



Ecological and Phylogenetic Correlates to Body Size in the Indriidae

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I investigated ecological and phylogenetic correlates to body size variations in 10 taxa of extant Indriidae (Indri, Avahi, and Propithecus). I also tested for phylogenetic niche conservatism as a model for the evolution of indriid body size. Phylogenetic niche conservatism refers to the shared attributes that related taxa have acquired because they tend to have occupied similar niches during their evolutionary history. I collected species-specific data on body mass, climate, density, and chemical properties of food items from the literature. I used 2 phylogenies in independent contrasts methods to control for phylogenetic relationships (Indri and Propithecus as sister taxa vs. Indri basal taxa to all indriids). Multivariate models indicated that lemur density and resource quality are the strongest ecological correlates to indriid body size variations. Partitioning methods revealed that 52.4–67% of indriid body size variation is explained by phylogenetic niche conservation. Thus, indriid body size variations may be the result of stabilizing selection. Though it is possible to identify constraints on lower than average body size, there are few data on selection against larger than average body size in indriids. Large body size in subfossil lemurs further complicates identification of constraints on larger than average body size in extant indriids. Researchers using independent contrast methods to control for phylogeny should be aware that some ecology-phenotype relationships are best explained as the result of the synergistic effects of ecology and phylogeny.

KEY WORDS: density; food quality; Indriidae; phylogenetic niche conservation; stabilizing selection.

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INTRODUCTION

One of the most perplexing problems in primate evolutionary biology is understanding the relationship between body size and various ecological variables (Conroy, 2003; Gaston and Blackburn, 1996; Lovegrove and Haines, 2004). Interspecific allometry (IA) in adult body size is often linked to diet, particularly for folivores (Peters, 1986). Folivory tends to be characterized as a low-quality diet because of the difficulties involved with cellulose digestion, the low energy value of leaves, and the presence of plant secondary compounds in many leaves (Glander, 1982; Milton and May, 1976). Folivores have evolved adaptations of the gut tract to host colonies of symbiotic microorganisms that process fibrous plant material (Moir, 1965). Because a larger gut surface area maximizes nutrient absorption and larger animals tend to have higher energy requirements than those of small-bodied taxa, folivores are characterized by large body size. However, obligate folivores do not always represent the largest-bodied lemurs (Ganzhorn, 1999). For example, *Avahi laniger* weighs only 1.03–1.32 kg and is almost exclusively folivorous (Faulkner and Lehman, 2005; Ganzhorn *et al.*, 1985; Smith and Jungers, 1997). Conversely, the largest extant lemur, *Propithecus diadema diadema* (6.5 kg), has an annual diet that is composed of both young leaves (42% of total diet) and fruits (38.3% of total diet: Powzyk, 2003). *Propithecus diadema diadema* is sympatric throughout its range with *Avahi laniger*, so the differences are not likely the result of habitat variation. Moreover, body size variations are often linked to phylogenetic relationships between closely related taxa (Smith *et al.*, 2004). Therefore, the question arises as to how ecology and phylogeny influence interspecific body size variations in folivorous lemurs.

Many researchers have cited geographic variation in rainfall as the proximate factor influencing lemur evolutionary ecology (Albrecht and Miller, 1993; Albrecht *et al.*, 1990; Ganzhorn, 2002; Godfrey *et al.*, 1990, 2004; Lehman *et al.*, 2005; Ravosa *et al.*, 1993, 1995; Wright, 1999). Ultimately, rainfall is taken as an indirect measure of forest productivity (Kay *et al.*, 1997). Resource seasonality may apply to some extant Indridae (*Indri*, *Avahi*, and *Propithecus*) in that the largest *Propithecus* live in the eastern humid forests with progressively smaller forms inhabiting the dry forests of western, northern, and southern Madagascar (Albrecht *et al.*, 1990; Ravosa *et al.*, 1993, 1995). Albrecht *et al.* (1990) hypothesized that the ecogeographic pattern of size variations in frugivorous lemurs was a result of differential resource productivity. For folivores, regions characterized by low rainfall and therefore low productivity should normally select for larger body size. The resource seasonality hypothesis can be rephrased as a statistical prediction that there should be a negative correlation between

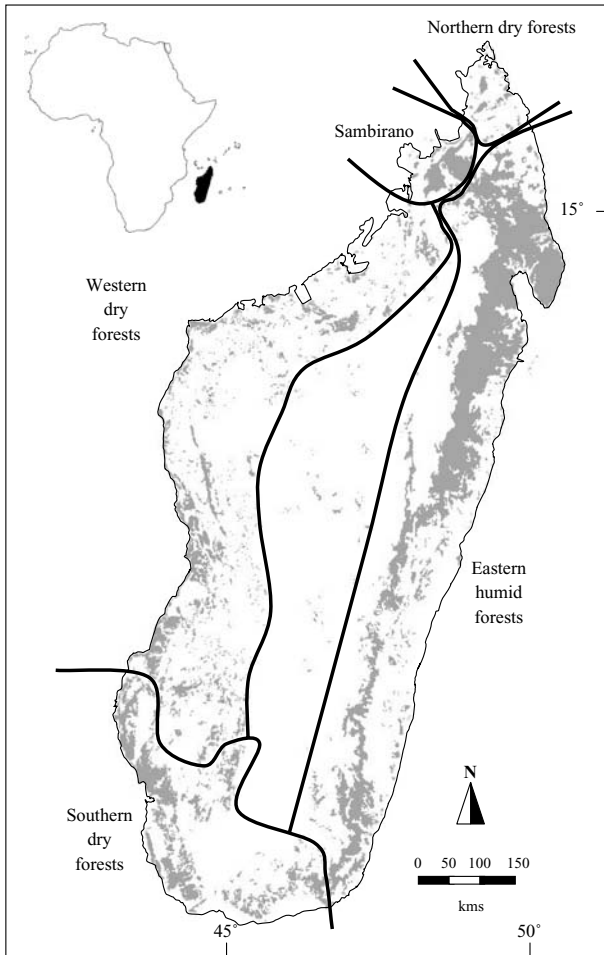


Fig. 1. Location of major biogeographic forest and climatic zones in Madagascar. (based on Nicoll and Langrand, 1989).

mean annual rainfall and adult body size in folivorous lemurs. Recent studies provide support for some aspects of the resource seasonality hypothesis for lemurs (Ganzhorn, 1999; Lehman *et al.*, 2005; Ravosa *et al.*, 1995). The main biogeographic regions for forest habitats can be classified as humid forests along the eastern part of the island and dry forests located in the south, west, and northern regions of the country (Fig. 1). Seasonal fluctuations in rainfall are more pronounced in dry forests versus humid forests (Ganzhorn, 1994, 2002; Ganzhorn *et al.*, 1997). Further, the length of the

dry season tends to be longer in the dry forests versus the eastern humid forests (Ganzhorn *et al.*, 1999). New leaves are often available throughout the year in eastern humid forests (Hemingway, 1998; Johnson, 2002; Meyers and Wright, 1993; Overdorff, 1993), though there is a small increase in new leaf availability around the time of the warm, rainy season (ca. October–February). Conversely, young leaves are usually available only during the November–March rainy season in dry forests (Ganzhorn, 1995; Meyers and Wright, 1993; Yamashita, 2002). Fruiting patterns show a different biogeographic pattern between dry and humid forests. Ganzhorn *et al.* (1999) observed that fruit availability is more predictable in western dry forests than in eastern humid forests. Based on the biogeographic data, low annual rainfall and a long dry season should result in reduced food abundance and therefore produce strong selective pressures for larger adult body size in folivores. However, a recent study of ecogeographic size variations in sifakas showed a positive rather than negative correlation between body size and rainfall (Lehman *et al.*, 2005).

Researchers have also cited resource quality as an important covariate to folivore biomass and body size variations (Chapman *et al.*, 2002; Ganzhorn, 1992; Milton and May, 1976; Ravosa *et al.*, 1995). For folivores, researchers have often measured resource quality as a protein-to-fiber (P:F) ratio in leaves (Milton and May, 1976). Leaves with low P:F ratios inhibit digestibility because folivores must devote considerable time and gut space to dealing with the indigestible fiber content. Ganzhorn (1992, 1999) documented higher P:F ratios for leaves in dry forests compared to leaves from trees in eastern humid forests. There tends to be lower mineral content in the soils of eastern humid forests, which may result in low-quality food resources for folivores (Ganzhorn *et al.*, 1999). There is also general biogeographic patterns of body size variations in folivorous lemurs that have been associated with difference in the quality of leaves between dry and humid forests (Albrecht *et al.*, 1990; Godfrey *et al.*, 1990; Ravosa *et al.*, 1995). For example, the larger-bodied *Avahi laniger* (body mass 0.9–1.17 kg) lives in poorer quality eastern humid forests whereas the smaller sized *A. occidentalis* (body mass 0.7–0.99 kg) ranges into higher-quality dry forests (Faulkner, 2005). If leaves are characterized by low P:F ratios at the landscape or biome levels, then there should be strong selective pressures for larger body size in the folivores that inhabit eastern humid forests. The relationship is known as the food quality hypothesis. However, Lehman *et al.* (2005) found that food quality is not a significant covariate of body size for *Propithecus* taxa in either dry forests or humid forests.

Energy availability and use may also relate to indriid body size variations. Though lemurs reach adult body mass faster than anthropoids, growth rates are slower in folivorous lemurs than in frugivorous lemurs

(Godfrey *et al.*, 2004; Leigh and Terranova, 1998). Moreover, many researchers have noted a biogeographic pattern of high densities for small-bodied folivores in low-quality habitats compared to low densities for large-bodied folivores in high-quality habitats (Damuth, 1981; Ganzhorn, 1999; Haugaasen and Peres, 2005; Silva and Downing, 1995; Sussman, 1999). The inverse relationship between population density and body size is referred to as the energetic equivalent rule (Damuth, 1981). Specifically, the energetic equivalent rule predicts that body mass (W) and population density (β) correlate negatively and exhibit a $W^{-.75} = \beta$ relationship. Despite considerable debate regarding the applicability of the energetic equivalent rule and $-.75$ slope for mammals (Arneberg and Andersen, 2003; Morgan Ernest, 2005; Nunn and Barton, 2000), Silva and Downing (1995) have applied it successfully to moderately-sized (0.1–100 kg) herbivores. Most importantly, slope variances can provide insights into why some taxa are larger than others. Griffiths (1986) suggested that if the slope of the body size-population density relationship is more than $-.75$, then the pattern may indicate that larger individuals control a disproportionately greater amount of energy. Conversely, if the slope is less than $-.75$, then smaller individuals may control a disproportionately greater amount of energy.

Testing and controlling for phylogenetic relationships are critical in IA studies. As Felsenstein (1985) noted, most statistical tests require independence between data points, a requirement that is often violated when comparing taxa with close phylogenetic relationships. Phylogenetic independent contrasts (IC) is the standard method to control for phylogeny in comparative studies (Felsenstein, 1985; Garland *et al.*, 1992, 1993). One derives the IC data by calculating pairwise comparisons at all levels of a phylogeny, using each branch only once, and can then consider the resulting analyses of the transformed data to be free of the confounding effects of phylogenetic history among taxa. For example, Smith and Cheverud (2002) found that phylogenetic relationships influenced the scaling of sexual size dimorphism in Catarrhini. Thus, the mixed success of previous studies to find consistent support for either the resource quality or abundance hypotheses may indicate the presence of phylogenetic inertia. Phylogenetic inertia, as it applies to body size, refers to the influence of an ancestor on the phenotype of a descendant (Blomberg and Garland, 2002). However, there is some evidence that interspecific body size variations are not related exclusively to ecology or phylogenetic inertia (Lord *et al.*, 1995). Desdevises *et al.* (2003) noted the value of incorporating both phylogeny and ecology as covariates to mammalian body size variations. The model is known as phylogenetic niche conservatism (Grafen, 1989; Harvey and Pagel, 1991; Plavcan and van Schaik, 1997). It is possible to define phylogenetic niche conservatism as the shared attributes that related taxa have acquired

because they tend to have occupied similar niches during their evolutionary history (Grafen, 1989; Harvey and Pagel, 1991). The conservatism is the result of stabilizing selection (Hansen, 1997; Webb *et al.*, 2002). Stabilizing selection selects for an intermediate body size that maximizes fitness in a habitat (Smith *et al.*, 2004). If indriid body size evolution reflects phylogenetic niche conservatism, then IA analyses may offer a better model than IC methods (Desdevises *et al.*, 2003; Smith and Cheverud, 2002).

The Indriidae is an excellent monophyletic taxon to test hypotheses on ecological and phylogenetic correlates to body size. There are data on body size, chemical properties of leaves exploited as food items, and phylogenetic relationships for most taxa of indriids (Table I). I tested if indriid body size variations relate to ecology or phylogeny or both. I then investigated if the data provide support for phylogenetic niche conservatism in indriids. The multivariate approach is important for understanding the evolutionary ecology of primates (Harcourt *et al.*, 2005).

METHODS

I collected data on body mass, density, climate, and chemical properties of food items from the literature for 10 taxa of indriids (Table I). I determined dry season length (months) using descriptions by primary sources specific to sites at which the researchers collected other variables on the indriid taxa were collected. For *Propithecus diadema perrieri*, I used climatic data from Ankarana (Wilson *et al.*, 1989), which lies within the historic range of the subspecies (Tattersall, 1982). I subjected all variables to \log_{10} transformations to linearize relationships.

It is important to test for spatial autocorrelation before conducting correlations among variables that represent different geographic regions (Fortin and Jacquez, 2000; Legendre and Fortin, 1989; Legendre *et al.*, 2002). Spatial autocorrelation is the pattern of relatedness of a set of spatially located data: the extent to which adjoining or neighboring spatial units are more likely to have similar magnitude than by chance alone (Fortin *et al.*, 2002). Spatial autocorrelation can inflate type I errors in statistical analyses and lead to false-positive results in correlations (Lennon, 2000). I tested for spatial autocorrelation for all variables via a Mantel's test (Z), which is a linear estimate of the relationship between 2 square distance matrices of variables taken at the same sampling locations (Mantel, 1967). The first matrix comprised the Euclidean distances between each site for which I selected indriid data. The second matrix contained the difference between each ecological variables by each site, e.g., rainfall at a site of *Avahi laniger*—rainfall at one of *Propithecus tattersalli*. I then normalized

Table 1. Body size, climatic data, and ecological data for 10 taxa of Indriidae

Taxa	Mean body mass (kg) ^d	Mean annual rainfall (cm) ^b	Dry season (months) ^c	Density (no. of ind./km ²) ^d	Protein-to-fiber ratio in leaves ^e	Habitat ^f
<i>Avahi lamiger</i>	1.05	1700	5	72.00	.113	Humid forest
<i>A. occidentalis</i>	.79	750	8	67.00	—	Dry forest
<i>Propithecus diadema perrieri</i>	4.34	1250	7	2.00	.326	Dry forest
<i>P. d. candidus</i>	5.27	2500	6	9.00	-	Humid forest
<i>P. d. edwardsi</i>	5.87	2650	5	7.65	.208	Humid forest
<i>P. d. diadema</i>	6.45	3721	4	1.50	.221	Humid forest
<i>P. v. verreauxi</i>	3.09	750	8	15.00	.477	Dry forest
<i>P. v. coquereli</i>	3.99	1500	6	6.00	.316	Dry forest
<i>P. tattersalli</i>	3.49	1639	7	22.50	.200	Dry forest
<i>Indri indri</i>	6.43	3721	4	5.20	.087	Humid forest

^aRazanahoera-Rakotomalala, 1981; Smith and Jungers, 1997; Lehman *et al.*, 2006.

^bGanzhorn, 1992; Hemingway, 1998; Meyers, 1993; Overdorff, 1991; Tan, 1999; Wilson *et al.*, 1989; Wright, 1999.

^cGanzhorn, 1992; Hemingway, 1998; Meyers, 1993; Overdorff, 1991; Powzyk, 1997; Wilson *et al.*, 1989; Wright, 1999.

^dGanzhorn, 1988; Hemingway, 1998; Irwin *et al.*, 2005; Powzyk, 1997; Vargas *et al.*, 2002; Lehman, unpublished data.

^eGanzhorn, 1992; Ganzhorn *et al.*, 1985; Meyers, 1993; Powzyk, 1998.

^fGanzhorn *et al.*, 1999; Lehman *et al.*, 2005.

a Mantel's statistic (Z) into a correlation coefficient (r) that corresponds to the intensity of spatial autocorrelation for 2 variables (Fortin and Dale, 2005). I conducted Mantel's tests and associated significance values via Rndom Project (Jadwiszczak, 2002), and determined the correlation coefficient with the PopTools add-in for Excel (Hood, 2004). There is no evidence of spatial autocorrelation for indriid body size ($Z = 2338.4$, Mantel's $r = .103$, $p = .478$), rainfall ($Z = -1440.1$, Mantel's $r = .001$, $p = .761$), dry season ($Z = 673.0$, Mantel's $r = .025$, $p = .255$), density ($Z = 376.5$, Mantel's $r = -.060$, $p = .255$), or P:F ratios ($Z = 1776.6$, Mantel's $r = 0.009$, $p = 0.303$).

I then tested for covariation among ecological variables via a Pearson correlation coefficient. If there was a significant correlation between the ecological variables, then I investigated the relationships via a partial correlation to indriid body size. Partial correlations compute correlation coefficients that describe the linear relationship between 2 variables while controlling for the effects of an additional variable. I conducted traditional IA measures of ecological correlates to indriid body size. I then used stepwise regression models to determine if indriid body size covaried with a specific set of ecological variables (rainfall, dry season, density, and P:F ratios). I assessed significance values via permutation methods to avoid normality issues in standard regression models (Legendre, 2002). The analyses refer to the ecological component of indriid body size, with an unaccounted component of phylogeny.

Though body size strongly correlates with phylogenetic history, it is important first to test the data for significant phylogenetic autocorrelation (Abouheif, 1999; Blomberg *et al.*, 2003; Cheverud *et al.*, 1985). Phylogenetic autocorrelation is the pattern of relatedness of a set of phylogenetically related data, the extent to which closely related taxa are more likely to have similar magnitude than by chance alone (Blomberg *et al.*, 2003). If there is no phylogenetic autocorrelation, then one can use traditional IA measures. Per Abouheif (1999), I conducted a test for serial independence (C) to determine if there was phylogenetic autocorrelation in the indriid size data. I conducted the test via PI (phylogenetic independence) with significance levels determined by 1000 iterations of the original data set (Reeve and Abouheif, 2003). Though analyses of molecular and morphological data have resolved many of the nodal relationships at the generic, specific, and subspecific levels for *Propithecus* and *Avahi* (Delpero *et al.*, 2001; Mayor *et al.*, 2004; Pastorini *et al.*, 2001; Razafindraibe *et al.*, 1997), the placement of *Indri indri* within the indriid clade is unresolved (Fig. 2). Thus, I used 2 phylogenies: 1 in which *Indri indri* is a sister taxa to *Propithecus* (phylogeny 1) and another in which *I. indri* is basal to all other indriids (phylogeny 2). Serial independence tests indicate positive phylogenetic autocorrelation

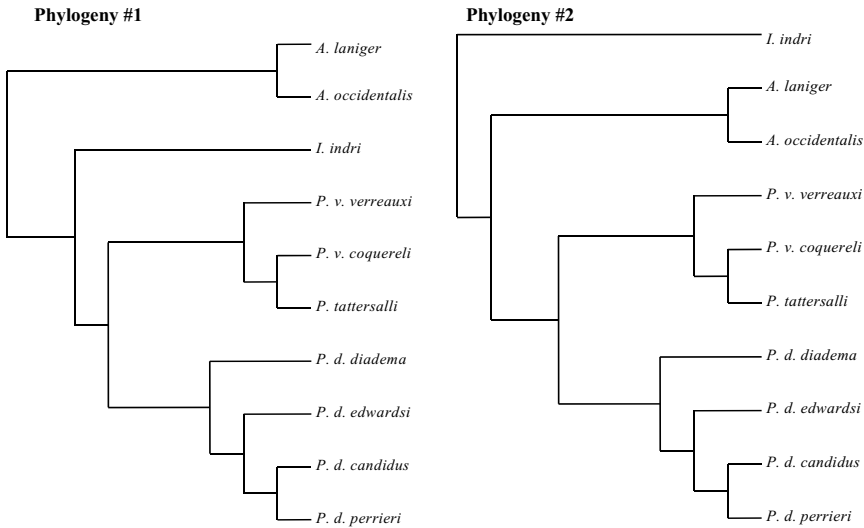


Fig. 2. Two phylogenies of Indriidae used in this study: phylogeny 1 in which *Indri indri* is a sister taxa to *Propithecus* and phylogeny 2 in which *I. indri* is basal to all other indriids. (Based on Mayor *et al.*, 2004; Pastorini *et al.*, 2001; Yoder, 1997.)

for indriid body size in phylogeny 1 ($C = .252$, $p = .001$) and phylogeny 2 ($C = .390$, $p = .017$). Thus, there is a phylogenetic component to body size variations in indriids.

I used IC to determine ecological correlates to body size in indriids after taking their phylogenetic relatedness into account. I transformed body size and ecological data via PDTREE (Garland *et al.*, 1992, 1999, 2002). Though IC methods require detailed information on phylogenetic relationships for the test population (Felsenstein, 1985), there are few data on branch lengths for indriids (Pastorini *et al.*, 2001). I used a default procedure in which I assigned all branches the same length (Purvis *et al.*, 1994; Symonds, 1999). The advantage of the approach is that it allows more contrasts to be performed, increasing the power of subsequent statistical tests. However, Felsenstein (1985) noted that branch lengths should represent expected units of evolutionary change. Thus, ICs must be adequately standardized so that they have equal expected variance in subsequent regression models (Garland *et al.*, 1992). I achieved the test by regressing the absolute values of the standardized contrasts on the square root of the expected variance. Ideally, none of the correlations should be statistically significant. It is also important to test for heterogeneity of variance in the residuals. The predicted values of the dependent variables (body size and density) are directly proportional to the contrasts in the predictor variable because one

derives the residuals by regression through the origin (Diaz-Uriarte and Garland, 1996). To complete the diagnostic test, I regressed the absolute values of the residuals against the standardized contrasts in each independent variable—rainfall, dry seasons, density, and P:F ratios. Again, none of the resulting correlation values should be statistically significant. If any of the diagnostic tests were significant, then I made branch length corrections via PDTREE.

I used linear regression analyses to determine if IC body size in indriids covaried with IC data on density, seasonality (annual rainfall and dry season length), and P:F ratios. For all IC regressions, I forced the slope of the regression equation through the origin (Garland *et al.*, 1992). I then used a *t*-test to determine the probability that the slope for each independent contrasts regression model differed significantly from 0 (Garland *et al.*, 1992). If the statistical probability for the independent contrasts slope was $> .05$, then I accepted the null hypothesis and inferred no causal relationships. Conversely, if the statistical probability for the independent contrasts slope was $< .05$, then I rejected the null hypothesis and determined that the independent variable is an important covariate of body size in Indriidae. The analyses provide information on the relationship between indriid body size and ecology once phylogeny is taken into account.

Per Desdevises *et al.* (2003), I used a partitioning method to determine if indriid body size variations reflect phylogenetic niche conservatism. The method partitions variation in a dependent variable among the following components: 1) a part strictly due to ecology, 2) phylogenetically structured environmental variation (PSEV), 3) a part strictly due to phylogeny, and 4) an unexplained component. The PSEV component refers to phylogenetic niche conservatism. I conducted the partitioning method separately for each of the 2 phylogenetic trees. First, I conducted a multivariate regression of body size on the various ecological variables, retaining the R^2 coefficient from the best model, which is equal to the components of $a + b$. I used the coefficient for both indriid phylogenies. Second, I derived a patristic distance matrix for each phylogenetic tree after any branch length transformations via PDDIST (Garland *et al.*, 2002). I performed a principal coordinate analysis on the matrix via The R Package version 4.0 (Casgrain and Legendre, 2000). I used a forward regression selection procedure to select the PC(s) that significantly contributed to the explanation of body mass. A multivariate regression conducted on the relationship between body size and the PC(s) yielded a R^2 coefficient that represents the fraction $b + c$. A final multivariate regression of body size on the ecological variable(s) from step 1 and the PC(s) provided a R^2 coefficient equal to the fraction of $a + b + c$. I obtained fractions a , b , c , and d by subtraction:

Table II. Pearson correlation coefficients between ecological variables

Variables	Dry season	Density	P:F ratios
Rainfall	-.916***	-.860**	-.703
Dry season	—	.659*	.736*
Density	—	—	.525

* $p \leq .0001$; ** $p \leq .001$; *** $p \leq .05$.

$a = (a + b + c) - (b + c)$; $b = (a + b) - (a)$; $c = (b + c) - (b)$; and $d = 1 - (a + b + c)$. I conducted all regression models via SPSS 11.5.

RESULTS

Rainfall correlates negatively with dry season and lemur densities (Table II). Length of the dry season correlates positively with lemur density and P:F ratios. Indriid body size correlates positively with rainfall and negatively with density (Table III). The slope of the density (dependent variable) on body size (independent) regression is higher than but not significantly different from the predicted value of $-.75$ ($t = .922, p = .369$). Visual inspection of the plots indicates that data for the 2 species of *Avahi* may be outliers (Fig. 3). However, removal of the data for *Avahi* results in a change from significant ($p < .05$) to nonsignificant ($p > .05$) only for the density (dependent variable) on body size (independent) regression model. None of the other nonsignificant models (dry season and P:F ratios) become statistically significant after one removes the data for *Avahi*. Moreover, removal of the possible outliers actually improves the explanatory power of the body size regression coefficients for the rainfall (increase to $R^2 = .871$) and density models (increase to $R^2 = .785$). After one controls for dry season, rainfall still correlates with indriid body size ($r = .679, df = 7, p = .044$). Conversely, rainfall is not a significant covariate of indriid body

Table III. Linear regression models of ecological correlates to body size and density in 10 taxa of indriids (all data \log_{10} transformed)

Dependent	Independent	<i>R</i>	<i>R</i> ²	<i>F</i>	Df	<i>p</i>	Slope	SE of slope
Body size	Rainfall	.673	.453	6.62	1, 8	.033	.859	.334
	Dry season	.473	.223	2.29	1, 8	.168	-1.351	.892
	Density	.713	.508	8.25	1, 8	.021	-.460	.160
	P:F ratio	.115	.013	.08	1, 6	.787	.122	.430
Density	Body size	.713	.508	8.25	1, 8	.021	-1.104	.384

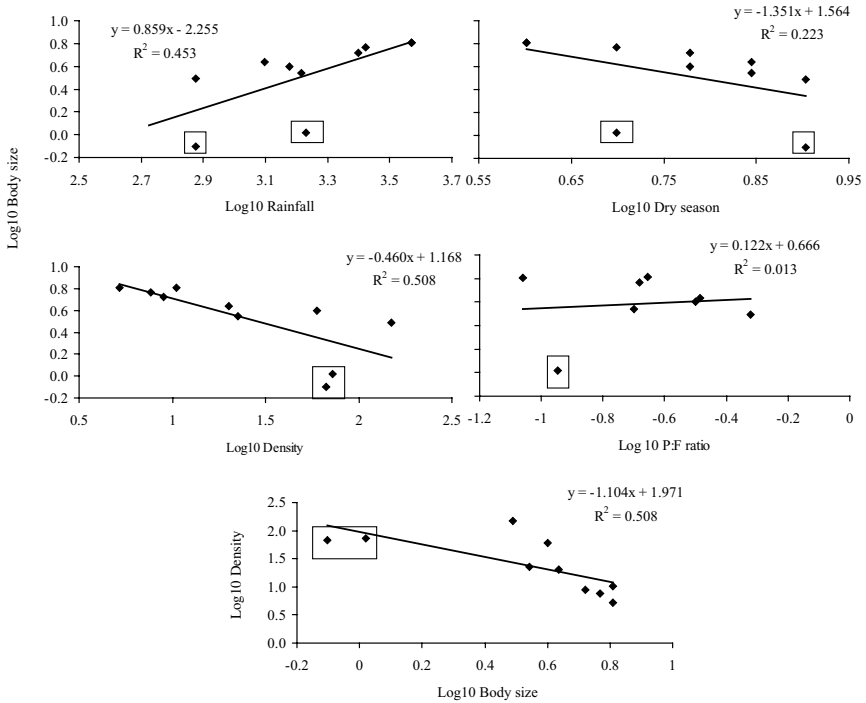


Fig. 3. Traditional IA plots of log₁₀ transformed data on ecological and body size correlates in indriids. Boxes indicate data for *Avahi* spp. Removal of the possible outliers influenced only the statistical significance for the density (dependent) on body size (independent) model.

size after one controls for density ($r = .166$, $df = 7$, $p = .668$). Further, there is no significant relationship between indriid body size and density ($r = -.605$, $df = 7$, $p = .084$) after one controls for rainfall. The partial correlations support a multivariate rather than univariate approach to body size variations in indriids. Stepwise regression analyses indicate that density and P:F ratios are the strongest covariates to indriid body size (Table IV), explaining 84.1% of the variation in the dependent variable.

Table IV. Stepwise regression models of ecological correlates to indriid body size

Variable(s)	R	R ²	F	df	p	Slope(s)	SE of slope(s)
Density, P:F ratio	.917	.841	13.26	2, 5	.01	-.538, .718	.105, .222
Density	.714	.510	6.23	1, 6	.047	-.359	.144

Table V. Independent contrast correlates to indriid body size and density

Model	Variables		Best branch lengths					Diagnostics ^a		
	Dependent	Independent	Transformation	Slope	SE of slope	R	p	R residuals	R x-axis	R y-axis
Phylogeny 1	Body size	Rainfall	Equal	.626	.205	.733	.018	.069	.245	.620
		Dry season	Equal	-1.274	.489	-.677	.035	.063	.060	-.568
		Density	Equal	-.350	.123	-.710	.025	-.188	.668	-.635
Phylogeny 2	Density	P:F ratio	Equal	-.252	.409	-.244	.565	-.182	-.323	.368
	Body size	Body size	Equal	-1.439	.504	-.710	.025	.132	.602	-.635
		Rainfall	Equal	.675	.240	.705	.026	-.043	.025	.604
	Dry season	Dry season	Equal	-1.336	.583	-.629	.056	.186	-.177	-.655
	Density	Density	Equal	-.383	.141	-.692	.030	-.058	.450	-.608
	P:F ratio	P:F ratio	Equal	-.086	.448	-.077	.856	.084	.291	.280
	Body size	Body size	Equal	-1.249	.461	-.692	.030	.090	.665	-.647

^aThe first column refers to IC correlates to residuals. Other columns refer to IC correlates to standard deviations. None of the correlations are statistically significant (i.e., $p < .05$).

Table VI. Comparison of IA and IC slopes for indriid phylogeny 1 and 2

Variables		Phylogeny 1		Phylogeny 2	
Dependent	Independent	<i>t</i> -test	<i>p</i>	<i>t</i> -test	<i>p</i>
Body size	Rainfall	.596	.559	.448	.660
	Dry season	.080	.937	.014	.989
	Density	.915	.372	.497	.625
	P:F ratio	.775	.448	.309	.761
Density	Body size	.740	.469	.218	.830

For the IC transformed data, rainfall correlates positively and density negatively with body size for phylogeny 1 and phylogeny 2 (Table V). Though IC dry season correlates with IC body size in phylogeny 1, the relationship approaches significance only for phylogeny 2. I conducted a stepwise regression model on the 2 IC data sets for body size as a function of rainfall, dry season, and density. It was not possible to include P:F ratios in the test because of the missing data for *Avahi occidentalis* and *Propithecus diadema candidus*. Stepwise regression analyses indicate that IC density is the only significant covariate to IC indriid body size for phylogeny 1 ($R = .710$, $F = 8.14$, $p = .011$) and phylogeny 2 ($R = .692$, $F = 7.35$, $p = .042$). Moreover, IC body size (independent variable) explains 50.1% of the variation in IC density (dependent variable) for phylogeny 1 and 47.2% of the variation in density for phylogeny 2. There is no significant difference in slopes between the IA and IC data for any of the linear regression models (Table VI). The slopes of the IC density (independent) to body size (dependent) regressions are higher than but not significantly different from the predicted value of $-.75$ for phylogeny 1 ($t = 1.367$, $p = .202$) and phylogeny 2 ($t = 1.083$, $p = .304$). Though visual inspection of the IC plots reveals possible outliers, correcting for the data points did not alter any of the significant correlates to indriid body size (Figs. 4 and 5). However, removal of the 2 outliers for phylogeny 1 IC body size on density regression model altered the significance threshold, i.e., $p > .05$.

I then tested for the effects of phylogenetic niche conservatism on indriid body size variations (Fig. 6). I retained the R^2 value (.836) from the IA stepwise regression model, with density and P:F ratios as the main covariates to indriid body size variation, as the component $a + b$ for phylogenies 1 and 2. For phylogeny 1, the forward regression model retained PC 1 and PC 2 from the principal component analysis of the patristic data matrix. The multivariate regression of the PCs on body size is statistically significant ($R^2 = .802$, $F = 14.14$, $p = .006$). A final multivariate regression of density, P:F ratios, and the 2 PCs on indriid body size yields the component

$a + b + c$ ($R^2 = .973, F = 26.53, p = .011$). For phylogeny 2, the forward regression model retained PC 2, which is a significant covariate to indriid body size ($R^2 = .538, F = 9.31, p = .016$). A multivariate regression of density, P:F ratios, and PC 2 on body size explains 85.5% of the variation in the dependent variable ($R^2 = .855, F = 7.88, p = .037$). The final partitioning models reveals that the PSEV component (52.4–67.0%) comprises a larger proportion of body size variation than either ecology (17.1–31.7%) or phylogeny (1.4–13.2%).

DISCUSSION

Density and P:F ratios are the ecological variables most strongly associated with interspecific variations in indriid adult body size. Moreover, there is a synergistic effect of phylogeny and ecology on the evolution of

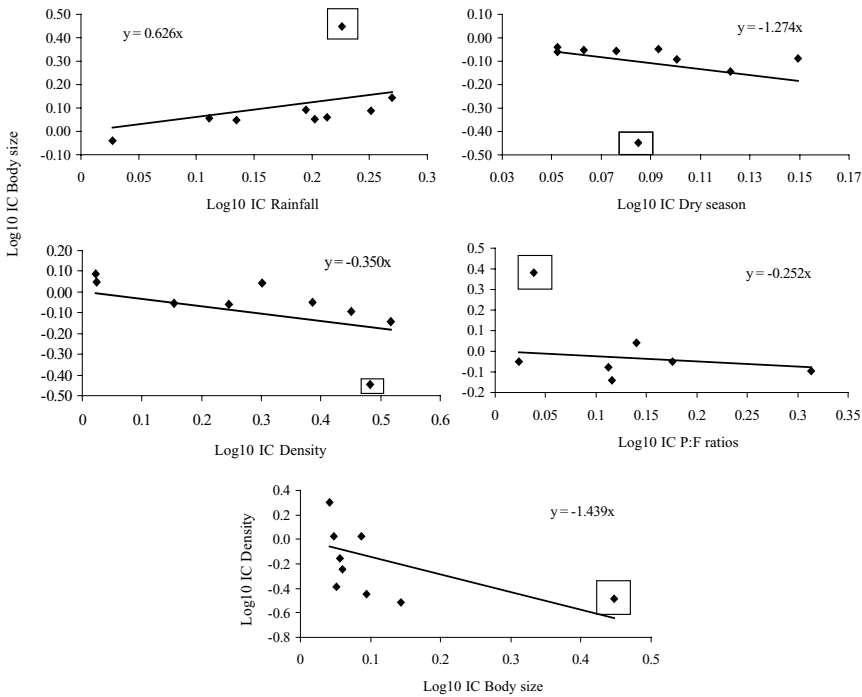


Fig. 4. IC plots of ecological correlates to body size in indriids for phylogeny 1. Boxes indicate possible IC outliers. Removal of the outliers influenced only the statistical significance for the IC density (dependent) on IC body size (independent) model.

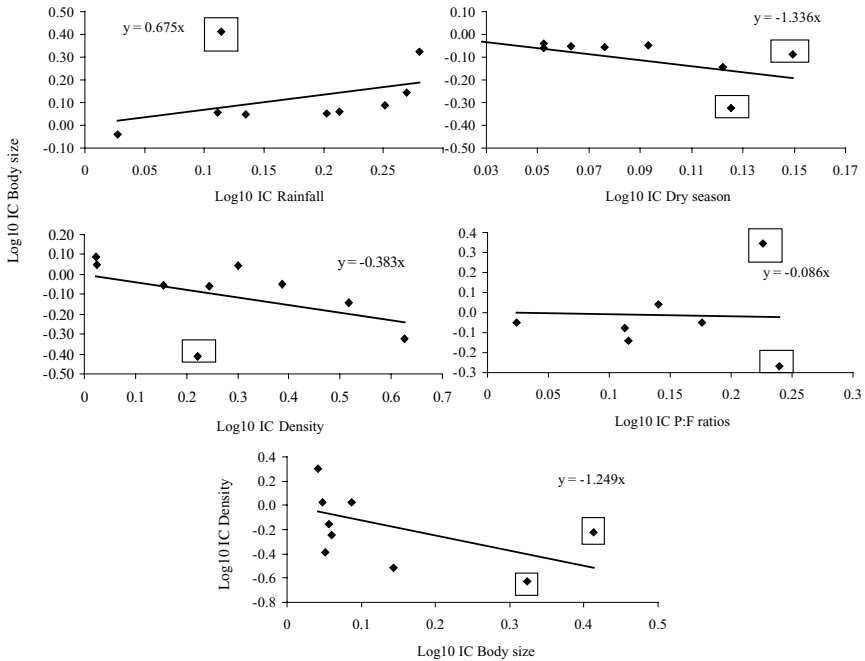


Fig. 5. IC plots of ecological correlates to body size in indriids for phylogeny 2. Boxes indicate possible IC outliers. Removal of the outliers did not alter the statistical significance threshold for any of the models.

indriid body size. Based on the data, indriid body size evolution may result from phylogenetic niche conservation and stabilizing selection. If closely related indriids had completed the invasion of ecologically similar niches and the taxa and their descendants had remained in similar environments with similar selective pressures, then stabilizing selection might have selected a body size in extant taxa that approximated that of the ancestral condition (Harvey and Pagel, 1991). Phylogenetic evidence for stabilizing selection is present when basal branch lengths are longer than terminal (species) branch lengths because phenotypic changes are small as a result of constraints (Diniz-Filho, 2004). Phylogenetic studies of lemurs provide some support for stabilizing selection as a key factor influencing indriid evolution (Pastorini *et al.*, 2001; Viguier, 2002). Specifically, Pastorini *et al.* (2001) analyzed *Propithecus* mtDNA sequences and found that branch lengths were an order of magnitude longer for basal branches compared to terminal (species) branch lengths. Researchers have also noted stabilizing selection as a strong force operating on the body size and genetic structure

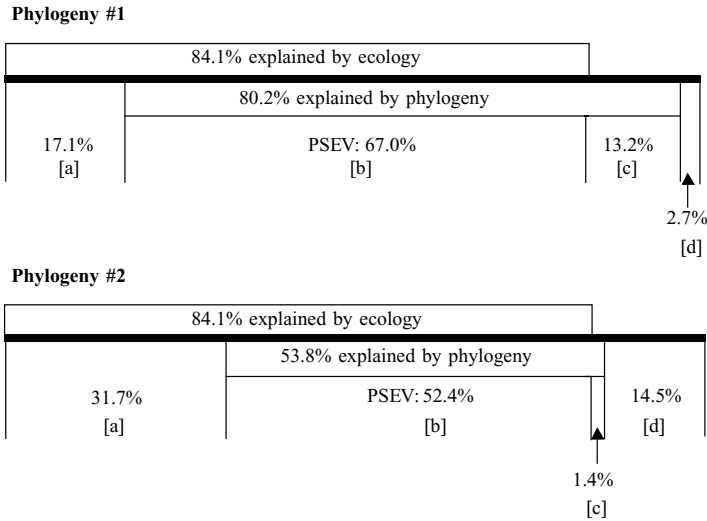


Fig. 6. Indriid body size variation (thick horizontal line) partitioned among ecology (density and P:F ratios) and phylogeny to quantify phylogenetically structured environmental variation for 2 phylogenies. Individual components are as follows: (a) ecology, (b) phylogenetically structured environmental variation, (c) phylogeny, and (d) unexplained.

of mammals (Lemos *et al.*, 2005; Peterson *et al.*, 1999; Smith *et al.*, 2004). For example, Peterson *et al.* (1999) conducted a phylogenetic study of ecological niches in 37 taxa of birds, butterflies, and mammals in Mexico. They documented niche conservatism over several million years of independent evolution, and suggested that it resulted from active constraints, i.e., stabilizing selection.

If stabilizing selection has selected for intermediate body sizes in indriids, then it is necessary to identify the constraints at each end of the body size spectrum. Ideally, the data should come from studies of individuals in which a phenotypic character, such as body size, have differential survival probabilities (Smith *et al.*, 2004). Despite the importance of the comparative life history data, most studies of body size and stabilizing selection have focused on birds and nonprimate mammals (Covas *et al.*, 2004; Endler, 1986; Peterson *et al.*, 1999). For example, Covas *et al.* (2004) investigated survival in relation to body mass in sociable weavers (*Philetairus socius*). They were able to capture, weigh, and measure 70–100% of the birds in the study area. They documented a significantly lower survival rate for juveniles and adults that were lighter or heavier than the mean body size. Covas *et al.* (2004) suggested that the selective pressures were increased

starvation risks for smaller than average individuals and increased predation rates for larger than average individuals. It would be difficult to conduct similar studies on most primates because their generally long life span, particularly for large-bodied taxa, issues with determining death vs. dispersal, and issues associated with annual capture-and-release. It is possible to suggest general patterns of differential survivability for individual individuals at different body sizes. Individuals at a smaller than average body size tend to have low fat reserves and are at greater risk for starvation (Altmann and Alberts, 2003a; Cuthill and Houston, 1997), particularly in highly seasonal environments like Madagascar (Pochron *et al.*, 2004; Sauther *et al.*, 2002; Wright, 1999). Low maternal body size also tends to be associated with reduced fertility (Altmann and Alberts, 2003b), though Pochron *et al.* (2004) suggested that fertility was not influenced by resource use in *Propithecus diadema edwardsi*. Individuals with larger than average body size are better able to deal with prolonged resource fluctuations (McNamara and Houston, 1990). Conversely, large-bodied folivores are more at risk for parasitic infections (Vitone *et al.*, 2004). Despite reports that large-bodied individuals incur higher predation pressures in birds (Ekman, 2004), recent studies indicate that large-bodied, folivorous lemurs have reduced predation rates versus smaller-bodied, sympatric taxa (Goodman, 2003; Hart, 2000; Karpanty, 2003). Karpanty (2003) observed that most avian predators attack younger, smaller individuals rather than the larger adults in folivorous *Propithecus diadema edwardsi*.

Extant individuals do not represent the largest lemurs if one includes subfossil lemurs as part of the primate community. Estimated body masses for subfossil lemur taxa are an order of magnitude higher than the heaviest extant individuals (Godfrey *et al.*, 1997). For example, *Paleopropithecus cf. ingens* was likely folivorous, weighed 35 kg, and may have survived to the point of European discovery of Madagascar in 1500 A.D. (Bachmann *et al.*, 2000; Burney *et al.*, 2004; Godfrey *et al.*, 1997). Researchers have recovered no subfossil lemur from sites in eastern humid forests (Godfrey and Jungers, 2003), where extant individuals achieve their largest adult body masses. The subfossil lemurs are from areas currently associated with dry forest habitats. Though specific extinctions may have opened new ecological space (Peres and Dolman, 2000), some niches may simply have disappeared in dry forests (Godfrey *et al.*, 1997). For example, Ganzhorn (1997) investigated lemur community composition in humid and dry forests and found that lemur communities in dry forests appear to be missing functional groups associated with the extinction of subfossil lemurs. Conversely, humid forests were at an equilibrium state, i.e., all functional dietary roles are filled. Thus, classic arguments for stabilizing selection against small body size may hold for individuals, but except for

increased parasitic loads among large individuals, may not explain selection against larger than average body size in all extant, folivorous indriids.

None of the IA or IC regression slopes for density as a function of body size differed significantly from the predicted value of $-.75$. Thus, my data support Damuth's (1981) energetic equivalent rule for indriids. However, all density-body size regression slopes are greater than the predicted value of $-.75$. Griffiths (1986) suggested that a slope greater than the predicted value of $-.75$ indicates a disproportionately greater amount of energy controlled by larger individuals. Thus, large-bodied indriids may be controlling more energy in eastern humid forests. Ganzhorn (1999) noted higher specific richness, particularly for frugivores, and greater habitat heterogeneity in eastern humid versus western dry forests. Though habitat heterogeneity is generally associated with increased opportunities to specialize and to avoid competition, Ganzhorn (1997, 1999) and Yoder *et al.* (2000) suggested that interspecific competition is an important factor influencing lemur evolution and community dynamics. Specifically, if leaves are of poor quality and fruiting resources are scarce in the more speciose eastern humid forests, then large-bodied indriids (*Indri indri*, *Propithecus diadema diadema*, and *P. d. edwardsi*) may be at an advantage in interspecific competition for scarce fruit resources (Clutton-Brock and Harvey, 1983). Fruit resources are particularly relevant to the energy hypothesis because they contain more easily extractable energy, in the form of sugars, than leaves do (Dasilva, 1992; Milton, 1999; Wasserman and Chapman, 2003).

My data support resource quality, i.e., P:F ratios, only as a covariate with density to indriid body size variations. The explanatory power of P:F models lies in the importance of protein in the primate diet. Though protein requirements per unit of body mass tend to diminish with increasing total body mass, primatologists have not determined protein requirements for most species in the wild. Oftedal (1991) suggested that most primates require little protein in their diets because they have slower growth rates than those of other mammals. Oftedal (1991) estimated that folivorous primates inhabiting low-quality habitats would require ≥ 7 –11% of their daily food intake to be protein for growth and maintenance, and 14% for reproduction. Prosimians differ from other primates in having depressed metabolic rates (Ross, 1992; Snodgrass *et al.*, 2000), which may account for their low protein needs. Moreover, protein absorption can be negatively affected by the presence of tannins in leaves (Foley and McArthur, 1994; Robbins *et al.*, 1987). Leaves eaten by indriids contain on average only 2–10% available protein per total dry mass (Ganzhorn, 1992; Powzyk, 1998). Powzyk (1998) estimated that the annual diet of *Indri indri* contained on average only 4.1% protein per total dry mass. Thus, either Oftedal's (1991)

estimates for protein requirements may not be applied to indriids or the lemurs have lower protein requirements than previously suggested.

Though I found a correlation between mean annual rainfall and indriid body size, the positive slope does not match the prediction of the resource seasonality hypothesis. However, the positive slope may actually relate to biogeographic patterns of soil characteristics and resource quality for indriids (Baden *et al.*, 2005; Ganzhorn *et al.*, 1999; Ravosa *et al.*, 1995). Ganzhorn *et al.* (1999) presented preliminary data on soil characteristics for 1 site each in eastern humid and western dry forests. They suggested that high rainfall levels result in mineral leaching and reduced forage quality in eastern humid forests. If leaching reduces leaf quality at the landscape level, then rainfall may have an indirect effect on body size variations in indriids. It is interesting to note that geophagy by indriids occurs only among taxa found in eastern humid forests (*Propithecus diadema edwardsi*, *P. d. diadema*, and *Indri indri*) and not in any taxa that range into dry forests (Krishnamani and Mahaney, 2000). Though there is some statistical support for dry season as a possible covariate to indriid body size, I suggest that length of the dry season may be a spurious correlate to variations in body mass in sifakas. Annual rainfall strongly correlates to the length of the dry season. Controlling for dry season is not negate the IA relationship of rainfall to indriid body size. Moreover, dry season is not a significant factor in the IA or IC multivariate models. Therefore, my multivariate analyses and published data on soil properties provide some support for the resource quality hypothesis.

It is important to note 4 methodological issues with determining ecological and phylogenetic correlates to indriid body size variations. First, there are few data on forest productivity and the chemical properties of lemur food items in Madagascar. Researchers have often inferred measures of forest productivity and above-ground biomass from intersite correlates between broadly similar habitat types instead of from direct measurements in each forest site (Chave *et al.*, 2004). Though *Propithecus diadema edwardsi* exploit 73–83 plant species for food (Hemingway, 1998), researchers have collected and analyzed chemical properties of only 32 total leaf samples (Ganzhorn, 1992). Issues with sample sizes are often due to the difficulty of collecting and preparing plant specimens in the field. Small sample sizes combined with lack of data on P:F ratios for foods eaten by *Avahi occidentalis* and *Propithecus diadema candidus* indicate that the relationship of the food quality variable to indriid body size should be viewed with caution. There are also few data on temporal and spatial variations in food quality for most indriids. The data are important because indriids range into and have differing diets in a variety of habitat types and forest fragments of differing sizes (Hemingway, 1998; Powzyk, 2003; Wright, 1995;

Lehman *et al.*, 2006). For example, Arrigo-Nelson (2005) found differences in seasonal patterns of leaf exploitation by *Propithecus diadema edwardsi* at logged and unlogged sites in SE Madagascar. Second, I used a phylogenetic model in which I considered all branch lengths to be equal. Though others have used the approach widely (Lindenfors and Tullberg, 1998; Purvis *et al.*, 1994; Symonds, 1999), it necessarily implies a speciation model of evolution. As Smith and Cheverud (2002) noted, there are few genetic data supporting a speciation model of evolution. Use of a speciation model requires data on all speciation events throughout the phylogeny (Garland *et al.*, 1992); there are few data on the events for lemurs. Third, the correct placement of *Indri indri* within the indriid phylogeny is important for understanding the evolutionary ecology of this monophyletic group. The methodological issues may be mitigated to some degree by my diagnostic tests and the fact that stabilizing selection is better understood via IA versus IC methods (Harvey and Pagel, 1991; Smith and Cheverud, 2002). Also, I found a generally consistent pattern for phylogenetic niche conservation for both phylogenies. Data on branch lengths for *Propithecus* are available (Pastorini *et al.*, 2001), and I hope that similar data will soon be available for *Indri* and *Avahi*. Finally, both the IA and IC models for the relationships between density and body size were sensitive to the presence of outliers. The results indicate the need for further testing with larger sample sizes of lemur densities as a function of species-specific body sizes. For example, future studies should include data on other lemur taxa, such as *Lepilemur* and *Eulemur*. Therefore, researchers using independent contrast methods to control for phylogeny should be aware that some ecology-phenotype relationships are best explained as the result of the synergistic effects of ecology and phylogeny.

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