectives on primate ecology. In *Primate communities* (eds JG Fleagle, C Janson, KE Reed), pp. 92–115. New York, NY: Cambridge University Press.
53. Thierry B. 2008 Primate socioecology, the lost dream of ecological determinism. *Evol. Anthropol.* **17**, 93–96. (doi:10.1002/evan.20168)
54. Kamilar JM, Guidi LM. 2010 The phylogenetic structure of primate communities: variation within and across continents. *J. Biogeogr.* **37**, 801–813. (doi:10.1111/j.1365-2699.2009.02267.x)
55. Kamilar JM. 2009 Environmental and geographic correlates of the taxonomic structure of primate communities. *Am. J. Phys. Anthropol.* **139**, 382–393. (doi:10.1002/ajpa.20993)
56. Mitani JC, Rodman PS. 1979 Territoriality: the relationship of ranging pattern and home range size to defendability, with an analysis of territoriality in primates. *Behav. Ecol. Sociobiol.* **5**, 241–251. (doi:10.1007/BF00293673)
57. Arnold C, Matthews LJ, Nunn CL. 2010 The 10kTrees website: a new online resource for primate

- phylogeny. *Evol. Anthropol.* **19**, 114–118. (doi:10.1002/evan.20251)
58. R Development Core Team. 2009 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
59. Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
60. Dunbar RIM, Shultz S. 2007 Understanding primate brain evolution. *Phil. Trans. R. Soc. B* **362**, 649–658. (doi:10.1098/rstb.2006.2001)
61. Smith FA *et al.* 2004 Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *Am. Nat.* **163**, 672–691. (doi:10.1086/382898)
62. Kappeler PM, Heymann EW. 1996 Nonconvergence in the evolution of primate life history and socioecology. *Biol. J. Linn. Soc.* **59**, 297–326. (doi:10.1111/j.1095-8312.1996.tb01468.x)
63. Kay RF. 1975 The functional adaptations of primate molar teeth. *Am. J. Phys. Anthropol.* **43**, 195–216. (doi:10.1002/ajpa.1330430207)
64. Fleagle JG. 1999 *Primate adaptation and evolution*, 2nd edn. San Diego, CA: Academic Press.
65. Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
66. Freckleton RP, Harvey PH. 2006 Detecting non-Brownian trait evolution in adaptive radiations. *PLoS Biol.* **4**, 2104–2111. (doi:10.1371/journal.pbio.0040373)
67. Price TD, Helbig AJ, Richman AD. 1997 Evolution of breeding distributions in the Old World leaf warblers (genus *Phylloscopus*). *Evolution* **51**, 552–561. (doi:10.2307/2411127)
68. Soligo C. 2006 Correlates of body mass evolution in primates. *Am. J. Phys. Anthropol.* **130**, 283–293. (doi:10.1002/ajpa.20298)
69. Brown JH, Marquet PA, Taper ML. 1993 Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584. (doi:10.1086/285558)
70. Harvey PH, Clutton-Brock TH. 1985 Life history variation in primates. *Evolution* **39**, 559–581. (doi:10.2307/2408653)
71. Tecot SR, Baden AL, Romine N, Kamilar JM. 2012 Infant parking and nesting, not allomaternal care, influence Malagasy primate life histories. *Behav. Ecol. Sociobiol.* **66**, 1375–1386. (doi:10.1007/s00265-012-1393-5)
72. Kleiman DG. 1977 Monogamy in mammals. *Q. Rev. Biol.* **52**, 39–68. (doi:10.1086/409721)
73. Schradin C. 2004 Territorial defense in a group-living solitary forager: who, where, against whom? *Behav. Ecol. Sociobiol.* **55**, 439–446. (doi:10.1007/s00265-003-0733-x)
74. Fooden J. 1982 Ecological segregation of macaque species. *Primates* **23**, 574–579. (doi:10.1007/BF02373969)
75. Wrangham R. 1980 An ecological model of female-bonded primate groups. *Behaviour* **75**, 262–300. (doi:10.1163/156853980X00447)
76. van Schaik CP. 1983 Why are diurnal primates living in groups? *Behaviour* **8**, 120–143. (doi:10.1163/156853983X00147)
77. Nunn CL, Altizer SM. 2006 *Infectious diseases in primates: behavior, ecology and evolution*. Oxford, UK: Oxford University Press.
78. Kamilar JM, Paciulli LM. 2008 Examining the extinction risk of specialized folivores: a comparative study of colobine monkeys. *Am. J. Primatol.* **70**, 1–12. (doi:10.1002/ajp.20553)
79. Davies AG, Oates JF. 1994 *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge, UK: Cambridge University Press.
80. Kamilar JM, Ledogar JA. 2011 Species co-occurrence patterns and dietary resource competition in primates. *Am. J. Phys. Anthropol.* **144**, 131–139. (doi:10.1002/ajpa.21380)
81. Beaudrot LH, Marshall AJ. 2011 Primate communities are structured more by dispersal limitation than by niches. *J. Anim. Ecol.* **80**, 332–341. (doi:10.1111/j.1365-2656.2010.01777.x)
82. Clutton-Brock TH, Harvey PH. 1977 Species differences in feeding and ranging behaviour in primates. In *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes* (ed. TH Clutton-Brock), pp. 557–584. London, UK: Academic Press.
83. Nunn CL. 1999 The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* **46**, 1–13. (doi:10.1007/s002650050586)
84. Kamilar JM, Bribiescas RG, Bradley BJ. 2010 Is group size related to longevity in mammals? *Biol. Lett.* **6**, 736–739. (doi:10.1098/rsbl.2010.0348)
85. Janson CH, Goldsmith ML. 1995 Predicting group size in primates: foraging costs and predation risks. *Behav. Ecol.* **6**, 326–336. (doi:10.1093/beheco/6.3.326)
86. Fleagle JG, Reed KE. 1996 Comparing primate communities: a multivariate approach. *J. Hum. Evol.* **30**, 489–510. (doi:10.1006/jhev.1996.0039)