Testing Bergmann's Rule and the Resource Seasonality Hypothesis in Malagasy Primates Using GIS-Based Climate Data

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ABSTRACT We tested four major hypotheses on the ecological aspects of body mass variation in extant Malagasy strepsirrhines: thermoregulation, resource seasonality/scarcity, resource quality, and primary productivity. These biogeographic hypotheses focus on the ecological aspects of body mass variation, largely ignoring the role of phylogeny for explaining body mass variation within lineages. We tested the independent effects of climate and resource-related variables on variation in body mass among Malagasy primates using recently developed comparative methods that account for phylogenetic history and spatial autocorrelation. We extracted data on lemur body mass and climate variables for a total of 43 species from 39 sites. Climatic data were obtained from the WorldClim database, which is based on climate data from weather stations compiled around the world. Using generalized linear models that incorporate parameters to account for phylogenetic and spatial autocorrelation, we found that diet and climate variables were weak predictors of lemur body mass. Moreover, there was a strong phylogenetic effect relative to the effects of space on lemur body mass in all models. Thus, we failed to find support for any of the four hypotheses on patterns of geography and body mass in extant strepsirrhines. Our results indicate that body mass has been conserved since early in the evolutionary history of each genus, while species diversified into different environmental niches. Our findings are in contrast to some previous studies that have suggested resource and climate related effects on body mass, though these studies have examined this question at different taxonomic and/or geographic scales. Am J Phys Anthropol 147:401–408, 2012.

Among the most frequently cited macroecological patterns is the positive correlation between body mass and latitude (Bergmann, 1847; James, 1970; Boyce, 1979; Blackburn et al., 1999), although the mechanism driving this trend has received less attention (Ho et al., 2010; Watt et al., 2010). Most commonly, these patterns have been demonstrated at the within-species or within genus level (Blackburn et al., 1999; Ashton et al., 2000; Meiri et al., 2004). More recently, researchers have also examined the macroecology of body mass variation at a broad interspecific level, which included species across numerous lineages (Blackburn and Hawkins, 2004; Rodriguez et al., 2008; Harcourt and Schreier, 2009). Blackburn et al. (1999) provide an extensive review of the rationale and evidence for Bergmann's rule at multiple taxonomic levels.

Four main hypotheses have been invoked to explain patterns of geography and body mass:

1. Thermoregulation: among different species of endothermic animals, body mass tends to increase with decreasing environmental temperature because larger-bodied organisms have a lower surface-area to volume ratio than smaller organisms, and therefore lose less heat energy to the environment. Large-bodied organisms thus have an advantage in cold environments because they expend relatively less energy to maintain homeothermy than small-bodied endothermic organisms. This hypothesis is widely known as Bergmann's rule (*sensu* Bergmann, 1847; James, 1970; Watt et al., 2010).

2a. Resource seasonality (*sensu* Boyce, 1979; Lindstedt and Boyce, 1985): where the environment is more seasonal, natural selection favors larger individuals because they are better able to store energy, and thus have greater fasting endurance. Larger individuals can live longer on stored reserves during the lean season than smaller individuals, and have greater survival rates. Larger individuals therefore have greater fitness than smaller individuals because they are released from density-dependence

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when small individual mortality is high over the period of resource scarcity. These selection patterns are also known as the fasting endurance hypothesis (Boyce, 1979; Lindstedt and Boyce, 1985).

2b. Resource seasonality (*sensu* Terborgh and van Schaik, 1987): seasonality constrains available energy in an ecosystem, and thus the body mass of the animals in the system. Thus, in more seasonal habitats where resources are limited, smaller body mass is predicted. Recent research has supported a negative correlation between body mass and resource seasonality in Malagasy strepsirrhines (Ravosa et al., 1993; Lehman et al., 2005; Lehman, 2007; Muldoon and Simons, 2007).

3. Resource quality: because larger species have larger digestive tracts and relatively slower metabolisms than smaller species, they can be sustained on a lower quality diet (Chivers and Hladik, 1984). This relationship between body mass and diet has been demonstrated both across and within species (Kay, 1984; Kamilar and Pokempner, 2008), with regard to fruit, leaf, and insect consumption. Resource quality is often related to local climate and/or habitat conditions (Ganzhorn, 1992; Huston and Wolverton, 2009; Ho et al., 2010), and therefore, may be a driver of body mass variation (Ravosa et al., 1993; reviewed in McNab, 2010). In addition, if dietary niches are conserved within an evolutionary lineage, then the optimal body mass related to diet may also be the product of the history of lineages.

4. Primary productivity: where productivity is low there is limited energy, leading to selection for smaller body mass. The relationship is not necessarily linearly positive and may be curvilinear because body mass may increase to a point with increasing primary productivity, and then level off when energy reaches and passes some optimum (Rosenzweig, 1968a,b).

These biogeographic hypotheses focus on the ecological aspects of body mass variation, largely ignoring the role of phylogeny (Revell et al., 2008). A growing body of research indicates that taxa in some lineages exhibit phenotypic conservatism despite exploitation of novel habitats. For example, across all mammals, body mass is strongly conserved at the ordinal level, and overall there is little variation in body mass among sister species within genera (Smith et al., 2004). Within Primates, Harcourt and Schreier (2009) demonstrated a significant effect of latitude on body mass, yet, this effect is mostly driven by cercopithecines. They found no effect in strepsirrhines, platyrhines, or hylobatids. Furthermore, the lemurs of Madagascar were not included in their analyses because they occupy a relatively small latitudinal range. It is also important to note that latitude was used as a proxy for temperature, but latitude is also related to the resource hypotheses, and thus the effects of seasonality, resource quality, and quantity cannot be teased apart.

Within mammals, the primates of Madagascar offer a unique opportunity to test the effects of climate, geography, and evolutionary history on body mass variation. First, lemurs are speciose: genera tend to be widely distributed across the island, while species tend to be geographically restricted and adapted to unique niches (Mittermeier et al., 2006). Further, a single radiation of lemurs have evolved in isolation since their initial colonization of Madagascar 50–60 million years ago (Yoder et al., 1996; Yoder and Yang, 2004). Likewise, the major ecoregions (Burgess et al., 2004) of the island evolved gradually and are relatively ancient (Wells, 2003). Finally, while lemurs occupy a relatively moderate latitudinal range (-12 to -25°S), they occupy a wide range of climatic niches (temperature range of 7–35°C, rainfall range of 420 to ~6,000 mm/year, Kremen, 2003; Hijmans et al., 2005; Kamilar, 2009; Kamilar and Muldoon, 2010). Thus, the unique and diverse lemur species are an excellent study system for examining the mechanisms behind body mass variation.

Body mass variation in some lemur species has been explained by the resource seasonality hypothesis (*sensu* Terborgh and Van Schaik, 1987; Ravosa et al., 1993; Lehman et al., 2005; Lehman, 2007; Muldoon and Simons, 2007). Predictions that smaller body size evolves in more seasonal habitats, *contra* Boyce (1979), is partly based on the idea that in seasonal habitats, there is a long time period of low resource availability, particularly of high-protein immature leaves. However, the ratio of protein to fiber in leaves eaten by lemurs is highest in sites with long dry seasons and is negatively correlated with mean annual rainfall (Ganzhorn, 1992). In other words, although resources are more seasonal in the western dry forests, they are higher quality when they are available. In the same vein, the effect of resource quality alone might drive the increased body mass in non-seasonal environments because resource quality (protein-to-fiber ratio) declines with increasing rainfall (Ganzhorn, 1992). This pattern has been suggested to drive the larger body mass in eastern rainforest sifakas (*Propithecus* sp.) compared to small-bodied western species (Lehman, 2007).

The use of proxies for climate and seasonality (e.g., latitude), rather than climate variables themselves, can obfuscate our understanding of the mechanisms driving geographic variation in body mass. Although latitude is correlated with many environmental variables such as temperature, rainfall, and seasonality, these variables are also influenced by multifaceted aspects of geography, such as topography, wind currents, and proximity to bodies of water. Latitude alone may not be a good predictor of body mass in many cases. For example, pair-wise comparisons of sister taxa suggest that lemur body mass is correlated with the ecoregions of Madagascar, such that in ecoregions with lower rainfall and long dry seasons, populations within species, and species within genera, are smaller than in ecoregions with higher rainfall and short dry seasons (Albrecht et al., 1990; Muldoon and Simons, 2007). It is difficult to tease apart the potential effects of climate and resources because these variables are imbedded within the definitions of ecoregions. There is a relationship between rainfall-related measures of resource seasonality and body mass within one family of lemurs, the Indriidae (Lehman et al., 2005; Lehman, 2007). These studies found higher body mass in rainforests and lower mass in dry forests, with an additional phylogenetic effect. Studies that have tested the effects of resource seasonality and quality have not included temperature variables (Ravosa et al., 1993; Lehman et al., 2005; Lehman, 2007; Muldoon and Simons, 2007), making it difficult to test the relative effects of thermoregulation and resource availability. In addition to the aforementioned relationships between climate variables and resource quality and seasonality, overall plant productivity should increase as rainfall levels increase (Kay et al., 1997). Therefore, we expect to find a rainfall effect if primary productivity influences body mass variation.

In this study, we test the independent effects of climate and resource-related variables on variation in body mass among Malagasy primates using recently developed comparative methods that account for phylogenic and spatial autocorrelation. Unlike previous studies, we use a range of GIS-based climate data gathered from the same sites where lemur body mass data have been collected.

MATERIALS AND METHODS

Study sites and data collection

We extracted data on lemur body mass and climate variables for a total of 43 species from 39 sites around Madagascar. We selected studies that report field measures of body mass at each site and used adult body mass only. Typically, reported body masses were an average for males and females combined, and the sample sizes in the studies selected ranged from one individual to 46. Where studies reported masses for males and females separately, we took the average of the two values because several studies have noted that there is little or no sexual dimorphism in lemurs (Albrecht et al., 1990; Smith and Jungers, 1997). Where there were multiple reports of body mass from several populations of a species, we took the median value. In addition, some cheirogaleid species exhibited measurable changes in body mass during different seasons. In these cases, we used the weighted mean mass based on the number of individuals with recorded mass data. We examined the sensitivity of this approach by conducting additional analyses using the seasonal minimum or maximum mass values for these species. We included only studies that report clear locality data, and extracted geographic coordinates using geographic information system (GIS) software. The raw data are available in electronic Supporting Information Table 1.

We included data on the dietary niches of the species in our analysis from Muldoon and Goodman (2010), who classified taxa as folivores, frugivores, or omnivores. They defined these categories as ". . . the food that is eaten most often throughout the majority of the year determined a species' dietary category. . . . A species is defined as an omnivore if relatively equal proportions of animal and plant matter are included in its diet" (Muldoon and Goodman, 2010). We dummy coded diet into two dichotomous variables to represent the three categories.

We extracted climatic data from the WorldClim database, which interpolates a geographic grid of climate data (raster layer) from weather station data compiled around the world (Hijmans et al., 2005). We extracted the climate data for our sample sites in Madagascar using the "Extract-by-point" operation in ArcGIS 9 (ESRI). The WorldClim database includes numerous temperature and precipitation variables measuring different aspects of climatic variation. After culling highly correlated variables, we chose eight variables from this dataset that quantified mean climate and climate seasonality: (1) annual mean temperature, (2) temperature seasonality (standard deviation of monthly mean temperature $\times$ 100), (3) minimum temperature of coldest month, (4) temperature annual range (maximum temperature of warmest month – minimum temperature of coldest month), (5) annual precipitation, (6) precipitation of warmest quarter, (7) precipitation of wettest month, and (8) precipitation of driest month. These variables allowed us to effectively test the hypotheses explaining body mass variation. Similar to body mass, we used median values for species with data from more than one population.

Data analyses

We used a generalized linear model that incorporates parameters to account for phylogenetic and spatial autocorrelation designed by Freckleton and Jetz (2009), implemented in the R statistical environment (R Development Core Team, 2009). Phylogenetic comparative methods have been widely used in biology for more than two decades (Felsenstein, 1985). In contrast, accounting for spatial autocorrelation in biological data has been recognized (Sokal and Oden, 1978) for many years, but only recently has gained increased popularity due to advances in quantitative techniques and computer technology (Diniz-Filho et al., 2003; Kamilar 2009; Rangel et al., 2010; Kamilar and Bradley, 2011). The Freckleton and Jetz (2009) method incorporates a parameter to account for phylogenetic autocorrelation in the regression model, λ', based on Pagel's lambda (Pagel, 1997, 1999). The λ' statistic ranges from 0 (no effect of phylogeny) to 1 (trait evolution perfectly follows a Brownian model). The regression model of Freckleton and Jetz (2009) also estimates the value of a parameter for the relative effect of spatial autocorrelation, Φ, the tendency of things that are closer together in geographic space to be more similar than things farther apart. As in the phylogenetic parameter, Φ ranges from 0 (no spatial effect) to 1 (all trait variance explained by geographic distance). Both parameters are simultaneously estimated using a maximum likelihood approach (details in Freckleton and Jetz, 2009). A final metric is calculated as the model variance independent of both phylogeny and space (γ). These three parameters sum to one, and each range in practice from 0.01 to 0.99.

We are also interested in the degree of phylogenetic signal in body mass itself. We used the R package, Geiger, to calculate Pagel's lambda (Pagel, 1999). Pagel's lambda ranges from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). We used a log likelihood ratio test to examine if lambda was significantly greater than zero. It is important to note that this is a different measure of phylogenetic signal than the one in the regression model. Phylogenetic comparative methods account for phylogenetic effects within the context of a regression model (i.e., modifying the error structure of the model), yet this is not necessarily related to the degree of phylogenetic signal in the variables themselves. This was elegantly demonstrated in a recent paper by Revell (2010).

Our taxonomic scheme follows Mittermeier et al. (2006). To test the possible effects of phylogenetic uncertainty, we ran three versions of our model, each with a different phylogeny of Malagasy primates, one from Arnold et al. (2010) based on the "10 k trees" project (http://10ktrees.fas.harvard.edu/), one from Chatterjee et al. (2009), and one from Bininda-Emonds et al. (2007). Each phylogeny contained a different set of species; therefore our models vary in sample size: 28 species for Bininda-Emonds et al. (2007), 37 species for Chatterjee et al. (2009), and 43 species for Arnold et al. (2010). We used Mesquite (Madison and Madison, 2007) to plot body mass on each phylogeny, which allowed us to better visualize body mass variation in a phylogenetic context.

We included six predictor variables in our models, including the two dietary variables and four climate variables. We reduced our eight climate variables to four by performing two principal component analyses (PCA),

TABLE 1. Results of principal components analysis for temperature variables, including axis loadings and the importance of each axis

Variable	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 4
Annual mean temperature	−0.868	−0.471	0.140	0.071
Temperature seasonality	0.896	−0.167	0.411	−0.001
Min temperature of coldest month	−0.975	−0.087	0.188	−0.076
Temperature annual range	0.377	−0.911	−0.166	−0.029
Eigenvalue	2.650	1.087	0.251	0.012
Proportion of total variance	0.663	0.272	0.063	0.003

TABLE 2. Results of principal components analysis for rainfall variables, including axis loadings and the importance of each axis

Variable	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 4
Annual precipitation	−0.942	0.241	0.193	0.132
Precipitation of wettest month	−0.617	0.778	−0.002	−0.121
Precipitation of driest month	−0.689	−0.692	0.194	−0.097
Precipitation of warmest quarter	−0.901	−0.255	−0.349	0.020
Eigenvalue	2.554	1.207	0.197	0.042
Proportion of total variance	0.639	0.302	0.049	0.010

one for the rainfall variables and one for the temperature variables. We used the first two components of each PCA in our regression models. This allowed us to use fewer predictor variables in our models, which was desirable because of our relatively small sample size (Quinn and Keough, 2002). In addition, conducting two PCA enabled us to better evaluate the separate effects of rainfall and temperature for influencing body mass variation. All climate variables were natural log transformed before being entered into the PCA.

RESULTS

The first two axes of the temperature and rainfall PCAs explained 93.5% and 94.1%, respectively, of the variation in the original variables (Tables 1 and 2). Three variables loaded heavily on the first PCA axis for temperature: annual mean temperature (−), temperature seasonality (+), and minimum temperature of the coldest month (−). Temperature annual range displayed a strong negative loading on PCA axis two (Table 1). For the rainfall variables, mean annual precipitation (−) and precipitation of the warmest quarter (−) loaded strongly on PCA axis 1. The precipitation of the wettest (+) and driest months (−) were the variables most strongly correlated with PCA axis 2.

Our predictive models of Malagasy primate body mass produced consistent results using different phylogenies (Table 3). In all models, diet and climate variables were weak predictors of body mass. The best predictor of body mass was folivory, yet p values were at the 0.201 level using the Arnold et al. (2010) phylogeny and 0.153 for the Chatterjee et al. (2009) phylogeny. The first rainfall PCA axis was the best predictor of mass using the Bininda-Emonds et al. (2007) phylogeny, with $P = 0.392$. In addition, the full model results for each regression produced r^2 values less than 0.10. Using seasonal minimum and maximum mass values for cheirogaleid species produced qualitatively similar results.

TABLE 3. Predictors of body mass in lemuriformes, while accounting for phylogeny and space

Predictor	Estimate	SE	*t*	*P*
Phylogeny based on Arnold et al. (2010)				
frugivore	0.703	0.574	1.224	0.229
folivore	0.799	0.613	1.304	0.201
temp_pca1	0.022	0.101	0.220	0.827
temp_pca2	−0.043	0.127	−0.337	0.738
rain_pca1	−0.086	0.124	−0.690	0.495
rain_pca2	−0.018	0.101	−0.180	0.858
Full model: $r^2 = 0.087$, $P = 0.761$, $n = 43$				
Phylogeny based on Chatterjee et al. (2009)				
frugivore	0.934	0.681	1.372	0.181
folivore	0.996	0.679	1.466	0.153
temp_pca1	0.009	0.119	0.075	0.941
temp_pca2	−0.005	0.130	−0.040	0.968
rain_pca1	−0.011	0.128	−0.090	0.929
rain_pca2	−0.043	0.125	−0.341	0.735
Full model: $r^2 = 0.094$, $P = 0.800$, $n = 37$				
Phylogeny based on Bininda-Emonds et al. (2007)				
frugivore	0.397	0.699	0.568	0.576
folivore	0.573	0.730	0.785	0.442
temp_pca1	−0.031	0.164	−0.189	0.852
temp_pca2	−0.165	0.269	−0.615	0.546
rain_pca1	−0.220	0.252	−0.874	0.392
rain_pca2	−0.084	0.257	−0.325	0.749
Full model: $r^2 = 0.068$, $P = 0.956$, $n = 37$				

Model parameters for each analysis: Phylogenetic (λ') = 0.980, Spatial (Φ) = 0.010, Independent (γ) = 0.010.
temp_pca1 = Annual Mean Temperature (−), Temperature Seasonality (+), Min Temperature of Coldest Month (−).
temp_pca2 = Temperature Annual Range (−).
rain_pca1 = Annual Precipitation (−), Precipitation of Warmest Quarter (−).
rain_pca2 = Precipitation of Wettest Month (+), Precipitation of Driest Month (−).

The other consistent result in our models was the relative importance of phylogeny and space. In all three regressions, the λ' value was 0.98, indicating that there is a strong phylogenetic effect in each model (Table 3). Conversely, the Φ values were 0.01 in all models, indicating that space has little role in the relationship between the predictor variables and body mass. The metric quantifying the variance independent of both phylogeny and space was very low, at 0.01. Similarly, we found the highest possible degree of phylogenetic signal in body mass for each of the three phylogenies we employed in our analyses (Table 4 and Fig. 1A–C).

DISCUSSION

We failed to find support for any of four hypotheses (thermoregulation, resource seasonality, resource quality, and primary productivity) to explain interspecific variation in body mass across extant Malagasy strepsirrhines. We found that across Malagasy primates, there is a strong effect of phylogeny on variation in body mass, whereas the effect of space, diet, and climate were small and did not significantly explain mass variation. These results were consistent across the three phylogenies we examined. Within families and especially genera, body

TABLE 4. Results of phylogenetic signal analyses for Malagasy primate body mass using three different phylogenies

Phylogeny	N	λ_{max}	Log likelihood$_{\lambda_{max}}$	Log likelihood$_{\lambda_0}$	Log likelihood$_{\lambda_1}$	Log likelihood ratio$_{p\ value}$
Arnold et al. (2010)	43	1.00	−30.02	−80.53	−30.02	<0.001
Chatterjee et al. (2009)	37	1.00	−28.03	−63.97	−28.03	<0.001
Bininda-Emonds et al. (2007)	28	1.00	−28.50	−46.38	−28.50	<0.001

Body mass exhibits the highest possible phylogenetic signal for all phylogenies.

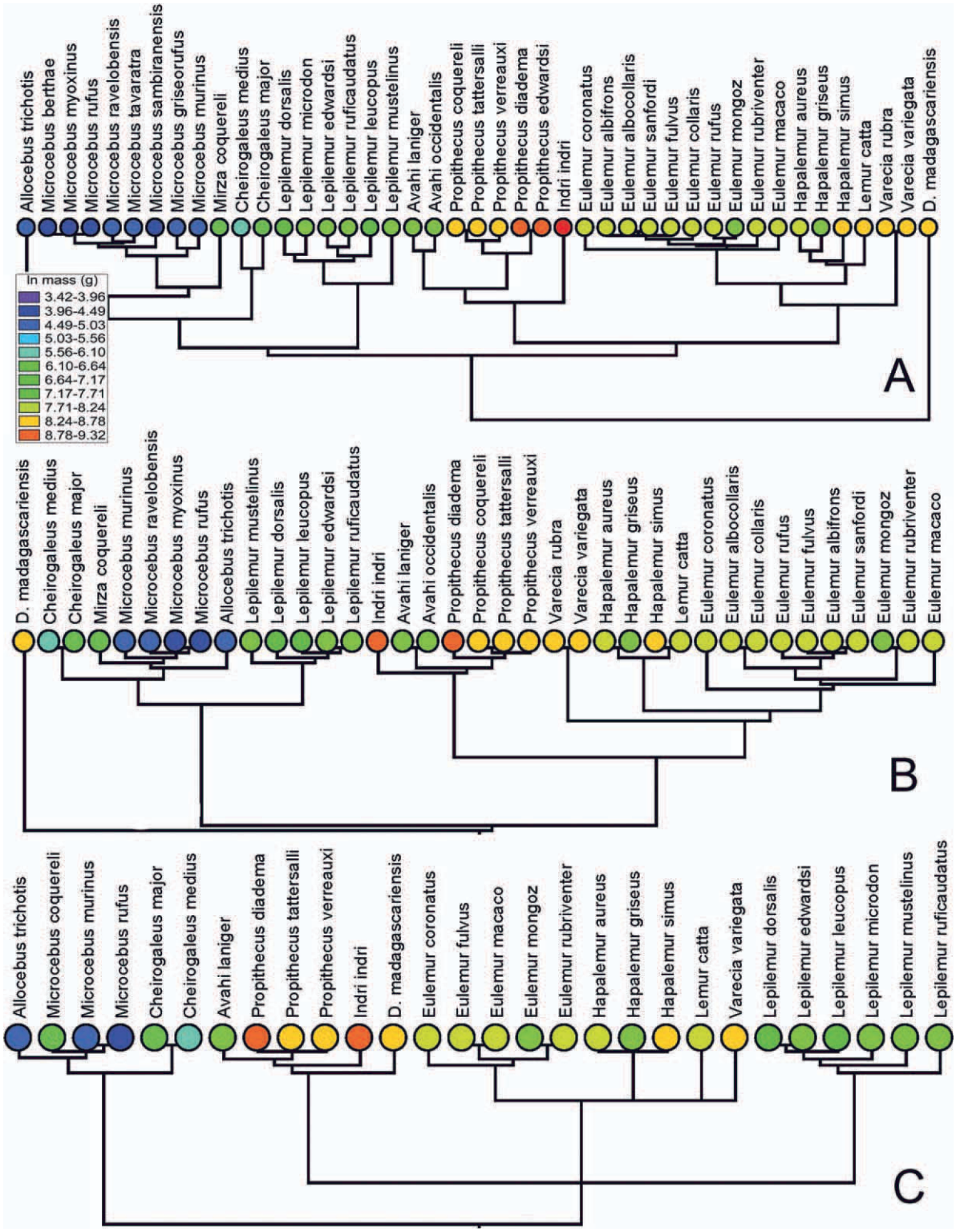

Fig. 1. Body mass in an evolutionary context using the phylogeny presented in: (**A**) Arnold et al. (2010), (**B**) Chatterjee et al. (2009), (**C**) Bininda-Emonds et al. (2007). Phylogenetic signal for body mass is Pagel's lambda = 1.0, $P < 0.001$ for all phylogenies.

mass does not vary greatly (Fig. 1A–C). Species range from medium to large body mass in only one family, Indriidae, while small body mass is characteristic of the cheirogaleids. In the other families (Lepilemuridae, Daubentonidae, and Lemuridae), body mass has been conserved at intermediate values. Body masses are also more consistent at the intrageneric level. Our findings are especially striking considering the large diversity of climatic and habitat niches occupied by species within most genera (Kamilar and Muldoon, 2010). Thus, our results fail to find support for the underlying patterns commonly thought to govern Bergmann's Rule.

Our findings are in contrast to a recent study of Bergmann's rule in primates by Harcourt and Schreier (2009). They found a primate-wide effect of latitude on body mass variation, though this finding was driven primarily by Old World monkeys. Although they did not examine climate or habitat characteristics specifically, Harcourt and Schreier (2009) logically argue that the wide range of habitats occupied by these species (e.g., tropical to temperature habitats) is the main mechanism for body size variation. Conversely, the lack of a Bergmann's effect for platyrrhines and non-Malagasy strepsirrhines may be due to the more uniform environmental conditions that they occupy. A recent study of New World mammals provided similarly interesting results. Rodriguez et al. (2008) showed that Nearctic mammals follow the expected relationship of increasing body mass at latitudes, being driven primarily by mean annual temperature. This is in accord with a thermoregulatory mechanism for increasing body size over evolutionary time. In contrast, they found that temperature and body size were positively correlated for Neotropical mammals, yet there was a strong interaction effect with topography. In particular, there were fewer large species in high elevation locales. Rodriguez et al. (2008) argued that this was due to reduced habitat sizes in mountainous regions.

Although Malagasy primates are distributed across a relatively narrow latitudinal range, they do experience a large amount of climate and habitat variation (Jury, 2003; Kamilar and Muldoon, 2010). The fact that we do not detect an effect of climate on body mass across lemur species, suggests that body mass has been conserved since early in the evolutionary history of each genus, while species diversified into different environmental niches. This result follows closely with a recent study that found among mammals, sister species within genera do not differ in body mass, despite separation in geography and climate (Smith et al., 2004). Of course, other selective forces may affect the evolution of body size, and result in deviations from Bergmann's rule (e.g., Dayan et al., 1991; Meiri and Dayan, 2003; Meiri and Thomas, 2007). For example, many Malagasy primates exhibit behavioral or physiological traits to mediate variable environmental conditions. Some cheirogaleids enter prolonged periods of torpor and hibernation during the cold, dry season when resource availability is low, and only emerge in the austral "spring" when resources like flowers, fruits and insects become abundant (Schülke and Ostner, 2007; Schmid and Ganzhorn, 2009; Blanco and Rahalinarivo, 2010; Kobbe and Dausmann, 2010). Larger species in the genera *Lemur*, *Varecia*, *Indri*, and *Propithecus* deal with low temperatures by sunbathing and/or huddling in groups (Jolly, 1966; Richard, 1978; Morland, 1993; Powzyk, 1997). Other proposed adaptations to the harsh Malagasy environment include low basal metabolic rate, small group sizes, highly fibrous diets and strict synchrony in the timing of weaning across species, despite other life history traits being differing drastically (Wright, 1999).

Previous researchers have hypothesized that vicariant speciation may result in body mass conservatism because when lineages are split by some barrier to gene flow, divergent selection on body mass is not necessarily inferred as a result, and often the separated species continue to maintain the same ecological niches (Smith et al., 2004). Recently, some scientists have suggested that vicariance due to habitat isolation during periods of Quaternary climate shifts have resulted in speciation in lemurs (Goodman and Ganzhorn, 2004; Wilmé et al., 2006; Vences et al., 2009). If so, this model of speciation may fit with our finding of body mass being evolutionarily conserved in Malagasy primates. Though, it is important to note that many closely related Malagasy primate species currently occupy distinct climatic niches (Kamilar and Muldoon, 2010).

Our results have important implications for the conservation biogeography of lemurs. Rapid climate change is a potentially powerful selective force operating on lemurs and their forest habitats, as it does on many plant and mammal communities (Malcolm et al., 2006). Although our study did not specifically seek to determine how recent climatological variations, such as global warming, influence species persistence, it does indicate that the evolution of lemur body mass is a conserved character largely irresponsive to spatial variations in temperature and rainfall. The question arises whether short-term changes in climate will affect lemur biology, in general, and lemur body mass, in particular. We hypothesize that lemur responses to climate change may not involve changes in basic biology (i.e., changes in body mass) outside the existing range of seasonal variation already seen in many species; rather, they may involve behavioral and life history variations. Behavioral plasticity has been invoked either directly or indirectly as a major factor enabling extant lemurs to survive annual cyclones and, more recently, the massive anthropogenic conversion of forest landscapes (Dehgan, 2003; Wright, 2006). For example, Lahann and Dausmann's (2011) study of *C. medius* in littoral rainforest and dry deciduous forest documented spatial variations in life history variables, such as differing litter sizes and the number of litters. Therefore, studies of life history variables and fluctuations in lemurs may serve as a critical indicator of selection pressures due to climate change.

Additional studies have examined the ecological effects on body mass at fine taxonomic and/or geographic levels. At the within-species level, the body mass of *Propithecus diadema* populations varied between contiguous rainforest compared to fragmented rainforest (Irwin, 2008). Across closely related species, Albrecht et al. (1990) found that within genera, conspecifics are smaller in arid versus wet environments, despite samples not differing statistically. Similarly, Muldoon and Simons (2007) found that body size in congeneric lemur species differs significantly among arid and dry forest taxa.

Although our models indicate a strong effect of phylogeny on variation in lemur body mass, these results are not indicative of broad macroevolutionary processes, such as phylogenetic inertia (PI). PI is thought to occur when trait evolution operates slower than the rate of natural selection in environments undergoing rapid changes in abiotic or biotic characteristics (Blomberg and Garland, 2002), such as climate change. Consequently, species undergoing PI exhibit extended time periods to reach an optimum

range for a trait in a stochastic environment (Diniz-Filho et al., 1998). Theoretical biologists have noted issues with the lax application of PI to questions of phylogenetic niche and character change, with special attention being placed on defining and testing for specific mechanisms that constrain trait evolution (Cooper et al., 2010). However, rigorous statistical requirements for PI models, including well-estimated topologies and branch lengths, are still not available for all clades of extant strepsirrhines. As these data become available, then it will be possible for researchers to examine specific macroevolutionary models, such as PI, of body mass variation in lemurs.

In conclusion, the evolutionary history of Malagasy primates appears to have a strong relationship to interspecific body mass variation despite species occupying different climates. A variety of non-mass traits may be sufficient adaptations to the environmental niches species occupy, and part of a long evolutionary history in the relatively ancient ecoregions of Madagascar. Our findings are in contrast to some previous studies that have suggested resource and climate related effects on body mass, though these studies have examined this question at finer taxonomic and/or geographic scales.

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