



Test of the Optimal Body Size Model for Strepsirhines

Shawn M. Lehman,^{1,3} Mariam Nargolwalla,¹ Andrea Faulkner,² Nicole Taylor,¹ and Rochelle Lundy¹

Received March 8, 2005; revision September 30, 2005; accepted February 1, 2006;
Published Online February 15, 2007

We determined if data on strepsirhine body and home range sizes support an optimal body size (OBS) model of 100 g, as predicted from studies of energetics in terrestrial mammals. We also tested the following predictions of the OBS model: 1) relationships between body and home range sizes will change slope and sign above and below the OBS threshold of 100 g and 2) best-fit lines for OBS regression models (above and below the 100-g threshold) will intersect at ca. 100 g (range of 80–250 g). We collected data on body mass, home range size, and vertical ranging behavior for 37 strepsirhines from the literature. Linear regression analyses and phylogenetic independent contrasts methods revealed that body size is a significant determinant of both 2-dimensional (ha) and 3-dimensional (km³) home range sizes only in taxa weighing >100 g. There were consistent changes in the sign of the slopes above and below the OBS threshold. The intersections of the best-fit lines were within the OBS range for the body size to 3-dimensional home range comparisons. Thus, the data provide some support for the OBS model in strepsirhines. However, no regression model was statistically significant for the taxa below the OBS threshold, which may reflect small sample sizes. Also, no slope differed significantly between taxa above and below the OBS. Significant correlations between body and home range sizes for the complete data sets refute the \surd -shaped constraint space predicted via the OBS model.

KEY WORDS: independent contrasts; interspecific allometry; optimal body size; strepsirhines.

¹Department of Anthropology, University of Toronto, Toronto, Ontario, Canada M5S 3G3.

²Faculty of Nursing, University of Calgary, Calgary, Alberta, Canada T2N 1N4.

³To whom correspondence should be addressed; e-mail: slehman@chass.utoronto.ca.

INTRODUCTION

Mammalian body size tends to have a linear relationship to most life-history variables in logarithmic space (Leonard and Robertson, 2000). However, some allometric relationships to body size are not linear (Brown and Nicoletto, 1991; Brown *et al.*, 1993; Kelt and Van Vuren, 1999). Brown *et al.* (1993) and Brown (1995) produced a model to explain nonlinear relationships to body size in mammals. They argued that there is an energetically based optimal body size (OBS) for mammals of *ca.* 100 g (range of 80–250 g), which they referred to as M^* . The OBS is based on the following energetic definition of fitness: “. . .the rate that resources, in excess of those required for growth and maintenance of the individual, can be harvested from the environment and used for reproduction” (Brown *et al.*, 1993: 575). Thus, an optimally-sized organism is one that maximizes energy left over after growth and maintenance by converting the free energy into reproduction (Boback and Guyer, 2003). Two of the main assumptions of the OBS model are that interspecific allometric (IA) relationships between body size and ecological variables, such as home range size, should change slope and sign above and below M^* . Another assumption is that best-fit lines for OBS regression models should intersect at *ca.* 100 g (range of 80–250 g). The patterns occur because Brown *et al.* (1993) used standard allometric equations for acquisition of resources (scaled to .75 power) and transfer of energy to offspring (scaled to $-.25$ power). Thus, small-bodied individuals are best able to convert resources (energy) into reproduction, though their high metabolic needs limit the rate of resource acquisition for reproduction. Though large-bodied individuals have a greater capacity to acquire resources, they are limited in their reproductive potential. For example, Kelt and Van Vuren (1999) documented that the slopes of a body size vs. home range comparison were significantly negative below M^* and significantly positive above M^* , i.e., a \surd shaped constraint space, for 19 species of North American mammals.

Some theoretical and empirical studies do not support the OBS model. Kozlowski (1996) and Perrin (1998) criticized the assumption that the transfer of energy to offspring scales to the $-.25$ power. Use of the scaling relationship results in a prediction that female mouse lemurs (*Microcebus* spp.) weighing 33–63 g should produce more milk per day than female gorillas (*Gorilla* sp.) weighing 71–97 kg. Others have criticized the use of correlational values derived from measurements on individuals to then make inferences about body size in species (Chown and Gaston, 1997). The last assumption may be particularly problematic because of primate sexual dimorphism and the annual variations in body size that occur in many Malagasy strepsirhines (Atsalis, 1999; Clutton-Brock, 1985;

Ganzhorn and Schmid, 1998; Kappeler, 1991; Leutenegger and Cheverud, 1982; Plavcan and van Schaik, 1997; Smith and Cheverud, 2002). Some researchers have questioned the unimodal, right-skewed distribution that is inherent to the OBS model (Jones and Purvis, 1997; Kozłowski, 1996; Lovegrove and Haines, 2004). Lovegrove and Haines (2004) found that subdividing Afrotropical mammals—including primates—into specific locomotory modes—plantigrade, digitigrade, and unguligrade—resulted in a trimodal rather than unimodal pattern of body size distributions. Among empirical tests of the OBS model, Symonds' (1999) study of insectivores showed no relationship between body mass and life history variables after controlling for phylogeny. Symonds' (1999) study is one of the first to test the OBS model via phylogenetically independent contrasts (Felsenstein, 1985; Garland *et al.*, 1992, 1993). In phylogenetically IC (independent contrasts), comparisons are made at all levels of a phylogeny rather than just between species (Nunn and Barton, 2001). The comparisons are important because they provide phylogenetically independent data points, which one can then analyze via standard statistical methods. It is not yet known if predictions derived from the OBS model apply to primates and if any potential relationships will continue to exist after application of phylogenetic controls.

The Strepsirhini represents an excellent primate taxon to test the OBS model. There are data on body and home range sizes for many taxa (Table I). Strepsirhines straddle the hypothesized optimal body size of 100 g, with body sizes ranging from 33 g for *Microcebus berthae* to 6.7 kg for *Propithecus diadema diadema* (Smith and Jungers, 1997). Intersexual variations in body and home range sizes for some strepsirhines provide an additional opportunity to contrast potential energetic differences between males and females. Therefore, we examined relationships between body size and home range size in strepsirhine primates to test the OBS model. Specifically, we tested the following hypotheses: 1) the relationship between body and home range sizes will be significantly negative <100 g and significantly positive >100 g, 2) the signs of the slopes for the body size and home range size comparisons will change above and below 100 g, and 3) the best-fit lines for OBS regression models (above and below the 100-g threshold) will intersect at *ca.* 100 g (range of 80–250 g).

METHODS

We collected data on body mass and minimum home range size from the literature. Per Kelt and Van Vuren (1999), we used minimum home range size instead of estimates of mean or maximum sizes. We chose

Table I. Body size and home range size for 37 taxa of male and female strepsirrhines

| Species | Mean body size (kg) | | Minimum home range (ha) | | Minimum cubic home range (km ³ × 10 ⁻⁵) | | Minimum group size | Sources ^a |
|------------------------------|---------------------------|---------|-------------------------|---------|--|---------|--------------------|----------------------|
| | Males | Females | Males | Females | Males | Females | | |
| | <i>Microcebus berthae</i> | .033 | .033 | 4.90 | 2.50 | 2.450 | | |
| <i>M. myoxinus</i> | .037 | .037 | 4.30 | 1.00 | 4.515 | 1.050 | 1.0 | 3, 4 |
| <i>M. rufus A</i> | .043 | .042 | 7.00 | 3.00 | 9.800 | 4.200 | 1.0 | 3, 5 |
| <i>M. griseorufus</i> | .055 | .060 | 2.00 | 2.00 | 1.600 | 1.600 | 1.0 | 6 |
| <i>M. ravelobensis</i> | .056 | .062 | .40 | .60 | .396 | .558 | 1.0 | 7 |
| <i>M. murinus W</i> | .059 | .063 | 3.20 | 1.80 | 1.280 | .720 | 1.0 | 3, 8, 35 |
| <i>Galagoides demidoff</i> | .063 | .060 | .50 | .60 | 1.750 | 2.100 | 1.0 | 3, 9 |
| <i>G. zanzibariensis</i> | .149 | .137 | 1.90 | 1.60 | .950 | .800 | 1.0 | 3, 10 |
| <i>Galago moholi</i> | .187 | .173 | 1.50 | 4.40 | .600 | 1.760 | 1.0 | 3, 10 |
| <i>Cheirogaleus medius</i> | .188 | .172 | 4.00 | 4.00 | 2.800 | 2.800 | 1.0 | 3, 8, 11 |
| <i>Galago senegalensis</i> | .227 | .199 | .12 | .12 | .060 | .060 | 1.0 | 3, 12 |
| <i>Loris tartigradus</i> | .264 | .269 | 1.80 | 1.30 | .708 | .524 | 1.0 | 3, 13, 31 |
| <i>Galagoides alleni</i> | .277 | .269 | 3.00 | 8.00 | 57.000 | 15.200 | 1.0 | 3, 14 |
| <i>Mirza coquereli</i> | .304 | .326 | 4.00 | 2.50 | 2.000 | 1.250 | 1.0 | 3, 15, 33 |
| <i>Cheirogaleus major</i> | .438 | .362 | 4.00 | 4.00 | 5.200 | 5.200 | 1.0 | 3, 11 |
| <i>Phaner furcifer</i> | .460 | .460 | 3.80 | 4.00 | 2.660 | 2.800 | 1.0 | 3, 11, 32 |
| <i>Nycticebus coucang</i> | .679 | .626 | .80 | .40 | 2.640 | 1.320 | 1.0 | 3, 16 |
| <i>Haplemur griseus</i> | .748 | .670 | 2.00 | 2.00 | .133 | .133 | 4.5 | 3, 17 |
| <i>Lepilemur musidelinus</i> | .777 | .777 | .20 | .90 | .140 | .630 | 1.0 | 3, 8 |
| <i>Avahi occidentalis</i> | .814 | .777 | 3.00 | 3.00 | 2.850 | 2.850 | 1.0 | 3, 8, 18 |

Table I. Continued

| Species | Mean body size (kg) | | Minimum home range (ha) | | Minimum cubic home range (km ³ × 10 ⁻⁵) | | Minimum group size | Sources ^a |
|--------------------------------------|---------------------|---------|-------------------------|---------|--|---------|--------------------|----------------------|
| | Males | Females | Males | Females | Males | Females | | |
| | <i>A. laniger</i> | 1.030 | 1.320 | 1.00 | 1.00 | .800 | | |
| <i>Otolemur crassicaudatus</i> | 1.190 | 1.110 | 7.00 | 7.00 | 4.900 | 4.900 | 1.0 | 3, 20, 30, 35 |
| <i>Eulemur coronatus</i> | 1.280 | 1.080 | 6.00 | 6.00 | 2.344 | 2.344 | 6.4 | 3, 21 |
| <i>E. mongoz</i> | 1.410 | 1.560 | .50 | .50 | .273 | .273 | 2.8 | 3, 8 |
| <i>Hapalemur aureus</i> | 1.487 | 1.355 | 26.00 | 26.00 | 3.250 | 3.250 | 2.0 | 17 |
| <i>E. fulvus sanfordi</i> | 1.870 | 1.830 | 5.00 | 5.00 | 2.016 | 2.016 | 6.2 | 3, 21 |
| <i>E. macaco macaco</i> | 1.880 | 1.760 | 3.50 | 3.50 | .560 | .560 | 5.0 | 3, 8, 22 |
| <i>Eulemur rubriventer</i> | 1.980 | 1.940 | 15.00 | 15.00 | 15.000 | 15.000 | 2.0 | 3, 23 |
| <i>Hapalemur simus</i> | 2.150 | 1.300 | 4.00 | 4.00 | 5.500 | 5.500 | 4.0 | 3, 17 |
| <i>Eulemur fulvus rufus</i> | 2.180 | 2.250 | 9.00 | 9.00 | 3.000 | 3.000 | 6.0 | 3, 23 |
| <i>Lemur catta</i> | 2.210 | 2.210 | 6.00 | 6.00 | 2.400 | 2.400 | 5.0 | 3, 8 |
| <i>Daubentonina madagascariensis</i> | 2.620 | 2.490 | 17.30 | 35.60 | 255.450 | 53.400 | 1.0 | 3, 24 |
| <i>Propithecus verreauxi</i> | 3.250 | 2.950 | 3.00 | 3.00 | 2.250 | 2.250 | 2.0 | 3, 8, 25 |
| <i>P. tattersalli</i> | 3.390 | 3.590 | 8.00 | 8.00 | 4.000 | 4.000 | 3.0 | 3, 26 |
| <i>Varecia variegata variegata</i> | 3.630 | 3.520 | 25.00 | 25.00 | 4.688 | 4.688 | 8.0 | 3, 27, 28 |
| <i>Indri indri</i> | 5.830 | 6.840 | 17.00 | 17.00 | 33.150 | 33.150 | 2.0 | 3, 8, 29 |
| <i>P. diadema</i> | 6.500 | 6.700 | 33.00 | 33.00 | 22.000 | 22.000 | 3.0 | 3, 29 |

^a1 = Dammhahn and Kappeler, 2005; 2 = Schwab and Ganzhorn, 2004; 3 = Smith and Jungers, 1997; 4 = Schwab, 2000; 5 = Atsalis, 1998; 6 = F. Génin, pers. comm.; 7 = Weidt et al., 2004; 8 = Sussman, 1999; 9 = Charles-Dominique, 1977a; 10 = Harcourt and Bearder, 1989; 11 = Hladik et al., 1980; 12 = Grant et al., 1992; 13 = Nekaris, 2000; 14 = Charles-Dominique, 1977b; 15 = Kappeler, 1997; 16 = Wiens, 2002; 17 = Tan, 1999; 18 = Warren and Crompton, 1997; 19 = Ganzhorn et al., 1985; 20 = Nunn and Barton, 2000; 21 = Freed, 1996; 22 = Colquhoun, 1997; 23 = Overdorff, 1991; 24 = Sterling, 1993; 25 = Carrai and Lunardini, 1996; 26 = Meyers, 1993; 27 = Britt, 2000; 28 = Ratsimbazafy, 2002; 29 = Powzyk, 1998; 30 = Shoeninger et al., 1998; 31 = Nekaris and Jayewardene, 2004; 32 = Schülke, 2003; 33 = Kappeler, 2003; 34 = Goodman et al., 1993; 35 = Doyle and Bearder, 1977.

minimum home range sizes because methods primatologists commonly use, such as grid cell counts, result in overestimates of home range size (Pimley *et al.*, 2005a; Worton, 1987). We also controlled for the influence of group size on home range size by dividing minimum home range size by minimum group size for group-living strepsirhines (Leonard and Robertson, 2000; Milton and May, 1976). We selected minimum group sizes for sites where we collected body size and home range data. The control was necessary because the OBS model operates at the organismal rather than the group level. We eliminated taxa from the initial data set if body masses were available only for captive individuals and if data on body size, home range, and group size were each from different sites/protected areas. The data requirements resulted in a final data set of 37 taxa used for analyses (Table I).

Methods commonly used by researchers to estimate home range sizes may not accurately reflect the unique energy expenditures of arboreal species (Worton, 1987). Home range sizes in primates tend to measure only a 2-dimensional area (length \times width) and do not account for vertical ranging behavior (Grand, 1984). The third dimension contributes to the distance arboreal primates travel and energy they expend as well as the density of the resources they may encounter within their arboreal environment (Milton and May, 1976). Thus, we incorporated species-specific vertical ranging data into home range size to produce an approximation of home range size in 3 dimensions (length \times width \times height). The methodological issue is particularly relevant to the OBS model because it is based on and supported largely by studies of terrestrial mammals. We tested 2- and 3-dimensional measures of home range size separately as covariates to strepsirhine body size.

Though researchers believe that body size correlates strongly with phylogenetic history (Smith *et al.*, 2004), 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), we conducted a test for serial independence (*C*) to determine if there was phylogenetic autocorrelation in the body size and home range data. We conducted the tests via Phylogenetic Independence with significance levels determined via 1000 iterations of the original data set (Reeve and Abouheif, 2003). We used a consensus phylogeny Yoder (1997) produced as the main source for strepsirhine phylogenetic relationships (Fig. 1). The phylogeny was chosen because it is based on a meta-analysis of 9 genetic studies on

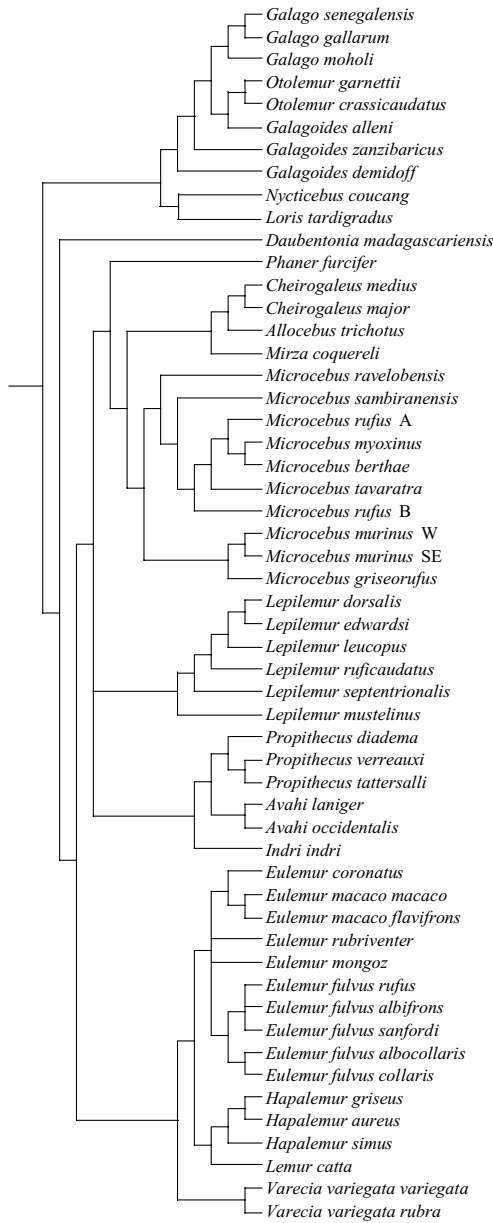


Fig. 1. The phylogeny of the strepsirhines in this study (Mayor *et al.*, 2004; Wyner *et al.*, 2000; Yoder, 1997, 2003; Yoder *et al.*, 2000).

strepsirhines, includes numerous regions of the genome, and supports many of the phylogenetic relationships reported from morphological studies. We supplemented the phylogeny with more recent genetic data (Delpero *et al.*, 2001; Mayor *et al.*, 2004; Poux and Douzery, 2004; Wyner *et al.*, 2000; Yoder *et al.*, 2000). Serial independence tests indicated significant phylogenetic autocorrelation for male body size ($C = .442$, $p = .001$) and female body size ($C = .685$, $p = .001$), but not for 2-dimensional home range size in males ($C = .169$, $p = .197$) and females ($C = .201$, $p = .171$). Further, there was no phylogenetic autocorrelation for 3-D home range sizes in males ($C = -.019$, $p = .103$) and females ($C = .054$, $p = .128$). Thus, it was necessary to control for phylogeny in the OBS analyses.

We used IC to determine the relationship between body size and home range in strepsirhines after taking their phylogenetic relatedness into account. We transformed body size and home range data via PDAP (Phenotypic Diversity Analysis Programs) to produce standardized IC data (Garland *et al.*, 2002). Because the OBS model makes no prediction about contrast values of body size, we split each strepsirhine data set into 2 phylogenetic subsets: 1) taxa whose body sizes were $< \log_{10}$ 100-g threshold and 2) taxa whose body sizes were $> \log_{10}$ 100-g threshold. IC methods require detailed information on phylogenetic relationships for the test population (Felsenstein, 1985). However, data on branch lengths are available for only some strepsirhines (Pastorini *et al.*, 2001; Yoder and Yang, 2004). Thus, we used an accepted default procedure in which we assigned the same length to all branches (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, one must adequately standardize ICs so that they have equal expected variance in subsequent regression models (Garland *et al.*, 1992). We 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 home range) are directly proportional to the contrasts in the predictor variable because the residuals are derived by regression through the origin (Diaz-Uriarte and Garland, 1996). To complete the diagnostic test, we regressed the absolute values of the residuals against the standardized contrasts in the independent variable. Again, none of the resulting correlation values should be statistically significant. If any of the diagnostic tests were significant, then we made branch length corrections via PDTREE (Garland *et al.*, 1992, 1999; Garland *et al.*, 2002).

We used linear regression analyses to determine if \log_{10} body mass (independent variable) was a significant determinant of 2-D and 3-D \log_{10} home range sizes (dependent variables) for the IA and IC data. Per Symonds (1999), we computed regression coefficients for males and females above and below the OBS threshold (i.e., 100 g). We also tested for a linear relationship between body mass and home range size for the complete male and female IA and IC data sets. We ran the regressions as a test of the proposed \surd -shaped constraint space. We used a *t*-test to determine if there was a significant difference in slopes above and below the OBS threshold within and between sexes. For IC regressions, we forced the slope of the regression equation through the origin (Garland *et al.*, 1992). We used a *t*-test to determine the probability that the slope for each IC regression model differed significantly from zero (Garland *et al.*, 1992). If the statistical probability for the IC slope was $>.05$, we accepted the null hypothesis and inferred no causal relationships. Conversely, if the statistical probability for the IC slope was $<.05$, we rejected the null hypothesis and determined that the independent variable is an important covariate of body size.

We conducted statistical analyses via SPSS 11.5 (SPSS Inc., Chicago, IL 60606). All statistical tests were 2-tailed and $\alpha = .05$.

RESULTS

There is a significant positive relationship between body size and 3-D home range sizes for male and female strepsirhines above the OBS threshold of 100 g (Table II). Moreover, there is a significant positive correlation between body size and 3-D home range size for all female strepsirhines. There is no statistically significant correlation for any of the other models. Further, there is no significant difference in slope above and below the OBS threshold for either 2-D or 3-D home range sizes in males. Despite the lack of a statistical effect, there are changes in sign above (positive slopes) and below (negative slopes) the OBS threshold for 2-D and 3-D home ranges in both males and females (Fig. 2). The intersections of the best fit lines fall within the range of OBS limits only for the 3-D measures of home range sizes in male and female strepsirhines.

We used equal branch lengths for all IC transformed data (Table III). None of the diagnostic correlations is significant, indicating that there is no statistical issue with the branch length transformation. For the IC data, body size in males above the OBS threshold correlates significantly with both 2-D and 3-D home range sizes. In female strepsirhines above the OBS threshold, body size correlates positively with 3-D home ranges. None of the other IC regression models is statistically significant for the OBS data

Table II. Regression coefficients and slope comparisons (*t*) for log10 body size and log10 home range sizes in male and female strepsirrhines

| Sex | Model | Dependent variable ^a | slope | SE of slope | R | R ² | F | p | t | P |
|--------------|---------------|---------------------------------|-------------|-------------|-------------|----------------|--------------|-------------|-------|------|
| Male | <OBS | 2-D HR | -3.125 | 1.396 | -.708 | .501 | 5.015 | .076 | | |
| | >OBS | 2-D HR | .365 | .267 | .250 | .062 | 1.860 | .185 | 2.455 | .067 |
| | <OBS | 3-D HR | -2.287 | 1.481 | -.568 | .323 | 2.383 | .184 | | |
| Female | > OBS | 3-D HR | .741 | .292 | .432 | .187 | 6.440 | .017 | 1.997 | .092 |
| | All | 2-D HR | .164 | .159 | .172 | .030 | 1.060 | .309 | | |
| | All | 3-D HR | .329 | .177 | .299 | .089 | 3.437 | .073 | | |
| | <OBS | 2-D HR | -1.050 | .952 | -.442 | .196 | 1.216 | .321 | | |
| | >OBS | 2-D HR | .323 | .224 | .263 | .069 | 2.080 | .161 | 1.404 | .148 |
| | <OBS | 3-D HR | -.694 | 1.047 | -.284 | .081 | .439 | .537 | 1.288 | .163 |
| > OBS | 3-D HR | .702 | .240 | .484 | .235 | 8.584 | .007 | | | |
| All | 2-D HR | .235 | .132 | .288 | .083 | 3.174 | .084 | | | |
| All | 3-D HR | .397 | .146 | .409 | .167 | 7.746 | .012 | | | |

Note. Statistically significant models are in bold.

^a2-D refers to home ranges (HR) measured as length × width (ha), 3-D refers to HR measured as length × width × height (km³).

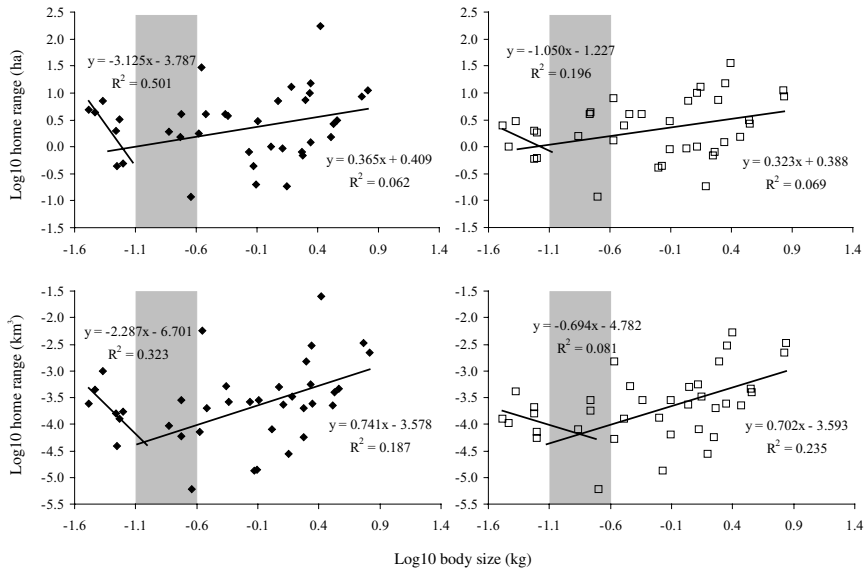


Fig. 2. Interspecific allometric relationships between log₁₀ body size and log₁₀ home range sizes (ha and km³) and for male and female strepsirhines above and below the presumed optimal body size threshold of 100 g. Males are designated by closed diamonds and females by open squares. Shaded areas refer to the log₁₀ optimal body size range (80–250 g). According to the OBS model, the intersection of the best-fit lines should occur within this range.

sets. There is no significant difference in IC regression slopes above and below the OBS thresholds for males or females, though there are consistent changes in the signs of slopes for both home range metrics. There are also significant positive correlations between body size and both 2-D and 3-D home range sizes for all male and female strepsirhines when phylogeny is taken into account.

DISCUSSION

Some of our data support the OBS model in strepsirhines. Though none of the slopes differs significantly between taxa above and below the OBS threshold, there are consistent changes in the sign of the slopes around the threshold. Specifically, all the slopes for taxa below the OBS threshold are negative, whereas the slopes for the taxa above the OBS threshold are positive. Further, controlling for phylogeny did not alter the patterns. Graphical comparisons of body and home range sizes result in a $\sqrt{\text{ }}$ -shaped

Table III. Regression coefficients and slope comparisons (*t*) for independent contrasts data on body and home range sizes in male and female strepsirrhines

| Sex | Model | Dependent variable ^a | Transformation | Best branch lengths | | | | Diagnostics ^b | | | | Slope comparisons | |
|--------|-------|---------------------------------|----------------|---------------------|-------------|-------------|----------------|--------------------------|-------------|----------|----------|-------------------|------|
| | | | | Slope | SE of slope | R | R ² | p | R residuals | R x-axis | R y-axis | t | p |
| Male | <OBS | 2-D HR | Equal | -2.194 | 2.556 | -358 | .128 | .430 | -.216 | -.013 | .327 | 1.206 | .176 |
| | >OBS | 2-D HR | Equal | .928 | .418 | .387 | .150 | .035 | .010 | .097 | -.238 | | |
| | <OBS | 3-D HR | Equal | -.495 | 3.010 | -.073 | .005 | .876 | .387 | -.013 | -.042 | .228 | .421 |
| Female | >OBS | 3-D HR | Equal | .190 | .059 | .522 | .272 | .003 | -.284 | .097 | -.236 | | |
| | All | 2-D HR | Equal | .852 | .318 | .413 | .170 | .011 | -.120 | .098 | -.084 | | |
| | All | 3-D HR | Equal | 1.082 | .342 | .471 | .222 | .003 | -.063 | .098 | -.101 | | |
| | <OBS | 2-D HR | Equal | -1.679 | 1.818 | -.382 | .146 | .398 | .480 | -.167 | -.285 | 1.287 | .163 |
| | >OBS | 2-D HR | Equal | .712 | .378 | .335 | .112 | .071 | .129 | .077 | -.351 | | |
| | <OBS | 3-D HR | Equal | -.700 | 2.148 | -.144 | .021 | .758 | .232 | -.167 | -.123 | .870 | .238 |
| | >OBS | 3-D HR | Equal | 1.198 | .391 | .501 | .251 | .005 | .273 | .077 | -.331 | | |
| | All | 2-D HR | Equal | .658 | .288 | .360 | .130 | .029 | .007 | .093 | -.303 | | |
| | All | 3-D HR | Equal | .877 | .310 | .432 | .186 | .008 | .015 | .093 | -.249 | | |

Note. Statistically significant models are in bold.

^a2-D refers to home ranges (HR) measured as length × width (ha), 3-D refers to HR measured as length × width × height (km³).

^bFirst column refers to IC correlates to residuals. Other columns refer to IC correlates to standard deviation.

constraint space in male and female strepsirhines, with the intersection of the best-fit lines within the OBS range for 3-D data. Though we recognize that there are undoubtedly issues with accuracy and precision in our vertical ranging data, the data represent an important consideration in determining an arboreal niche. Incorporating vertical ranging data into home range estimates provides a more accurate measure of the distance traveled and energy expended by arboreal primates as well as the density of the resources within their arboreal environment (Milton and May, 1976). Moreover, body size tends to be constrained to moderate sizes in arboreal mammals, such as most of the strepsirhines tested here (Bakker and Kelt, 2000), because of the physical and energetic costs of living in the forest canopy (Lovegrove and Haines, 2004). For example, arboreal taxa must be small enough for tree branches to support their body masses (Emmons, 1995). The constraints and the necessity of determining home ranges in 3-D space indicate that the OBS model may be applicable to some strepsirhines.

Despite our finding support for some aspects of the OBS model for strepsirhines, the complete data set for the 37 taxa support previous research in which body size was a significant determinant of home range size in primates (Clutton-Brock and Harvey, 1979; Mace *et al.*, 1983; Milton and May, 1976). The analyses do not support the OBS model because there should be no significant correlation between body and home range sizes for the entire data sets in males and females. In other words, there is not exclusive statistical support for a $\sqrt{\quad}$ -shaped constraint space. Other research refutes the main predictions of the OBS model (Jones and Purvis, 1997; Symonds, 1999). Lovegrove and Haines (2004) concluded that the diverse responses of mammals to natural selection in different regions should not produce a single optimum body size. For example, Jones and Purvis (1997) found no change in allometries of reproductive power above or below the OBS in chiropterans. They suggested that optimal body size was not found as a result of small sample sizes, the conservative life history characteristics of the taxon, and low variations in body masses across all chiropterans. Sample size is a potential issue in some of our data sets, particularly because we have data for only 7 taxa weighing <100 g. Nunn and Barton (2000) noted that there has been considerable debate regarding ecological correlates to body size in primates. They proposed that ecological factors, e.g., substrate use, home range overlap, and diet, confound analytical methods for determining how body size covaries with home range in primates. For example, some supposedly solitary strepsirhines—such as Mysore slender lorises (*Loris tardigradus lydekkerianus*)—form sleeping and feeding associations with conspecifics (Nekaris and Rasmussen, 2003). How can one control for group size for the supposedly solitary taxa (Pimley *et al.*, 2005b)?

Strepsirhines also have diverse dietary regimens, which may confound the OBS model. When one examines taxa representing different broad dietary categories—folivorous vs. frugivorous or omnivorous—separately, the positive relationship between body mass and home range size tends to be strengthened (Milton and May, 1976; Nunn and Barton, 2000). However, the methodology is not applicable to the question of OBS in strepsirhines because all the taxa weighing <100 g are insectivores whereas most of the taxa weighing >100 g are folivores or folivore/frugivores. Further, annual and intersite variations in the proportion of fruits vs. leaves in the diet influence primate ranging patterns (Chapman and Chapman, 1990; Chapman and Fedigan, 1990; Easley and Kinzey, 1986). Diet as a confounding variable may be particularly relevant to folivorous strepsirhines; all of which weigh >100 g. Most folivores have smaller home ranges than similarly-sized frugivores because leaves are ubiquitous compared to more widely and patchily distributed fruit resources (Clutton-Brock and Harvey, 1977; Milton and May, 1976). Finally, sociality may increase the efficiency of finding food resources, which may reduce home range size used by some group-living primates (Chapman and Fedigan, 1990).

Allometric studies of Malagasy strepsirhines may not be entirely free of the confounding effects of seasonality (Lehman *et al.*, 2005). Of the 37 primate taxa for which we have data, 78.3% ($N = 29$) are lemurs. Many lemurs undergo seasonal changes in body size, and in some cases, the variations are extreme (Wright, 1999). For example, mean monthly body masses vary significantly on a seasonal basis for female golden brown mouse lemurs (*Microcebus ravelobensis*) in the dry forests of NW Madagascar (Randrianambinina *et al.*, 2003). In male fat-tailed dwarf lemurs (*Cheirogaleus medius*), prolonged torpor results in mean body mass decreasing from 270 g before torpor to 152 g after torpor (Mueller, 1999). Further, there are seasonal variations in general activity patterns and home range use in many lemurs (Atsalis, 1999; Lemelin and Schmitt, 2004; Overdorff *et al.*, 1997). Brown mouse lemurs (*Microcebus rufus*) undergo prolonged seasonal torpor and reduced activity periods in the humid forests of eastern Madagascar (Atsalis, 1999; Randrianambinina *et al.*, 2003). Sussman (1992) notes that ring-tailed lemurs (*Lemur catta*) will adjust their home range sizes in different habitats. Therefore, the effects of seasonality and habitat variations on lemur body size and home range size may result in large standard deviations for any mean values. As a consequence of the variation, the biological and statistical significance of any resulting regression or correlation analyses may be questionable.

It is important to note some phylogenetic issues in our data. Our use of a phylogenetic model in which we considered all branch lengths to be equal necessarily implies a speciation model of evolution (Garland *et al.*, 1992).

Use of a speciation model requires data on all speciation events throughout the phylogeny (Purvis *et al.*, 1994). Smith and Cheverud (2002) note that there are few genetic data supporting a speciation model of primate evolution. Also, it is not known if the unresolved trichotomy of cheirogalids, lepilemurids, and indriids represents a hard or soft polytomy (Yoder, 2003). For example, genetic studies of lemurs result in differing phylogenies depending on phylogenetic method (parsimony, maximum likelihood) and which genes are used (Delpero *et al.*, 2001; Hapke *et al.*, 2005; Pastorini *et al.*, 2002). In addition, there is considerable debate regarding lorisiid systematics (Groves, 2001; Masters *et al.*, 2005; Yoder, 2005). Branch length data are becoming available for many lemurs (Pastorini *et al.*, 2001; Yoder and Yang, 2004), and we hope that a complete data set will soon be available for strepsirhines. The phylogenetic data will ultimately increase the power of phylogenetic controls, providing a better understanding of the applicability of the OBS model to strepsirhines.

In conclusion, we found some support for the OBS model for IA and IC data on body and 3-D home range size comparisons in strepsirhines. Specifically, we confirmed that relationships between body size and home range size changed sign above and below 100 g and that the best-fit lines for the 3-D home range models intersect within the predicted range of 80–250 g. However, none of the IA or IC regression models is statistically significant for the taxa below the OBS threshold, which may reflect issues with small sample sizes. Further, none of the slopes is significantly different above and below the OBS threshold. Also, significant correlations between body and home range sizes for the complete data sets do not provide exclusive support for the \surd -shaped constraint space implicit in the OBS model. A complete test of the OBS model in strepsirhines requires increased sample sizes for taxa weighing <100 g, more accurate data on 3-D home range sizes, measures of other characteristics, e.g., age at weaning, maximum lifespan, annual fecundity, and more robust phylogenetic measures.

ACKNOWLEDGMENTS

We thank Prof. Joerg Ganzhorn and Fabien Genin for providing unpublished data on body and home range sizes in *Microcebus griseorufus*, Richard Smith for advice on phylogenetic contrasts methods, as well as Michael Schillaci and the 2 reviewers for excellent comments on previous drafts of the manuscript. Our research was supported in part by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada, Connaught Foundation, an Ontario Graduate Scholarship, and The University of Toronto.

REFERENCES

- Abouheif, E. (1999). A method for testing the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.* 1: 895–909.
- Atsalis, S. (1998). *Feeding Ecology and Aspects of Life History in Microcebus rufus (Family Cheirogaleidae, Order Primates)*. Unpublished Ph.D. dissertation, City University of New York, New York.
- Atsalis, S. (1999). Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *Int. J. Primatol.* 20: 883–910.
- Bakker, V. J., and Kelt, D. A. (2000). Scale-dependent patterns in body size distributions of Neotropical mammals. *Ecology* 81: 3530–3547.
- Blomberg, S. P., Garland, T., Jr., and Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more liable. *Evolution* 57: 717–745.
- Boback, S. M., and Guyer, C. (2003). Empirical evidence for an optimal body size in snakes. *Evolution* 57: 345–351.
- Britt, A. (2000). Diet and feeding behaviour of the black-and-white ruffed lemur (*Varecia variegata variegata*) in the Betampona Reserve, eastern Madagascar. *Folia Primatol.* 71: 133–141.
- Brown, J. H. (1995). *Macroecology*. University of Chicago Press, Chicago.
- Brown, J. H., Marquet, P. A., and Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *Am. Nat.* 142: 573–584.
- Brown, J. H., and Nicoletto, P. F. (1991). Spatial scaling of species composition: Body masses of North American land mammals. *Am. Nat.* 138: 1478–1512.
- Carrai, V., and Lunardini, A. (1996). Activity patterns and home range use of two groups of *Propithecus v verreauxi* in the Kirindy Forest. *Primate Rep.* 46: 275–284.
- Chapman, C. A., and Chapman, L. J. (1990). Dietary variability in primate populations. *Primates* 3: 121–128.
- Chapman, C. A., and Fedigan, L. M. (1990). Dietary differences between neighboring *Cebus capucinus* groups: Local traditions, food availability or responses to food profitability? *Folia Primatol.* 54: 177–186.
- Charles-Dominique, P. (1977a). *Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa*. Columbia University Press, New York.
- Charles-Dominique, P. (1977b). Urine marking and territoriality in *Galago alleni* (Waterhouse, 1837-Lorisoidea, Primates)—A field study by radio-telemetry. *Zeit. Tierpsychol.* 43: 113–138.
- Cheverud, J. M., Dow, M. M., and Leutenegger, W. (1985). The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. *Evolution* 39: 1335–1351.
- Chown, S. L., and Gaston, K. J. (1997). The species-body size distribution: Energy, fitness and optimality. *Funct. Ecol.* 11: 365–375.
- Clutton-Brock, T. H. (1985). Size, sexual dimorphism, and polygyny in primates. In Jungers, W. L. (ed.), *Size and Scaling in Primate Biology*. Plenum Press, New York, pp. 51–60.
- Clutton-Brock, T. H., and Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool. (Lond.)* 183: 1–39.
- Clutton-Brock, T. H., and Harvey, P. H. (1979). Home range size, population density and phylogeny in primates. In Smith, E. O. (ed.), *Primate Ecology and Human Origins: Ecological Influences on Social Organization*. Garland, New York, pp. 201–214.
- Colquhoun, I. C. (1997). *A Predictive Socioecological Study of the Black Lemur (Eulemur macaco macaco) in Northwestern Madagascar*. Unpublished Ph.D. dissertation, Washington University, St. Louis, MO.
- Dammhahn, M., and Kappeler, P. M. (2005). Social system of *Microcebus berthae*, the World's smallest primate. *Int. J. Primatol.* 26: 407–435.
- Delpero, M., Masters, J. C., Cervella, P., Crovella, S., Ardito, G., and Rumpler, Y. (2001). Phylogenetic relationships among the Malagasy lemuriforms (Primates: Strepsirrhini) as

- indicated by mitochondrial sequence data from the 12S rRNA gene. *Zool. J. Linn. Soc.* 133: 83–103.
- Diaz-Uriarte, R., and Garland, T., Jr. (1996). Testing hypotheses of correlated evolution using phylogenetically independent contrasts: Sensitivity to deviations from Brownian motion. *Syst. Biol.* 45: 27–47.
- Doyle, G. A., and Bearder, S. K. (1977). The galagines of South Africa. In PR III and GH Bourne, G. H. (eds.), *Primate Conservation*. Academic Press, New York, pp. 1–35.
- Easley, S. P., and Kinzey, W. G. (1986). Territorial shift in the yellow-handed titi monkey (*Callicebus torquatus*). *Am. J. Primatol.* 11: 307–318.
- Emmons, L. H. (1995). Mammals of rain forest canopies. In Lowman, M. D., and Nadkarni, N. M. (eds.), *Forest Canopies*. Academic Press, New York, pp. 199–223.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* 125: 1–15.
- Freed, B. (1996). *Co-occurrence Among Crowned Lemurs* (Lemur coronatus) and *Sanford's Lemurs* (Lemur fulvus sanfordi) of Madagascar. Unpublished Ph.D. dissertation, Washington University, St. Louis, MO.
- Ganzhorn, J., Abraham, J. P., and Razahanahoera-Rakotomalala, M. (1985). Some aspects of the natural history and food selection of *Avahi laniger*. *Primates* 26: 452–463.
- Ganzhorn, J. U., and Schmid, J. (1998). Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. *Int. J. Primatol.* 19: 785–796.
- Garland, T., Jr., Dickerman, A. W., Janis, C. M., and Jones, J. A. (1993). Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* 42: 265–292.
- Garland, T., Jr., Harvey, P. H., and Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41: 18–32.
- Garland, T., Jr., Midford, P. E., and Ives, A. R. (1999). An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am. Zool.* 39: 374–388.
- Garland, T., Jr., Midford, P. E., and Jones, J. A. (2002). PDAP: Phenotypic Diversity Analysis Programs: 6.0, Department of Biology, University of California-Riverside, Riverside.
- Goodman, S. M., O'Connor, S., and Langrand, O. (1993). A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York, pp. 51–66.
- Grand, T. I. (1984). Motion economy within the canopy: Four strategies for mobility. In Rodman, P. S., and Cant, J. G. H. (eds.), *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes*. Columbia University Press, New York, pp. 54–72.
- Grant, J. W. A., Chapman, C., and Richardson, K. S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behav. Ecol. Socio.* 31:149–161.
- Groves, C. P. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.
- Hapke, A., Fietz, J., Nash, S. D., Rakotondravony, D., Rakotosamimanana, B., Ramanamanjato, J.-B., Randria, G. F. N., and Zischler, H. (2005). Biogeography of dwarf lemurs: Genetic evidence for unexpected patterns in southeastern Madagascar. *Int. J. Primatol.* 26: 873–901.
- Harcourt, C. S., and Bearder, S. K. (1989). A comparison of *Galago moholi* in South Africa with *Galago zanzibaricus* in Kenya. *Int. J. Primatol.* 10: 35–45.
- Hladik, C. M., Charles-Dominique, P., and Petter, J. J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*. Academic Press, New York, pp. 41–73.
- Jones, K. E., and Purvis, A. (1997). An optimum body size for mammals? Comparative evidence from bats. *Funct. Ecol.* 11: 751–756.
- Kappeler, P. M. (1991). Patterns of sexual size dimorphism in body weight among prosimian primates. *Folia Primatol.* 57: 132–146.

- Kappeler, P. M. (1997). Intrasexual selection in *Mirza coquereli*: Evidence for scramble competition polygyny in a solitary primate. *Behav. Ecol. Socio.* 41: 115–127.
- Kappeler, P. M. (2003). *Mirza coquereli*, Coquerel's dwarf lemur. In Goodman, S. M., and Benstead, J. (eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 1316–1318.
- Kelt, D. A., and Van Vuren, D. (1999). Energetic constraints and the relationship between body size and home range area in mammals. *Ecology* 80: 337–340.
- Kozłowski, J. (1996). Energetic definition of fitness? Yes, but not that one. *Am. Nat.* 147: 1087–1091.
- Lehman, S. M., Mayor, M., and Wright, P. C. (2005). Ecogeographic size variations in sifakas: A test of the resource seasonality and resource quality hypotheses. *Am. J. Phys. Anthropol.* 126: 318–328.
- Lemelin, P., and Schmitt, D. (2004). Seasonal variation in body mass and locomotor kinetics of the fat-tailed dwarf lemur (*Cheirogaleus medius*). *J. Morph.* 260: 65–71.
- Leonard, W. R., and Robertson, M. L. (2000). Ecological correlates of home range variation in primates: Implications for hominid evolution. In Boinski, S., and Garber, P. A. (eds.), *One the Move: How and Why Animal Travel in Groups*. University of Chicago Press, Chicago, pp. 628–648.
- Leutenegger, W., and Cheverud, J. M. (1982). Correlates of sexual dimorphism in primates: Ecological and size variables. *Int. J. Primatol.* 3: 387–402.
- Lovegrove, B. G., and Haines, L. (2004). The evolution of placental mammal body sizes: Evolutionary history, form, and function. *Oecologia* 138: 13–27.
- Mace, G. M., Harvey, P. H., and Clutton-Brock, T. H. (1983). Vertebrate home-range size and energetic requirements. In Swingland, I. R., and Greenwood, P. J. (eds.), *The Ecology of Animal Movement*. Clarendon Press, Oxford, pp. 32–53.
- Masters, J. C., Anthony, N. M., de Wit, M. J., and Mitchell, A. (2005). Reconstructing the evolutionary history of the Lorisidae using morphological, molecular, and geological data. *Am. J. Phys. Anthropol.* 127: 465–480.
- Mayor, M., Sommer, J. A., Houck, M. L., Zaonarivelo, J. R., Wright, P. C., Ingram, C., Engel, S. R., and Louis, E. E. (2004). Specific status of *Propithecus* spp. *Int. J. Primatol.* 25: 875–900.
- Meyers, D. M. (1993). *The Effects of Resource Seasonality on Behavior and Reproduction in the Golden-Crowned Sifaka (Propithecus tattersalli) in Three Malagasy Forests*. Unpublished Ph.D. dissertation, Duke University, Durham.
- Milton, K., and May, M. L. (1976). Body weights, diet and home range area in primates. *Nature* 259: 459–462.
- Mueller, A. E. (1999). Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): Inferences from body weights and trapping data. *Am. J. Primatol.* 49: 265–280.
- Nekaris, K. A. I. (2000). *The Socioecology of the Mysore Slender Loris (Loris tardigradus lydekkerianus) in Dindigul, Tamil Nadu, South India*. Unpublished Ph.D. dissertation, Washington University, St. Louis, MO.
- Nekaris, K. A. I., and Jayewardene, J. (2004). Survey of the slender loris (Primates, Lorisidae Gray, 1921: *Loris tardigradus* Linnaeus, 1758 and *Loris lydekkerianus* Cabrera, 1908) in Sri Lanka. *J. Zool.* 262: 327–338.
- Nekaris, K. A. I., and Rasmussen, D. T. (2003). Diet and feeding behavior of Mysore slender lorises. *Int. J. Primatol.* 24: 33–46.
- Nunn, C. L., and Barton, R. A. (2000). Allometric slopes and independent contrasts: A comparative test of Kleiber's Law in primate ranging patterns. *Am. Nat.* 156: 519–533.
- Nunn, C. L., and Barton, R. A. (2001). Comparative methods for studying primate adaptation and allometry. *Evol. Anthropol.* 10: 81–98.
- Overdorff, D. J. (1991). *Ecological Correlates to Social Structure in Two Prosimian Primates: Eulemur fulvus rufus and Eulemur rubriventer in Madagascar*. Unpublished Ph.D. dissertation, Duke University, Durham.
- Overdorff, D. J., Strait, S. G., and Telo, A. (1997). Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. *Am. J. Primatol.* 43: 211–223.

- Pastorini, J., Forstner, M. R. J., and Martin, R. D. (2001). Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. *Am. J. Primatol.* 53: 1–17.
- Pastorini, J., Forstner, M. R. J., and Martin, R. D. (2002). Phylogenetic relationships among Lemuridae (Primates): Evidence from mtDNA. *J. Hum. Evol.* 43: 463–478.
- Perrin, N. (1998). On body size, energy, and fitness. *Funct. Ecol.* 12: 500–502.
- Pimley, E. R., Bearder, S. K., and Dixon, A. F. (2005a). Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. *Int. J. Primatol.* 26: 191–206.
- Pimley, E. R., Bearder, S. K., and Dixon, A. F. (2005b). Social organization of the Milne-Edward's potto. *Am. J. Primatol.* 66: 317–330.
- Plavcan, J. M., and van Schaik, C. P. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 103: 37–68.
- Poux, C., and Douzery, E. J. P. (2004). Primate phylogeny, evolutionary rate variations, and divergence times: A contribution from the nuclear gene IRBP. *Am. J. Phys. Anthropol.* 124: 1–16.
- Powzyk, J. A. (1998). *The Socio-ecology of Two Sympatric Indrids, Propithecus diadema diadema and Indri indri: A Comparison of Feeding Strategies and Their Possible Repercussions on Species-Specific Behaviors*. Unpublished Ph.D. dissertation, Duke University, Durham.
- Purvis, A., Gittleman, J. L., and Luh, H.-K. (1994). Truth or consequences: Effects of phylogenetic accuracy on 2 comparative methods. *J. Theor. Biol.* 167: 293–300.
- Randrianambinina, B., Rakotondravony, D., Radespiel, U., and Zimmermann, E. (2003). Seasonal changes in general activity, body mass and reproduction of two small nocturnal primates: A comparison of the golden brown mouse lemur (*Microcebus ravelobensis*) in Northwestern Madagascar and the brown mouse lemur (*Microcebus rufus*) in Eastern Madagascar. *Primates* 44: 321–331.
- Ratsimbazafo, J. (2002). *On the Brink of Extinction and the Process of Recovery: Responses of Black-and-White Ruffed Lemurs (Varecia variegata variegata) to Disturbance in Manombo Forest, Madagascar*. Unpublished Ph.D. dissertation, Stony Brook University, Stony Brook, NY.
- Reeve, J., and Abouheif, E. (2003). Phylogenetic Independence: 2.0, Department of Biology, McGill University, Montreal.
- Schülke, O. (2003). *Phaner furcifer*, fork-marked lemur, vakihandry, tanta. In Goodman, S. M., and Benstead, J. (eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 1318–1320.
- Schwab, D. (2000). A preliminary study of spatial distribution and mating system of pygmy mouse lemurs (*Microcebus myoxinus*). *Am. J. Primatol.* 51: 41–60.
- Schwab, D., and Ganzhorn, J. (2004). Distribution, population structure and habitat use of *Microcebus berthae* compared to those of other sympatric Cheirogalids. *Int. J. Primatol.* 25: 307–330.
- Shoenering, M., Iwaniec, U. T., and Nash, L. T. (1998). Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Oecologia* 113: 222–230.
- Smith, F. A., Brown, J. H., Haskell, J. P., Lyons, S. K., Alroy, J., Charnov, E. L., Dayan, T., Enquist, B. J., Ernest, S. K. M., Hadly, E. A., Jones, K. E., Kaufman, D. M., Marquet, P. A., Maurer, B. A., Niklas, K. J., Porter, W. P., Tiffney, B., and Willig, M. R. (2004). Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *Am. Nat.* 163: 672–691.
- Smith, R. J., and Cheverud, J. M. (2002). Scaling of sexual dimorphism in body mass: A phylogenetic analysis of Rensch's Rule in primates. *Int. J. Primatol.* 23: 1195–1135.
- Smith, R. J., and Jungers, W. L. (1997). Body mass in comparative primatology. *J. Hum. Evol.* 32: 523–559.
- Sterling, E. (1993). Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy Mangabe. In Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York, pp. 1–10.
- Sussman, R. W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol.* 13: 395–413.

- Sussman, R. W. (1999). *Primate Ecology and Social Structure: Lorises, Lemurs, Tarsiers*. Pearson Custom Publishing, Needham Heights, MA.
- Symonds, M. R. E. (1999). Insectivore life histories: Further evidence against an optimum body size for mammals. *Funct. Ecol.* 13: 508–513.
- Tan, C. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int. J. Primatol.* 20: 547–566.
- Warren, R. D., and Crompton, R. H. (1997). A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *J. Zool.* 243: 397–415.
- Wiens, F. (2002). *Behavior and Ecology of Wild Slow Lorises (Nycticebus coucang): Social Organization, Infant Care System, and Diet*. Unpublished Ph.D. dissertation, Bayreuth University, Bayreuth.
- Worton, B. J. (1987). A review of models of home range for animal movement. *Ecol. Model.* 38: 277–298.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *Yrbk. Phys. Anthropol.* 42: 31–42.
- Wyner, Y., DeSalle, R., and Absher, R. (2000). Phylogeny and character behavior in the family Lemuridae. *Mol. Phylog. Evol.* 15: 124–134.
- Yoder, A. D. (1997). Back to the future: A synthesis of strepsirhine systematics. *Evol. Anthropol.* 6: 11–22.
- Yoder, A. D. (2003). Phylogeny of the lemurs. In Goodman, S. M., and Benstead, J. (eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 1242–1247.
- Yoder, A. D. (2005). Perfect congruence of molecular-phylogenetic and fossil-record divergence age estimates for the Lorisiiformes. *Am. J. Phys. Anthropol.* (Suppl) 40: 227–228.
- Yoder, A. D., Rasoloarison, R. M., Goodman, S. M., Irwin, J. A., Atsalis, S., Ravosa, M. J., and Ganzhorn, J. U. (2000). Remarkable species diversity in Malagasy mouse lemurs (Primates, *Microcebus*). *Proc. Natl. Acad. Sci. USA* 97: 11325–11330.
- Yoder, A. D., and Yang, Z. (2004). Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. *Mol. Ecol.* 13: 757–773.