

Environmental Correlates of Body Mass in True Lemurs (*Eulemur* spp.)

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Abstract An organism's body size is intrinsically related to its metabolic requirements, life history profile, and ecological niche. Previous work in primates generally, and lemurs specifically, has shown that body size often correlates with ecological parameters related to temperature and energy availability in the environment, although other studies indicate the absence of any such patterns in lemurs. Here we test hypotheses that predict that body mass in *Eulemur* should covary with 1) overall food availability or resource seasonality and/or 2) temperature, i.e., Bergmann's rule. We use data from 722 wild true lemurs to identify population-specific body mass for 27 populations representing 11 of the 12 described *Eulemur* species, and derive climatic data for each population from the WorldClim database. We use phylogenetic generalized least squares models to evaluate these hypotheses and find that body mass significantly negatively correlates with annual mean temperature and positively correlates with standard deviation of temperature, but does not significantly correlate with annual rainfall or number of dry months. These results indicate that body mass distribution across populations in *Eulemur* is consistent with Bergmann's rule, but does not track resource seasonality as seen in other lemurs, e.g., *Propithecus*. We suggest that the fact that body mass in various lemur radiations correlates with different environmental variables may result in these patterns being obscured when such taxa are combined in a single analysis. This may help explain why some previous work has found little evidence of ecogeographical correlates with body mass across all Lemuriformes.

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Introduction

A variety of theoretical models predict that some combination of ecological variables may constrain adult body size in mammals. Two broad classes of hypotheses relate body mass to environmental variables. The first group is a collection of resource constraint hypotheses, in which adult body size is limited by resource quality, year round availability, or seasonal availability. The best supported of these hypotheses within primates appears to be a resource seasonality model, in which extended periods of resource scarcity select for smaller body size (Terborgh and van Schaik 1987). This may be mediated through selection for slow growth rates in seasonal environments to minimize the absolute metabolic needs during periods of resource scarcity (Altmann and Alberts 1987, 2005; Leigh and Shea 1996; Leigh and Terranova 1998; Ravosa *et al.* 1993). Alternatively, it has been suggested that the opposite pattern might occur, in which large body size is selected for in highly seasonal environments because larger individuals have greater reserves to survive periods with inadequate resources (Lindstedt and Boyce 1985).

The second general hypothesis is commonly referred to by the name of an empirical observation known as Bergmann's rule or the Bergmann effect (Bergmann 1847; Mayr 1956). As originally formulated, this is the observation that within a genus, species living in colder habitats tend to be larger than those in warmer environments, although temperature is often replaced with latitude as a proxy. Bergmann's proposed mechanism for this relationship is that if body shape stays constant as body size increases, then the ratio of surface area to volume will decrease, resulting in lower heat loss relative to mass (Bergmann 1847). This mechanism is typically referred to as the "heat conservation hypothesis" to distinguish it from other potential mechanisms driving Bergmann's rule (Blackburn *et al.* 1999), particularly because there have been challenges to this explanation (McNab 2010; Scholander 1955).

Empirical tests of these hypotheses in lemurs have investigated whether body size is dependent on habitat primary productivity, resource seasonality, resource quality, and/or thermoregulation (Albrecht *et al.* 1990; Gordon *et al.* 2013; Harcourt and Schreier 2009; Kamilar *et al.* 2012; Lehman 2007; Lehman *et al.* 2005; Muldoon and Simons 2007). This research provides a mixed picture as to whether ecological variables might be constraining body mass. Craniodental metrics in both extant and subfossil lemur species typically follow a pattern in which species found in the warmer, drier, and longer dry season ecoregions of Madagascar are smaller than metrics from congeners in regions that are cooler, wetter, and have shorter dry seasons (Albrecht *et al.* 1990; Godfrey *et al.* 1990; Muldoon and Simons 2007), consistent with multiple hypotheses relating body size to environmental constraints. In contrast, a recent study which used phylogenetic comparative methods to test several ecological constraint hypotheses across Lemuriformes found no evidence of any relationship between body mass and environmental variables (Kamilar *et al.* 2012). However, one possible confounding factor in that study is that it included species that varied substantially in size but that came from the same site; in this case, ecogeographic patterns might be obscured by high-magnitude generic- and family-level body size differences associated with identical values for environmental variables (Gordon *et al.* 2013).

One way to address that concern is to limit the taxonomic breadth of such analyses. For example, multiple studies on day-active indriids have found that species mean body size strongly correlates with proxies for primary productivity and resource seasonality (Lehman 2007; Lehman *et al.* 2005; Ravosa *et al.* 1993). These results have recently been borne out by an interspecific study in *Propithecus* that confirms the relationship between body mass and precipitation-based variables using novel population-level data and phylogenetic comparative methods (Gordon *et al.* 2013).

Published studies of comparisons at even lower taxonomic levels also exist, although sample sizes are typically too small for significance tests. For example, three populations of *Microcebus murinus* showed a negative relationship between body mass and temperature, although not between body mass and seasonality (Lahann *et al.* 2006). Johnson *et al.* (2005) compared one eastern and one western population of true lemur that were both considered at that time to belong to *Eulemur fulvus rufus*, although now would be placed in *E. rufifrons* and *E. rufus*, respectively. They found that the eastern rain forest population was larger bodied than the western population from a warmer, drier, and more seasonal environment, consistent with both the heat conservation and resource constraint hypotheses.

In the present study we examine the relationship between body mass and environmental variables across multiple populations of *Eulemur* species to investigate hypotheses relating body size to various environmental constraints. True lemur species (*Eulemur* spp.) are broadly similar to each other in morphology, behavior, and ecological niche (Overdorff and Johnson 2004), although they range over a variety of forest habitats with different climate characteristics in Madagascar (Kamilar and Muldoon 2010; Mittermeier *et al.* 2008) and exhibit approximately a twofold difference in mean body mass among the various species of *Eulemur* (Gordon 2006; Smith and Jungers 1997). Previous work specifically on ecogeographic variation in true lemur body size is limited, although several studies have noted that eastern rain forest true lemurs are larger than their counterparts in drier, warmer western habitats (Albrecht *et al.* 1990; Gerson 1999, 2000; Godfrey *et al.* 1990; Johnson *et al.* 2005).

We evaluate the resource constraint and heat conservation hypotheses in true lemurs by testing the following nonexclusive predictions. First, if body mass is constrained by primary productivity, then linear models should show a significant positive relationship between body mass and annual precipitation, which is typically used in the primate literature as a proxy for primary productivity. Second, if body mass is constrained by the duration of the seasonal periods of low resource availability, then there should be a significant negative relationship between body size and the number of dry months per year. Finally, if body mass is responding to temperature-induced selection on surface area to volume ratios, then body mass should have a negative relationship with annual mean temperature, i.e., Bergmann's rule.

Methods

Population Identification and Calculation of Population-Specific Variables

Field crews from the Madagascar Biodiversity Partnership (MBP) and Omaha's Henry Doorly Zoo and Aquarium's (OHDZA) Conservation Genetics Department collected

body mass and GPS coordinate data for 722 individual true lemurs from across Madagascar. These individuals represent all 12 currently recognized species of the genus *Eulemur* (IUCN 2014; Mittermeier *et al.* 2008). Data were collected from February 13, 1999 to April 17, 2014 in conjunction with conservation genetics and systematics research (Brenneman *et al.* 2012; Delmore *et al.* 2013; Johnson *et al.* 2008; Tokiniaina *et al.* 2009). We then assigned individuals to populations or excluded them as isolated individuals using the procedure described in the text that follows.

Geographic Cluster Analysis We identified populations within each species via a cluster analysis using a geographic distance matrix of capture locations for individual specimens following the procedure described in Gordon *et al.* (2013). Clusters were identified according to the following conditions: 1) the maximum distance between capture locations within a cluster was 20 km and 2) the distance between the geographic centroids of clusters exceeded 12 km. This procedure excludes isolated specimens from arbitrary inclusion in the nearest cluster, while also ensuring that clusters were geographically distinct. We treated the resulting clusters as distinct populations for identifying population-specific mass and climatic data.

Population-Specific Body Mass Degree of maturity was not recorded at the time of capture for several individuals in the sample, so mean values of all captured individuals would be biased downward by juveniles in some cases. Following Gordon *et al.* (2013), we excluded clusters with fewer than four males and four females of known mass to reduce the probability of inclusion of clusters composed exclusively of juveniles, and then we selected the largest female and male to represent the upper end of sex-specific adult mass in each of the remaining populations. We then averaged the male and female values to provide a single value of adult body mass for each population. Some *Eulemur* species exhibit slight body size dimorphism, although most appear to be effectively monomorphic (Delmore *et al.* 2011; Johnson *et al.* 2005; Kappeler 1990, 1991). We compared resulting values against published ranges for adult body mass from wild and free-ranging captive populations (Gordon 2006; Smith and Jungers 1997; Zehr *et al.* 2014) to ensure that they were plausible body mass values for adults. Application of this procedure resulted in the exclusion of all *E. flavifrons*, as no geographic cluster for that species met the minimum sample size requirement. Also, as we have noted previously (Gordon *et al.* 2013), MBP field crews collected data throughout the year and so some individuals would have been weighed during different seasons, but there is no evidence to suggest that there is a systematic bias in sampling times across sampling sites. Thus any seasonal variation in body mass is expected to add noise rather than bias to the relationship between body mass and environmental variables.

Environmental Variables To facilitate comparison with earlier work, we also followed Gordon *et al.* (2013) in using four measures of annual tendency and seasonality in rainfall and temperature derived from the WorldClim database (Hijmans *et al.* 2005): total annual rainfall, number of dry months in the year (≤ 60 mm of rain per month), annual mean temperature, and standard deviation of monthly mean temperatures. We calculated population-specific values for each variable as the mean of all WorldClim values from 30 arc-second resolution grids that fell within a 10 km radius of each

population's geographic centroid. Environmental variables were not transformed before inclusion in linear models; please refer to Gordon *et al.* (2013) for a discussion of using correlated environmental variables vs. principal components and nontransformed vs. log-transformed environmental variables.

Final Data Set The geographic clustering procedure and minimum population size sampling protocol resulted in 27 populations from 11 species of *Eulemur* represented by a total of 553 individuals (Fig. 1). Geographic location, body mass, and environmental variables averaged over a 10 km radius circle centered on each population are provided in Table I. Environmental variables correlate among themselves, with annual variables strongly negatively correlated with their own seasonality ($r^2 = 0.769$ for precipitation variables and 0.754 for temperature variables; Table II, Fig. 2). These correlations must be borne in mind when interpreting the results of linear models, because independent variables that themselves highly correlate with body mass may not have significant regression coefficients when added to models containing other independent variables with which they strongly correlate. However, what is of interest in this study is not the specific regression coefficients themselves, but rather the relative information content of each model (see "Evaluation of Models").

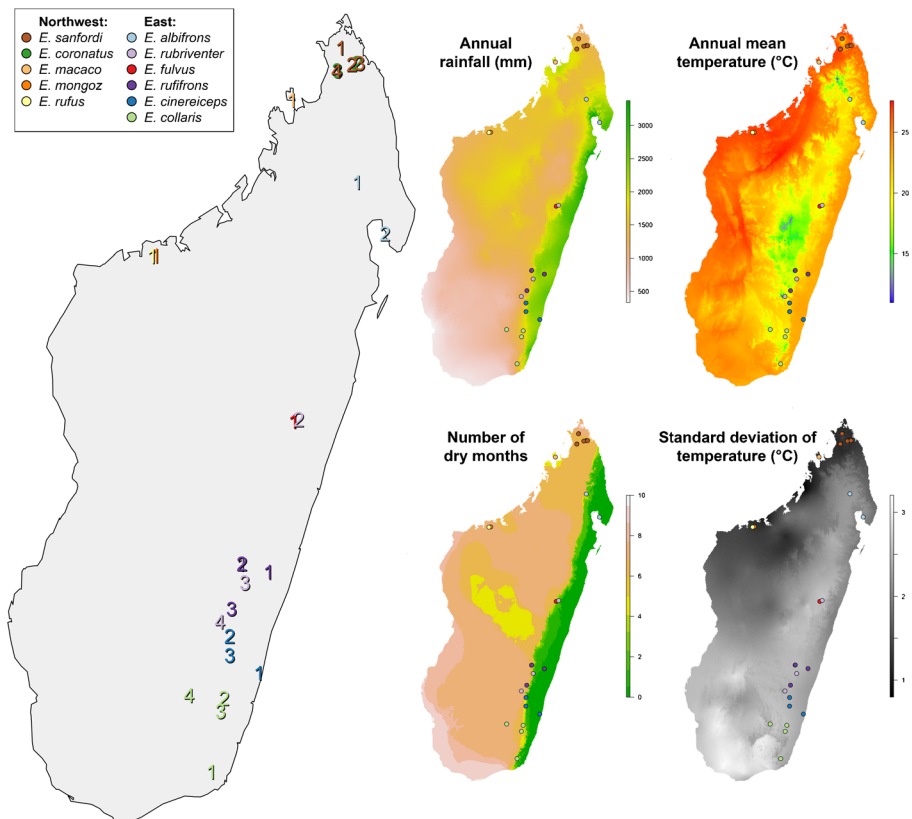


Fig. 1 Locations of populations of *Eulemur* included in this study ($N = 27$) and environmental variables derived from the WorldClim database (30 arc-second resolution). Numbers in left-most map correspond to population numbers in Table I.

Table 1 Population location, body mass, and environmental variables for the 27 populations of *Eulemur* identified in the geographical cluster analysis that meet the minimum sample size criterion of four individuals per sex

	Population	Longitude (°E)	Latitude (°S)	Mean elevation (m)	N_F	N_M	Max female mass (kg)	Max male mass (kg)	Combined mean mass (kg)	Annual rainfall (mm)	Number of dry months	Annual mean temp. (°C)	SD temp. (°C)
<i>E. albigrons</i>	1	49.466	14.793	1084.5	6	5	2.30	2.35	2.33	1734.3	4.22	19.55	2.32
	2	49.961	15.666	396.8	5	4	1.75	1.70	1.73	2551.9	0.00	22.18	2.17
	3	47.714	23.091	27.4	22	12	2.10	2.23	2.17	2369.7	0.00	23.27	2.47
<i>E. cinereiceps</i>	1	47.192	22.468	518.6	6	14	1.90	2.80	2.35	1764.1	3.71	21.37	2.61
	2	47.191	22.794	536.7	5	5	2.30	2.00	2.15	1785.8	3.64	21.15	2.63
	3	46.86	24.758	501.6	4	6	2.10	2.40	2.25	1281.9	3.90	21.14	2.57
<i>E. collaris</i>	1	47.09	23.519	725.6	4	6	2.60	2.50	2.55	1703.9	5.02	19.81	2.70
	2	47.026	23.742	830	4	6	2.40	2.50	2.45	1568.2	5.58	19.46	2.67
	3	46.465	23.466	1254	16	11	2.80	2.60	2.70	1086.4	7.00	18.76	2.61
<i>E. coronatus</i>	1	49.173	12.524	758.3	6	4	1.60	1.10	1.35	1347.8	6.25	21.94	1.39
	2	49.463	12.782	232.2	19	13	1.65	1.55	1.60	1375.7	6.00	24.96	1.32
	3	49.11	12.909	144.2	15	10	1.60	1.60	1.60	1608.4	6.00	25.83	1.25
<i>E. fulvus</i>	1	48.333	18.833	999.4	15	11	2.45	3.00	2.73	1679.7	3.95	19.19	2.73
	2	48.302	13.404	103.5	14	11	2.20	2.35	2.28	2076.9	5.09	26.00	1.34
<i>E. macaco</i>	1	45.864	16.037	23.9	11	9	1.20	1.30	1.25	1403.4	7.00	26.80	1.32
	2	47.401	21.248	1114.6	24	26	2.40	2.50	2.45	1582.2	5.63	18.16	2.68
<i>E. rubriventer</i>	1	48.423	18.802	1017.6	7	8	2.25	2.35	2.30	1760.7	2.60	19.21	2.75
	2	47.462	21.564	808.3	5	4	2.19	2.30	2.25	1821.4	3.78	19.62	2.64
	3	47.02	22.222	1199.9	7	7	2.20	2.34	2.27	1264.6	6.96	18.24	2.59
<i>E. ruffifrons</i>	1	47.886	21.382	166.5	21	13	2.70	2.70	2.70	2273.5	0.04	22.49	2.51
	2	47.41	21.243	1093.5	21	19	2.80	2.60	2.70	1609.3	5.46	18.26	2.68
	3	47.226	22.003	997.5	14	16	2.30	2.45	2.38	1408.0	6.68	19.00	2.62

Table 1 (continued)

Population	Longitude (°E)	Latitude (°S)	Mean elevation (m)	N_F	N_M	Max female mass (kg)	Max male mass (kg)	Combined mean mass (kg)	Annual rainfall (mm)	Number of dry months	Annual mean temp. (°C)	SD temp. (°C)
<i>E. rufus</i>	45.802	16.045	38.6	13	7	1.60	1.60	1.60	1390.4	7.00	26.68	1.34
<i>E. sanfordi</i>	49.172	12.525	764.4	6	4	2.10	2.00	2.05	1348.4	6.24	21.90	1.40
	49.369	12.804	336	9	8	2.10	2.40	2.25	1413.2	6.00	24.33	1.34
	49.51	12.787	223.6	13	6	2.55	1.84	2.19	1364.2	6.00	24.99	1.33
	49.103	12.914	132.1	6	10	1.75	2.15	1.95	1615.9	6.00	25.92	1.25

N_F = number of females with body mass data; N_M = number of males with body mass data; SD temp. = standard deviation of temperature

Table II Correlations among environmental variables for the 27 populations of *Eulemur* across eastern and northwestern Madagascar

	Annual rainfall	Number of dry months	Annual temp.	SD temp.
Annual rainfall	—	-0.820	0.107	0.225
Number of dry months	-0.877	—	0.112	-0.408
Annual temp.	0.069	0.110	—	-0.841
SD temp.	0.216	-0.411	-0.868	—

See Table I for locality information. Pearson correlations (r) are below the diagonal, Spearman correlations above

Data Analysis

To take into account phylogenetic relationships between populations, we ran phylogenetic generalized least squares (PGLS, Martins and Hansen 1997) models using the ‘caper’ package in R (Orme *et al.* 2012; R Development Core Team 2014) to investigate the relationship between body mass and environmental variables. We calculated nine models using different combinations of environmental variables as predictors of population-specific body mass (see “Linear Models”). To evaluate the relative strength of different environmental variables in these models, we compared the models using F -ratio significance tests (for nested models) and sample-size corrected Akaike Information Criterion (AICc) weights (for all models). Models with the lowest AICc values are the best performers in terms of maximizing the likelihood of the data given that particular model while exacting a penalty for the number of predictor variables. These AICc values can be transformed into weights between zero and one for a set of models, with higher values indicating better models according to this information criterion perspective; in addition, the relative importance of each predictor variable to the overall relationship between body mass and environmental variation can be estimated by summing the AICc weights for the models in which they appeared (Burnham and Anderson 2002; Symonds and Moussalli 2011).

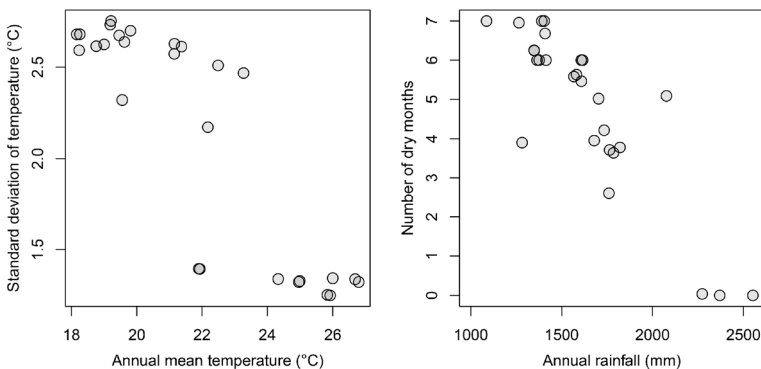


Fig. 2 Bivariate plots of seasonality variables against annual variables for temperature (left) and rainfall (right) for all 27 populations of *Eulemur* included in this study. Pearson and Spearman correlations are highly similar within each pair of variables and are provided in Table II.

Linear Models Following Gordon *et al.* (2013), we considered nine linear models in which \log_{10} body mass was the dependent variable and one or more environmental variables were the independent variables. In addition to a model that included all four environmental variables and models that included only one environmental variable, we built models that included as predictors either two variables of the same type (i.e., precipitation or temperature variables) or of the same temporal component (i.e., annual trend or seasonality variables). This resulted in the following models: 1) full: all four environmental variables as predictors, (2) annual: annual rainfall and annual mean temperature, 3) seasonality: number of dry months and standard deviation of temperature, 4) rainfall: annual rainfall and number of dry months, 5) temperature: annual mean temperature and standard deviation of temperature, and four models with only one environmental variable each – 6) annual rainfall, 7) number of dry months, 8) annual temperature, and 9) standard deviation of temperature.

Taxonomy and Phylogeny We follow Mittermeier *et al.* (2008) for our species-level taxonomy; species-level branching sequence and branch lengths in this study follow Markolf and Kappeler (2013). Because the residuals from linear models are not independent from each other for either species or populations within those species, the error structure of linear models must be adjusted to take into account phylogenetic relationships (Felsenstein 1985). As in Gordon *et al.* (2013), we modified the species-level phylogeny to include polytomies within each species that contributed multiple populations to the analysis because body mass and environmental variables are specific to populations in this study, not species. We determined consensus branch lengths for the phylogenetic distances between populations across all nine models using a maximum-likelihood method [Electronic Supplementary Material (ESM) Figs. S1, S2]. Once the consensus set of branch lengths was identified, we estimated Pagel's λ (Pagel 1997, 1999) for all PGLS models using the maximum likelihood estimation in *caper* (Orme *et al.* 2012). Pagel's λ is a parameter that adjusts the degree to which phylogenetic information is incorporated into the error structure of a linear model, and is generally interpreted as a measure of the strength of phylogenetic signal in the residuals of the model (where $\lambda = 1$ means that phylogenetic information is fully incorporated into the model, and $\lambda = 0$ means that phylogenetic information is ignored and the model is identical to an ordinary least squares model). To directly compare models using nested ANOVA F -ratios, branch lengths and branch scaling parameters such as λ must be identical in all of the models under consideration. We used the mean of λ for the nine models in the recalculation of all models so that they could be directly compared (Gordon *et al.* 2013).

Evaluation of Models The goal of this study is to determine whether particular climatic variables are more strongly associated with body mass of *Eulemur* than others, consistent with the various hypotheses outlined in the Introduction. To address this, we can compare the overall fit of models that include certain climatic variables to models that contain other climatic variables. As mentioned previously, these environmental variables correlate with each other, resulting in some degree of multicollinearity for those models that include more than one independent variable. However, although the inclusion of partially collinear variables will produce biased estimates of regression coefficients within a particular model, it has no effect on the overall information content

of a model. For example, consider two linear models: in the first model, body mass is dependent on four correlated predictors (e.g., the four climatic variables in this study), and in the second model, the same set of body mass data is dependent on the four statistically independent principal components that derive from the four correlated predictors. Although the regression coefficients and P -values for those coefficients will differ between models, all statistics pertaining to overall model fit will be exactly the same between the two models: e.g., AICc, r^2 , sum of squared error statistics, and overall model significance. Thus multicollinearity has no effect on the determination of whether one model fits the observed data better than another, whether that determination is made using standard ANOVA comparisons of nested models or an information criterion approach.

In this study, we used two complementary lines of evidence to evaluate the various proposed relationships across populations of *Eulemur*, i.e., whether precipitation variables or temperature variables were more strongly associated with variation in body mass. The first line of evidence was a standard significance testing approach, in which ANOVA comparisons of nested models were used to address whether the fit of a more complete model was significantly better than the fit of a nested model that excluded some variables (e.g., does the addition of temperature variables to a model that includes only precipitation variables significantly improve model fit, and vice versa?). The second line of evidence was based on evidence ratios (ER) derived from an information criterion approach. ER is a measure of how many times more likely the better model (i.e., the model with the lower AICc value) is than the worse model for any pair of models (Burnham and Anderson 2002). The evidence ratio is based on Δ_{AICc} , which is the difference between the AICc value for any particular model and the AICc value for the best model. The ER for any pair of models is calculated as follows (Symonds and Moussalli 2011):

$$\text{ER} = \frac{\exp\left(-\frac{1}{2} \Delta_i\right)}{\exp\left(-\frac{1}{2} \Delta_j\right)}$$

where Δ_i is the value for the better model, and Δ_j is the value for the worse model.

Ethical Note

All immobilizations, handling, sample collections, and export/import protocols adhered to and were approved by the OHDZA Institutional Animal Care and Use Committee (IACUC), the University of Calgary Animal Care Committee, the Convention on International Trade in Endangered Species, and U.S. Fish & Wildlife Services. Protocols for animal handling and immobilization may be found in previously published research (Delmore *et al.* 2011, 2013). This research was conducted with permission from the government of Madagascar, following legal requirements.

Results

Phylogenetic Signal in the Error Structure of the Model

Consensus branch lengths as identified by a maximum likelihood procedure resulted in a tree in which populations of the same species diverged from each other at 49.3% of the distance from tree tips to the divergence of each species from other taxa (ESM Fig. S1). Using those consensus branch lengths, we calculated all nine PGLS models using maximum-likelihood to estimate Pagel's λ for each model. In all cases, λ was estimated as a nonzero value (estimates ranged from 0.590 to 0.720), all 95% confidence intervals excluded $\lambda = 1$, and five of nine confidence intervals excluded $\lambda = 0$ (Table III). These results indicate the presence of some phylogenetic signal in the error structure of these models.

We recalculated all models using a consensus value of λ set equal to 0.672, the mean of the maximum likelihood value of λ across all models; this value of λ incorporates a majority of phylogenetic information into the error structure of the linear models and falls within the 95% confidence intervals for all estimated values of λ (Table IV). The difference between using model-specific maximum likelihood values of λ and the consensus value had little effect on model fits: the coefficient of determination (r^2) of the nine PGLS models that used the consensus value of λ were all within 0.009 units of the r^2 value for the corresponding model using individual-determined maximum likelihood λ , with five of nine pairs of models having identical r^2 values to three decimal places (compare r^2 values in Tables III and IV).

Ecogeographic Correlates of Body Mass

Variation in population-specific body mass was significantly associated with variation in temperature variables but not rainfall variables (Table IV). Based on AICc weights,

Table III Estimates of Pagel's λ for each linear model using consensus branch lengths for population divergences ($N = 27$ in all models)

	r^2	Model P	λ (95% CI)	F	df ₁	df ₂
Full	0.442	0.010	0.698 (0.000 to 0.936)	4.35	4	22
Annual	0.396	0.002	0.664 (0.023 to 0.915)	7.87	2	24
Seasonality	0.432	0.001	0.660 (0.000 to 0.910)	9.14	2	24
Rainfall	0.031	0.685	0.720 (0.149 to 0.949)	0.384	2	24
Temperature	0.434	0.001	0.635 (0.000 to 0.903)	9.22	2	24
Annual rainfall	0.000	0.981	0.706 (0.180 to 0.938)	0.000	1	25
Number of dry months	0.005	0.722	0.692 (0.140 to 0.933)	0.129	1	25
Annual temperature	0.393	<0.001	0.686 (0.121 to 0.916)	16.2	1	25
SD temperature	0.410	<0.001	0.590 (0.000 to 0.894)	17.3	1	25

Each model has population-specific body size dependent on one or more environmental variable (see the "Linear Models" section in [Methods](#) for more detail on each model). Model coefficients of determination and overall significance are also provided. Boldface indicates models significant at $\alpha = 0.05$. Note that all 95% confidence intervals for λ exclude 1

Table IV Model parameters based on consensus branch lengths and with Pagel's λ set equal to 0.672 ($N = 27$ in all models)

	r^2	Model P	AICc	Δ_i	AICc weight (w_i)	F	df_1	df_2	Annual rainfall P	No. of dry months P	Annual temp. P	SD temp. P
Full	0.442	0.010	-64.077	6.444	0.012	4.35	4	22	0.743 (> -0.0001)	0.993 (0.0001)	0.627 (-0.005)	0.216 (0.074)
Annual	0.396	0.002	-67.741	2.780	0.076	7.86	2	24	0.765 (< -0.0001)	•	<0.001 (-0.018)	•
Seasonality	0.432	0.001	-69.411	1.110	0.175	9.12	2	24	•	0.264 (0.006)	•	<0.001 (0.102)
Rainfall	0.030	0.694	-54.965	15.556	0.000	0.371	2	24	0.446 (> -0.0001)	0.398 (-0.013)	•	•
Temperature	0.432	0.001	-69.409	1.112	0.175	9.12	2	24	•	•	0.264 (-0.009)	0.214 (0.052)
Annual rainfall	0.000	0.990	-56.687	13.834	0.000	0.000	1	25	0.990 (< -0.0001)	•	•	•
Number of dry months	0.006	0.709	-56.840	13.681	0.000	0.142	1	25	•	0.709 (-0.002)	•	•
Annual temperature	0.393	<0.001	-70.182	0.339	0.257	16.2	1	25	•	•	<0.001 (-0.018)	•
SD temperature	0.401	<0.001	-70.521	0	0.305	16.7	1	25	•	•	•	<0.001 (0.091)
Independent variable AICc weights:										0.187	0.520	0.666

Each model has population-specific body size dependent on one or more environmental variable (see the "Linear Models" section in Methods for more detail on each model). Regression coefficients are given in parentheses with each P -value. Boldface indicates models and parameters significant at $\alpha = 0.05$. Dots indicate that a parameter is not included in that particular model. Note that collinearity may bias regression coefficient estimates and P -values associated with each variable in models with more than one predictor, although it has no effect on the P -value for the overall model in such cases. However, by definition collinearity cannot be present in those models that include only one predictor and thus has no effect on those coefficient estimates, i.e., the last four models in the table

the best model in this analysis had body mass dependent solely on standard deviation of temperature, followed closely by body mass dependent solely on annual mean temperature (Table IV). The next two highly weighted models were the seasonality model, in which standard deviation of temperature and number of dry months were both predictors (although only the temperature variable had a significant regression coefficient at $\alpha = 0.05$), and the temperature model, in which both temperature variables were predictors (Table IV). Although the temperature model was statistically significant ($P = 0.001$), neither of the two independent variables had a significant regression coefficient (Table IV). This is due to the strong negative correlation between these two variables ($r = -0.868$, $r^2 = 0.754$), resulting in neither temperature variable significantly improving model fit when the other temperature variable was already included in the model, despite the fact that both variables individually strongly correlate with body mass.

Both temperature variables had considerably higher summed AICc weights than the precipitation variables (Table IV). This stronger relationship between body mass and temperature rather than precipitation is also shown by the fact that neither model that used only one of the precipitation variables as the sole predictor was significant at $\alpha = 0.05$, nor was the rainfall model (which was dependent on both precipitation variables). In contrast, all models that included one or both temperature variable(s) were significant.

This overall pattern is also reflected in the pairwise comparison of models. Significance tests of nested models show that the addition of one or more temperature variables to a model that included only precipitation variables always significantly improved model fit, while addition of either precipitation variable to any model never significantly improved model fit (Table V). Evidence ratios derived from AICc values show the same pattern. For any comparison of a model containing only precipitation variables (i.e., the rainfall model, annual rainfall model, and number of dry months model) with a model containing only temperature variables (i.e., the temperature model, annual temperature model, and SD of temperature model), the temperature model is always the better model. Evidence ratios for these comparisons range from 536.2 to 2387.5 (Table V), meaning that the model with only temperature variables is always at least 536 times more likely to estimate the body mass data better than the model with only precipitation variables.

Considered as a whole, these results suggest that population-specific body mass is most strongly associated with standard deviation of temperature, followed closely by annual mean temperature, but with little or no relationship with rainfall variables. In addition, although we do not show the data here, the phylogenetic correlation of population-specific body mass with minimum temperature (which arguably is the most relevant temperature variable for the heat conservation hypothesis for Bergmann's rule) is even higher than it is with the standard deviation of temperature ($r^2 = 0.412$ vs. 0.401, respectively).

We can use the standard deviation of temperature PGLS model and annual mean temperature PGLS model to estimate expected \log_{10} body mass for "typical" true lemurs (i.e., controlling for phylogenetic variation in the data set) living at the extremes of these two variables in this data set (1.25 and 2.75°C for standard deviation of temperature, 18.16 and 26.80°C for annual mean temperature; Table I). These two models have intercepts of 0.110 and 0.682, respectively; estimated \log_{10} body masses for the extremes of standard deviation of temperature in this data set are 0.224 and 0.361 $\log_{10}[\text{kg}]$, and estimated mass for the extremes of annual mean temperature are

Table V Pairwise model comparisons using significance testing for nested models (*P*-values below the diagonal) and evidence ratios based on AICc for all models (ER above the diagonal)

	Full (4)	Annual (2)	Seasonality (2)	Rainfall (2)	Temperature (2)	Annual rainfall (1)	No. of dry months (1)	Annual temperature (1)	SD temperature (1)
Full (4)	—	<u>6.25</u>	<u>14.4</u>	95.2	<u>14.4</u>	40.2	37.3	<u>21.2</u>	<u>25.1</u>
Annual (2)	0.417	—	<u>2.3</u>	594.7	<u>2.30</u>	251.4	232.9	<u>3.39</u>	<u>4.01</u>
Seasonality (2)	0.822	—	—	1370.6	1.00	579.4	536.7	<u>1.47</u>	<u>1.74</u>
Rainfall (2)	0.002*	•	•	—	1369.2	<u>2.37</u>	<u>2.55</u>	2015.3	2387.5
Temperature (2)	0.822	•	•	•	—	578.8	536.2	<u>1.47</u>	<u>1.74</u>
Annual rainfall (1)	0.004*	<0.001*	•	0.398*	•	—	<u>1.08</u>	851.9	1009.3
Number of dry months (1)	0.005*	•	<0.001*	0.446*	•	•	—	789.2	935.0
Annual temperature (1)	0.599	0.765	•	•	0.214	•	•	—	<u>1.18</u>
SD temperature (1)	0.661	•	0.264	•	0.264	•	•	•	—

Each model has population-specific body size dependent on one or more environmental variable (see the “Linear Models” section in *Methods* for more detail on each model). For all models, *N* = 27. The number of independent variables in each model is given in parentheses after model name. **Below the diagonal**: *P*-values significant at $\alpha = 0.05$ in bold; significant values indicate that the additional variable(s) in the more complete model for a given pair of models significantly improves model fit. An asterisk (*) indicates that the model in the comparison with fewer variables is not significant at $\alpha = 0.05$. Dots indicate that neither model is nested in the other. **Above the diagonal**: evidence ratios (ER) for how much more likely the better model is than the other model for every pairwise comparison. The better model (lower AICc) is the model named on the row of the table unless underlined, in which case the model named in the column is the better model. Bolded ER values are for comparisons of models that contain only temperature variables with those that contain only precipitation variables

0.209 and 0.362 $\log_{10}[\text{kg}]$. These values correspond to an expected 37% increase in body mass (in kg) associated with an increase in 1.5°C of standard deviation of temperature, and an expected 42% increase in body mass associated with a decrease of 8.64°C of annual mean temperature. These expected differences control for the effects of phylogeny; note that the full range of body mass values in this data set is much greater than these differences in expected mass at environmental extremes, with the highest combined mean mass in Table I being 118% larger than the lowest, but also note that these values are drawn from different species (2.73 kg for *Eulemur fulvus* and 1.25 kg for *E. mongoz*).

Discussion

Overall, we found no support for the two resource constraint hypotheses. However, our results suggest that body size variation across *Eulemur* is generally consistent with Bergmann's rule, with about 40% of the variation in body size accounted for by variation in temperature across populations in this analysis (see r^2 values in Table IV). The slightly higher correlation of body size with the standard deviation of monthly mean temperatures rather than annual mean temperature is slightly puzzling at first glance. However, there is a strong negative correlation between these two temperature variables, such that those locations with the coolest annual mean temperature also have the greatest variability in monthly mean temperatures on average. Thus a high standard deviation of monthly temperature typically indicates a low baseline temperature with relatively high monthly variability, meaning that those locations will have months with the lowest temperatures overall. This is reflected in the even higher phylogenetic correlation of population-specific body mass with minimum temperature than with standard deviation of temperature. This result is consistent with the expectation of the heat conservation hypothesis that body mass should be highest in those areas that experience the coldest minimum temperatures to minimize the surface area to volume ratio (Bergmann 1847).

A point to consider is whether the lack of support for the resource constraint hypotheses may be due in part to the inclusion of sympatric populations of species with different body size. Owing to our sampling protocol in which we calculate the mean of environmental variables across a circle with a radius of 10 km, no two populations in our study share exactly the same values for all environmental variables (Table I). However, there are five areas where we have partial overlap between populations of different species, resulting in very similar values for those populations. Just as in the Kamilar *et al.* (2012) study, we might expect that the difference in body mass between populations living in the same place with the same values for environmental variables might obscure underlying patterns, even if the magnitude of body mass differences in sympatric populations is much smaller in this study and we only ever have a maximum of two species living sympatrically in our sample. However, if that is the case, we have no particular reason to believe that this confounding effect would impact precipitation variables more than temperature variables, so it should equally impair our ability to detect relationships between body mass and precipitation on the one hand and temperature on the other. Thus it is probably safe to conclude that even if some small component of body mass variation across *Eulemur* is constrained by resources, the effect of temperature variation is much greater.

Contextualizing this pattern in true lemurs within the broader pattern of evidence of Bergmann's rule in nonhuman primates is difficult because there are few such studies. Harcourt and Schreier (2009) investigated Bergmann's rule in non-Malagasy primates using the common approach of treating latitude as a proxy for temperature. They found that those primate clades whose ranges extended farthest from the equator had patterns consistent with Bergmann's rule, although this is due in part to a loss of species diversity at higher latitudes that results in the absence of both the smallest and largest bodied species. At lower taxonomic levels, patterns appear to vary. Also using a latitudinal approach, Fernandez-Duque (2011) found that intraspecific and intrapopulation variation in body mass of *Aotus* follows Bergmann's rule, while studies in *Nycticebus* and *Macaca* show a mixed pattern in which the relationship is observed in some species of these genera but not others (Ito *et al.* 2014; Ravosa 1998).

There are also few studies of Bergmann's rule in lemurs, and they tend to show different results at different taxonomic levels and within different clades at the same taxonomic level. An analysis across all lemurs showed no evidence for any ecogeographic effects on body mass (Kamilar *et al.* 2012), while at the generic level, comparisons of populations of *Propithecus* representing all extant sifaka species found support for resource constraint hypotheses but little to no support for Bergmann's rule (Gordon *et al.* 2013). Intraspecific analyses of some of the smallest bodied lemurs have produced conflicting results: whereas an analysis of three populations of *Microcebus murinus* showed a negative relationship between body mass and temperature, consistent with Bergmann's rule (Lahann *et al.* 2006), an analysis of populations of *Cheirogaleus crossleyi* showed no such evidence (Blanco and Godfrey 2014). However, the authors of the latter study note that dwarf lemurs are obligate hibernators, unlike mouse lemurs, and thus are not subject to year-round thermal stress. Finally, previous work comparing one population each of *Eulemur rufifrons* and *E. rufus* (which have previously been considered to belong to a single subspecies, *E. fulvus rufus*) showed a pattern consistent with both Bergmann's rule and resource constraint hypotheses (Johnson *et al.* 2005). Samples sizes in all of these intraspecific studies are too small to draw meaningful conclusions about statistical significance.

That said, there are at least two proposed general relationships that may account for the different patterns observed in lemurs. The first is that variation in pelage thickness and density should have a greater impact on thermoregulation in larger mammals than in smaller mammals, and thus Bergmann's rule should be more evident in small mammals than in large mammals (Stuedel *et al.* 1994). If correct, this might help explain why support for Bergmann's rule is found in mouse lemurs and true lemurs but not in sifakas. However, broad studies across mammals that find evidence for Bergmann's rule do not find evidence for a difference in the pattern between small and large mammals (Ashton *et al.* 2000; Blackburn and Hawkins 2004). A second possibility is that there is a more complex relationship among body mass, temperature, and resource seasonality. In their study of ecogeographic body mass variation in *Microcebus murinus*, Lahann *et al.* (2006) suggest that temperature negatively correlates with body mass, whereas resource seasonality positively correlates with longevity and negatively correlates with reproductive rate. It is likely that the relationship of all of these variables to each other vary depending on the specific constraints on life history parameters for any given species, considered in conjunction with the spatial and temporal distribution of food resources. For example, the difference in dietary niche

between *Eulemur* and *Propithecus* species (the former incorporating mostly fruit into their diet, and the latter being more folivorous) may have an interaction effect with climatic variables that produces the different patterns of ecogeographic body mass variation observed in these two genera; dietary differences also appear to affect ecogeographic relationships with body mass in carnivores (Meiri *et al.* 2007). Whether a particular model can be developed that successfully predicts adult body mass based on environmental parameters, diet, and life history parameters (other than growth rate and duration) remains to be seen.

Regardless of why some lemur taxa appear to follow Bergmann's rule or to support resource constraint hypotheses while others do not, the results of this study considered in conjunction with previous work on *Propithecus* suggest that comparative analyses of ecogeographic body mass variation in high-level taxa should be interpreted with caution. Kamilar *et al.* (2012) found no evidence any relationship between body mass and environmental variables, and we suggested that this might be due to multiple species sharing the same values for environmental variables but highly different body mass values (Gordon *et al.* 2013). An additional reason why such studies may not find a relationship between body mass and environmental factors is that different relationships may be present in various lower level taxa (e.g., temperature relationships in true lemurs and resource seasonality relationships in sifakas), and these different relationships may be due to unmeasured factors (e.g., interactions with dietary differences). The inclusion of these multiple taxa with their differing patterns into a single analysis will likely obscure those relationships. As a consequence, we recommend that future comparative studies attempt to determine whether patterns (or absence of patterns) observed at high taxonomic levels are consistent with those observed at lower taxonomic levels within the same data sets (Gordon 2006; Smith and Cheverud 2002), and if not, attempt to determine whether additional factors might be involved in these relationships, e.g., dietary niche, activity pattern, life history variables.

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