

Bioenergetic Constraints on Primate Abundance

David A. Raichlen · Adam D. Gordon ·
Wes Sechrest

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Abstract Explaining variation in primate population densities is central to understanding primate ecology, evolution, and conservation. Yet no researchers to date have successfully explained variation in primate population density across dietary class and phylogeny. Most previous work has focused on measures of food availability, as access to food energy likely constrains the number of individuals supported in a given area. However, energy output may provide a measure of energy constraints on population density that does not require detailed data on food availability for a given taxon. Across mammals, many studies have shown that population densities generally scale with body mass^{-0.75}. Because individual energy expenditures scale with body mass^{0.75}, population energy use (the product of population density and individual energy use) does not change with body mass, which suggests the existence of energy constraints on population density across body sizes, i.e., taxa are limited to a given amount of energy use, constraining larger taxa to lower densities. We examined population energy use and individual energy expenditure in primates and tested this energy equivalence across body mass. We also used a residual analysis to remove the effects of body mass on primate population densities and energy expenditures using basal metabolic rates (BMR; kcal/d) as a proxy for total daily energy expenditure. After taking into account phylogeny, population energy use did not significantly correlate with body mass. Larger primates, which use more energy per day, live at lower population densities than smaller primates. In addition, we found a significant negative correlation between residuals of BMR from body mass and residuals of population density from body mass after taking phylogeny into account. Thus, energy costs constrain population density across a diverse sample of

D. A. Raichlen (✉)
Department of Anthropology, University of Arizona, Tucson, AZ 85721, USA
e-mail: raichlen@email.arizona.edu

A. D. Gordon
Department of Anthropology, University at Albany—SUNY, Albany, NY 12222, USA

W. Sechrest
Global Wildlife Conservation, San Francisco, CA, USA

primates at a given body mass, and primate species that have relatively low BMRs exist at relatively high densities. A better understanding of the determinants of primate energy costs across geography and phylogeny will ultimately help us explain and predict primate population densities.

Keywords Allometric scaling · Basal metabolic rate · Energetics · Energy equivalence rule · Population density · Resting metabolic rate

Introduction

Primate population densities vary in time and space, and understanding this variation is an essential component of primate ecological studies (Chapman *et al.* 2004). Most of the variation in primate population densities is explained by body mass, with larger bodied primates living in lower local densities than smaller bodied primates (Damuth 1987; Fa and Purvis 1997). The negative correlation between body mass and population density is often attributed to resource limitations because larger bodied primates require greater total food resources owing to increased total energy expenditures, and therefore cannot live at high local densities.

There is strong evidence that energy costs constrain, to some degree, population densities in a wide range of taxonomic groups (Brown *et al.* 2004). Across taxa, including mammals, birds, invertebrates, and land plants, population densities generally scale with body mass^{-3/4}, whereas basal metabolic rates (BMRs) scale with body mass^{3/4} (Damuth 1987; Enquist *et al.* 1998; Enquist and Niklas 2001; Marquet *et al.* 1990; Nee *et al.* 1991; Savage *et al.* 2004; West *et al.* 1997; *cf.* Capellini *et al.* in press; Sieg *et al.* 2009; White *et al.* 2009). Thus, total population energy expenditure (BMR × population density; kcal day⁻¹ km⁻²) is independent of body mass (Damuth 1981, 1987), and this relationship is generally termed the Energy Equivalence Rule (EER). The EER suggests that basal metabolism constrains population density such that a given area can support only a fixed amount of energy consumption for a given species.

Here, we examine how and why resource limitations constrain primate population densities from a bioenergetics perspective. Many ecologists have examined this relationship because it suggests that energy requirements and environmental productivity interact to constrain population densities in mammals (White *et al.* 2007a). Support for the EER is often based on examinations of the scaling exponent of population density and body mass, assuming that metabolic costs scale with body mass^{0.75} (Allen *et al.* 2002; Enquist *et al.* 1998). However, several studies analyzing the scaling of population density with body mass have critiqued the EER and suggest that energy use may not strongly constrain abundance. One major problem with many previous studies critiquing the EER is the assumption that energy requirements always scale with body mass raised to the 0.75 power, and most critiques of EER focus only on deviations of the population density vs. body mass scaling exponent from -0.75 (Blackburn and Gaston 1999; Blackburn *et al.* 1993; Cohen *et al.* 2003; Greenwood *et al.* 1996; Griffiths 1992; Russo *et al.* 2003). Although BMR generally scales with body mass^{0.75} over large carefully compiled data sets (Savage *et al.* 2004), it is possible to find variation in subsets of these larger

comprehensive samples (Capellini *et al.* [in press](#); Isaac and Carbone [in press](#); Sieg *et al.* [2009](#); White *et al.* [2007b, 2009](#)).

Thus, to test the EER in a group of taxa, one must include an estimate of population energy use, or at least determine the scaling of metabolic costs and body mass within the sample. In addition, we must account for the evolutionary relationships among the taxa in a given sample (Felsenstein [1985](#)). BMR carries a strong phylogenetic signal (Blomberg *et al.* [2003](#); Capellini *et al.* [in press](#); Freckleton *et al.* [2002](#)), suggesting that important relationships may be lost when phylogeny is not taken into account, and that it is essential to understand the relationship between BMR and population density after the correlated evolution of BMR among taxa is taken into account (Capellini *et al.* [in press](#); Garland and Ives [2000](#)). Because individual species are not independent data points, violations of the EER found using traditional methods may not remain when phylogeny is taken into account.

If metabolic energy expenditure (e.g., BMR) constrains primate population density, then we can hypothesize that the availability of resources (i.e., energy intake) must also constrain population densities. Several researchers have examined this resource limitation hypothesis in primates from the perspective of forest productivity (Janson and Chapman [1999](#)). However, total forest productivity is notoriously difficult to measure (Janson and Chapman [1999](#)), and researchers often use surrogates such as annual rainfall totals or the ratio of protein to fiber in leaf resources. Using these surrogates, researchers have predicted primate community biomasses, and in some cases individual species population densities, with varying degrees of success (Chapman and Chapman [1999](#); Davies [1994](#); Dunbar [1992](#); Fimbel [1994](#); Gupta and Chivers [1999](#); Janson and Chapman [1999](#); Peres [1997](#); Mendes Pontes [1999](#); Milton [1982](#); Terborgh and van Schaik [1987](#)). Often, predictions are successful only when the diet class or phylogenetic group is restricted (e.g., when population density is predicted for folivores only, or for platyrrhines only) suggesting that it is very difficult to make more general arguments about constraints on primate abundance patterns across the entire order. We examine the other side of the resource limitation hypothesis by investigating the role of individual metabolic energy costs in determining primate abundance. Instead of relying on forest productivity, we test the hypothesis that individual and population-level energy costs limit primate population densities. This hypothesis would explain both the relationship between body size and population density in primates, as well as variation in population densities at a given size.

Hypothesis Testing and Predictions

To test the hypothesis that bioenergetics constrains population densities in primates, we examine the relationship between BMR and population density across the order. Although total energy expended (TEE) is likely the preferred variable to use in this type of study, BMR generally encompasses a large portion of TEE in mammals, BMR correlates with TEE, and the slope of this relationship does not significantly differ from unity (Ricklefs *et al.* [1996](#)). In addition, the relationship between BMR and TEE remains highly significant after removing the effects of body mass on each variable (Ricklefs *et al.* [1996](#)), and BMR also correlates with a number of life history traits (White and Seymour [2004](#)). Thus, BMR is likely proportional to TEE across a

large sample. Further, although TEE has been measured for only 3 nonhuman primates (*Alouatta palliata*: Nagy and Milton 1979; *Lepilemur ruficaudatus*: Drack *et al.* 1999; and *Microcebus murinus*: Schmid and Speakman 2000), BMR is available for substantially more taxa. For the three primates for which TEE is available, BMRs make up between 30% and 50% of measured TEE (Drack *et al.* 1999; Nagy and Milton 1979; Schmid and Speakman 2000).

If energy requirements limit primate population densities, then we predict that the energy used by a population—proportional to the product of population density and BMR—should not change with increasing body mass in primates. This prediction is based on the fact that larger animals have higher BMRs, and thus these taxa should live at lower population densities than smaller taxa. In addition, if this prediction is correct, then BMR relative to body mass should correlate negatively with population density relative to body mass (e.g., relatively high BMRs should be associated with relatively low population densities). It is important to note that, owing to the known phylogenetic signal carried by BMR in mammals (Blomberg *et al.* 2003; Capellini *et al.* in press; Freckleton *et al.* 2002), these results should be tested using phylogenetic comparative methods. Finally, it is possible that dietary differences in a sample can confound analyses of EER (Marquet *et al.* 1995; Russo *et al.* 2003). We include diet in our analysis to account for the possibility that primate dietary preferences affect the relationship between population density and BMR across our sample.

Methods

We collected data for BMR and population density from published sources ($n=26$; Table 1). Body masses used in the population density analyses are mean female body mass for each species (see Table 1 for sources). If metabolic rate data from multiple individuals of the same species were available, we pooled data and calculated mean BMRs for inclusion in this study. If data were available for both sexes, means were taken. Although other sources include data from studies of both basal and resting metabolism (RMR; Snodgrass *et al.* 2007), we used only data from studies that collected basal metabolism (i.e., subjects were resting, normothermic, postabsorptive, inactive, and conscious). Because RMR is calculated under conditions that differ significantly across studies, we cannot assume that RMR is proportional to TEE across these studies. In addition, many primate BMR data points come from studies of juveniles. Juvenile BMRs often differ from those of adults (Glazier 2005), so we excluded all studies of juveniles from the data set (exclusion criterion: body mass was >30% below mean female body mass for that species). Although these criteria limit the sample size, they allow us to be sure that we are comparing adult metabolic data collected under similar conditions such that BMRs can be considered proportional to TEE.

We examined energy equivalence by calculating population energy use as the product of population density and BMR. We investigated relationships between BMR and population density further via a residual analysis. Although multiple regression may be preferred over residuals to investigate the relationship between population density and BMR at a given body size, we used 2 sets of body mass

Table I Primate data included in this analysis

Species	BMR (kcal/day)	Body mass (kg)	BMR reference	Population density (indiv./km ²)	Body mass (kg)	Diet
<i>Alouatta palliata</i>	231.9	4.67	Milton <i>et al.</i> (1979)	51.0 ^a	5.28 ^c	FL
<i>Aotus trivirgatus</i>	51.6	0.915	Scholander <i>et al.</i> (1950)	100 ^a	0.736 ^d	FR
<i>Callithrix jacchus</i>	22.8	0.360	White and Seymour (2003)	900 ^a	0.381 ^d	I
<i>Cercocebus torquatus</i>	196.2	4.00	Bruhn (1934)	12.3 ^b	5.50 ^d	FR ^c
<i>Cercopithecus mitis</i>	398.1	8.649	Muller <i>et al.</i> (1983)	42.0 ^a	4.25 ^d	FL
<i>Colobus guereza</i>	357.9	10.45	Muller <i>et al.</i> (1983)	112 ^a	9.20 ^d	FL
<i>Eulemur fulvus</i>	87.5	2.374	Daniels (1984)	221 ^b	2.08 ^d	FL
<i>Euoticus elegantulus</i>	24.9	0.262	Hildwein (1972)	17.5 ^a	0.261 ^d	FR
<i>Galago demidoff</i>	7.68	0.062	Lovegrove (2000)	58.4 ^b	0.0596 ^d	I
<i>G. moholi</i>	13.9	0.155	White and Seymour (2003)	172 ^b	0.194 ^c	I
<i>G. senegalensis</i>	18.1	0.215	Knox and Wright (1989)	90.4 ^b	0.225 ^c	I
<i>Lemur catta</i>	45.1	2.68	Snodgrass <i>et al.</i> (2007)	250 ^a	2.21 ^d	FL
<i>Lepilemur ruficaudatus</i>	27.6	0.680	Snodgrass <i>et al.</i> (2007)	260 ^b	0.755 ^c	FL ^f
<i>Loris tardigradus</i>	14.8	0.280	Muller <i>et al.</i> (1983)	72.8 ^b	0.269 ^d	I
<i>Macaca fascicularis</i>	245.8	4.209	Bromham <i>et al.</i> (1996)	25.0 ^a	3.41 ^c	FR
<i>M. mulatta</i>	231.9	5.38	Bruhn (1934)	35.0 ^a	5.37 ^d	FL
<i>Microcebus murinus</i>	4.90	0.050	Armstrong (1985)	215 ^a	0.0672 ^c	I
<i>Nycticebus coucang</i>	31.1	1.129	Muller (1979)	20.0 ^b	0.626 ^d	FR
<i>Otolemur crassicaudatus</i>	53.6	0.994	Muller and Jaksche (1980)	88.5 ^b	1.11 ^d	I
<i>O. garnettii</i>	81.1	1.314	White and Seymour (2003)	38.0 ^b	0.734 ^d	I
<i>Pan troglodytes</i>	848.0	25.9	Bruhn (1934)	1.64 ^b	40.4 ^d	FR
<i>Papio anubis</i>	342.9	9.50	Proppe and Gale (1970)	10.3 ^a	13.3 ^c	FR
<i>Perodicticus potto</i>	40.1	0.933	Hildwein and Goffart (1975)	9.00 ^a	0.998 ^c	FR
<i>Propithecus verreauxi</i>	86.8	3.08	White and Seymour (2003)	175 ^a	2.98 ^c	FL
<i>Saimiri sciureus</i>	68.8	0.850	White and Seymour (2003)	25.0 ^a	0.723 ^c	I
<i>Varecia variegata</i>	69.9	3.51	Snodgrass <i>et al.</i> (2007)	27.8 ^a	3.52 ^d	FR

All diet category data taken from Muchlinski (2010) unless otherwise specified. Superscripts refer to data source, as follows: ^a Damuth (1987), ^b Jones *et al.* (2009), ^c Gordon (2006), ^d Smith and Jungers (1997), ^e Mitani (1989), ^f Godfrey *et al.* (2004).

values for each species because we collected population density and BMR data on different samples within each species (Table I). Therefore, we could not include all 3 variables—body mass, population density, and BMR—in a single multiple regression analysis, and thus we used a residuals analysis.

As mentioned previously, the phylogenetic pattern of primate scaling relationships must be taken into account when conducting residual analyses. Extant strepsirhines are both hypometabolic relative to extant haplorhines (Kurland and Pearson 1986; Snodgrass *et al.* 2007) and smaller in body mass than haplorhines on average. The resulting size-biased grade shift will cause traditional regression to overestimate the slope of the scaling relationship between BMR and body mass, and thus will produce misleading residuals. Further, a lemur and a monkey of identical BMR and body mass would have identical residuals from a traditional regression,

even though they would not actually be identical in the difference of their BMR from similarly sized congeners owing to the difference in metabolic rate scaling patterns between primate suborders. To take these scaling differences into account, we used phylogenetically independent contrasts (PIC) for our analysis.

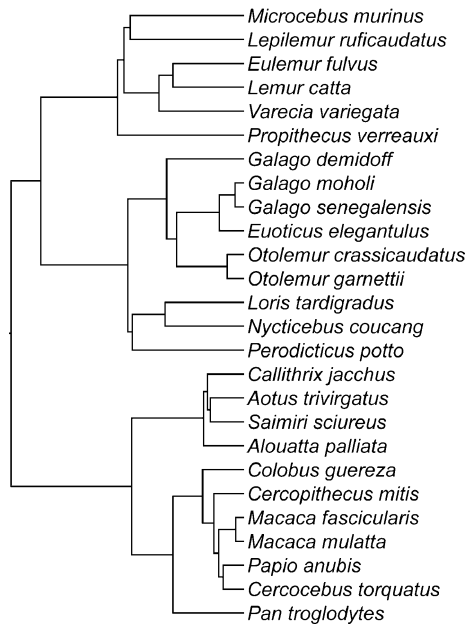
We calculated independent contrasts for logged values of BMR, population density, body mass from the BMR data set, and body mass from the population density data set using the “analyses of phylogenetics and evolution (ape)” package (version 2.5) in the statistical programming environment *R* (version 2.10.1) (Paradis *et al.* 2004; R Development Core Team 2009). We used the phylogenetic branching sequence and branch lengths based on divergence dates of Fabre *et al.* (2009), which yielded a fully resolved branching topology with no polytomies for the species included in this analysis (Fig. 1). Absolute values of the resulting contrasts did not correlate with contrasts standard deviations, indicating that contrasts were adequately standardized by the branch lengths used in this analysis (Garland *et al.* 1992). We calculated residuals from OLS regression lines against log body mass contrasts, where the intercept was constrained to equal zero (Garland *et al.* 1992). We calculated correlations between residuals for log population density contrasts and log BMR contrasts to identify the degree to which variation in population density is related to variation in BMR.

To address the possible additional effects of diet on population density in this sample, we ran 2 linear models in which residual population density contrasts were dependent on contrasts for diet categories. We obtained diet categories from Muchlinski (2010), except for 2 species not included in that analysis, in which case we used Godfrey *et al.* (2004) and Mitani (1989) (Table 1). We follow Muchlinski (2010) in grouping taxa as frugivores if $\geq 60\%$ of their diet is made up of fruit; if not, taxa are grouped as either folivores or insectivores based on whether the nonfruit portion of the diet was primarily made up of leaves or insects. We coded dietary categories as binary dummy variables, and calculated PIC values for all nodes in the phylogeny. A PIC analysis using continuous contrasts of binary dummy variables will produce identical results as a phylogenetic generalized least squares (PGLS) analysis used to perform a phylogenetic ANOVA or ANCOVA using species data, as opposed to contrasts data; the same phylogeny as the PIC analysis; and a Brownian motion model of evolution (Rohlf 2001). We considered 2 phylogenetic linear models for this study: 1 in which residual population density contrasts were dependent on residual BMR contrasts and dietary contrasts, and 1 in which residual population density contrasts were dependent on dietary contrasts alone.

Results

Allometric relationships between BMR and body mass using PIC regression in this sample have a slope that encompasses $3/4$; however, the 95% confidence intervals of the slope do not exclude other exponents including $2/3$ ($r^2=0.908$; $p<0.01$; OLS slope [95% CI]=0.743 [0.643–0.843]; Fig. 2a). Also, there is a negative relationship between population density and body mass in this sample that encompasses $-3/4$, although the relationship is considerably weaker than for BMR ($r^2=0.183$; $p=0.03$; OLS slope [95% CI]=−0.539 [−1.02 to −0.059]; Fig. 2b). Notably, population

Fig. 1 Primate phylogeny used in this study. Branch lengths are proportional to time as estimated in Fabre *et al.* (2009).



energy use does not appear to change with body mass ($r^2=0.021$; $p=0.48$; Fig. 2c). Residuals of BMR from body mass correlate significantly negatively correlated with residuals of population density from body mass when controlled for phylogeny ($r^2=0.155$; $p=0.05$; Fig. 3; Table II).

The inclusion of diet and residual BMR as independent variables in a phylogenetic linear model increases the proportion of variation in residual population density accounted for over that of residual BMR alone, but the model is less significant ($F=2.35$, $df=3,22$, $r^2=0.243$; $p=0.10$; Table II), indicating the relatively weak contribution of diet to the relationship between energy use and population density in this sample of primates. The coefficients for all independent variables are nonsignificant in this model, with the reduced significance for the effect of residual BMR indicating that residual BMR and diet overlap to some extent in the portion of variance in residual population density accounted for by these variables. The second model in which residual population density was dependent on diet alone was also nonsignificant, with all coefficients nonsignificant as well ($F=2.65$, $df=[2,23]$, $r^2=0.187$; $p=0.09$; Table II), demonstrating that diet alone cannot account for residual population density in this sample of primates.

Discussion

Our results show that population level energy use does not vary significantly with body mass in primates. This result is predicted by the EER and is a clear indication that energy use is an important factor in determining population densities across a wide range of primate body masses. In addition, the negative correlation between residuals of BMR from body mass and residuals of population density from body mass provide further support for the EER and suggest that individual metabolic costs

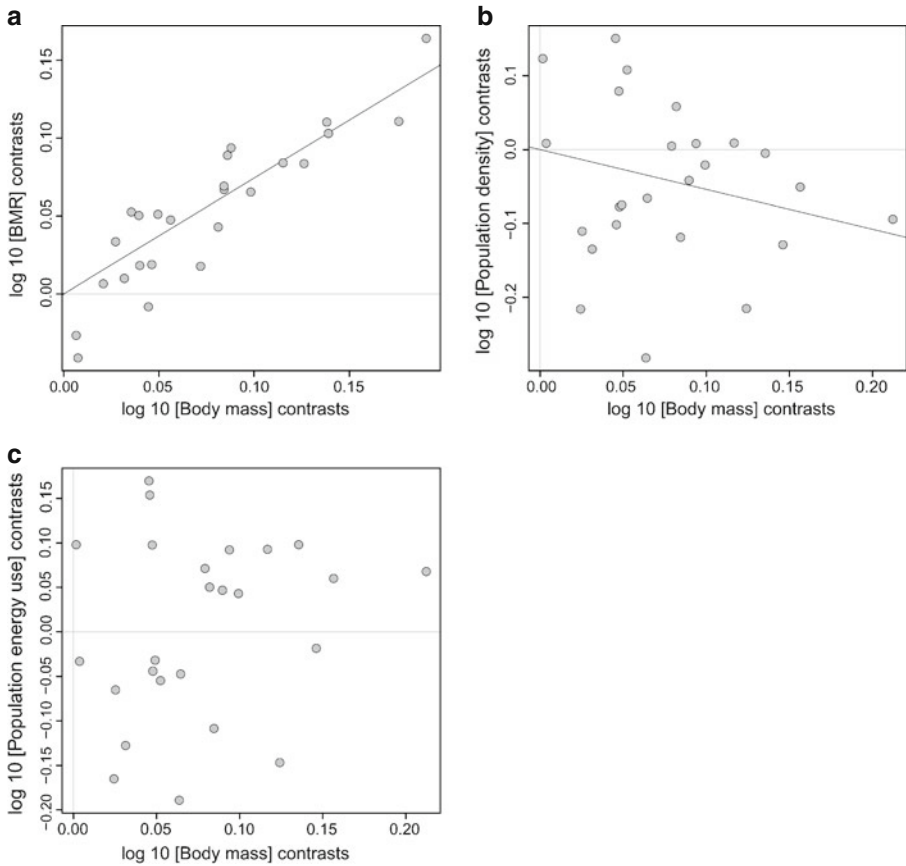
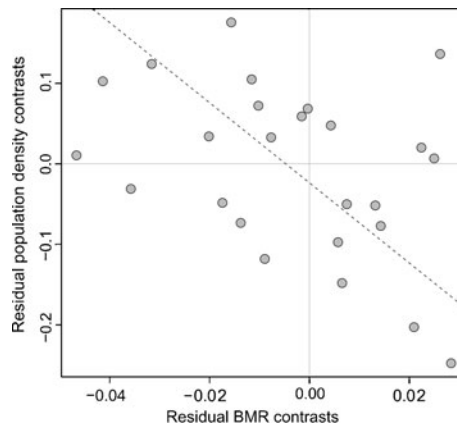


Fig. 2 Body mass scaling relationships using phylogenetically independent contrasts. Diagonal lines are ordinary least squares regression slopes (regression lines are forced through the origin). **a** Significant scaling of logged BMR with logged body mass. **b** Significant scaling of logged population density with logged body mass. **c** Bivariate plot of logged population level energy use and logged body mass. Population level energy use is the product of individual BMR and population density. There is no significant change in population level energy use with increasing body mass in primates. See text and Table II for statistics.

may partially constrain population densities in primates at a given body mass. Diet does not appear to have a strong effect on population density in this sample of primates once energy requirements have been taken into account. This result supports the hypothesis that larger primates live at lower population densities because they expend a greater amount of energy than smaller primates, and that bioenergetics play a further role in constraining variation in population density at a given body mass.

These bioenergetic constraints on population density support the long-held contention that food availability must also constrain population density (Chapman *et al.* 2002; Oates *et al.* 1990; Plumptre and Reynolds 1994; Rode *et al.* 2006). However, examining primate energy output does allow us to test this resource limitation hypothesis across diet classes and phylogenetic groups where measures of forest productivity generally fail. Our measure of energy use is a proxy for TEE, and

Fig. 3 Negative relationship between variation in population density and variation in BMR. Points are residuals from the OLS regression lines in Fig. 2a and b. Dashed diagonal line is reduced major axis best fit line to indicate correlation; this line is for visualization purposes only and is not meant to imply that a regression has been performed.



the use of this proxy measure likely weakens our results. Although we found a relationship between BMR and population density after controlling for body mass and phylogeny, BMR is only a portion of TEE and hence TEE may in fact provide a better explanation of population density than BMR. However, as previously discussed, data for TEE are available for only 3 primate taxa, and estimates of TEE based on activity budgets are often highly inaccurate (Leonard *et al.* 1997). The somewhat low correlation coefficient in our sample may be due to taxa having similar BMRs yet very different TEEs. For example, a frugivorous taxon may have a similar BMR compared to a folivore, but activity levels are likely higher in the frugivore (Gaulin 1979; Leonard and Robertson 1997; Milton and May 1976), possibly leading to larger TEEs and therefore lower possible population densities. Thus, our results suggest that bioenergetics constrains population density; however, more data on TEE are required to clarify this relationship.

Our analysis does not suggest that energy requirements alone determine population densities in primates. Several studies have shown that food availability plays an important role in determining population densities in specific taxa or in specific dietary classes (Chapman *et al.* 2004; Dunbar 1992; Janson 1984). Thus, population density is constrained by a combination of energy expenditure (likely TEE, which differs both among species and likely within species) and energy

Table II Correlation statistics and significance values for relationships among body size, BMR, population density, population energy use, and diet

Model	r	r^2	P
Correlation of \log_{10} [BMR] contrasts and \log_{10} [body mass] contrasts	0.953	0.908	<0.01
Correlation of \log_{10} [population density] contrasts and \log_{10} [body mass] contrasts	-0.428	0.183	0.03
Correlation of \log_{10} [population energy use] contrasts and \log_{10} [body mass] contrasts	0.145	0.021	0.48
Correlation of residual BMR contrasts and residual population density contrasts	-0.394	0.155	0.05
Phylogenetic linear model: Residual population density dependent on residual BMR and diet	—	0.243	0.10
Phylogenetic linear model: Residual population density dependent on diet alone	—	0.187	0.09

availability (which differs among habitats and dietary components). Based on the results of this study, we suggest that the inclusion of BMR and other bioenergetic measures will enhance our ability to predict population densities across broad ranges of primate taxa when combined with analyses of habitat productivity.

Using BMR to Explain Abundance

One advantage of using metabolic costs in addition to, or even in place of, measures of forest productivity, is that productivity measures are most useful when they are species-specific (Dunbar 1992; Janson 1984), or confined to one dietary class, e.g., protein-to-fiber ratios for folivores; Chapman *et al.* 2004). For example, Chapman *et al.* (2004) showed convincingly that the protein-to-fiber ratio of preferred dietary components (mature leaves) strongly predicts colobine biomass both within a forest at different sites, and across a wide range of sites spanning both Africa and Asia. Their results support the conclusions of several previous studies that suggest protein-to-fiber ratios are a major determinant of folivore abundance (Chapman *et al.* 2002; Ganzhorn 2002; Oates *et al.* 1990; Waterman *et al.* 1988).

Predictions of frugivore abundance are generally less successful than those of folivores (Chapman and Chapman 1999). Across taxa, general measures of fruit availability such as fruiting tree abundance or average monthly rainfall do not predict frugivore abundance (Chapman and Chapman 1999). This could be due to variation in fruit availability, both temporally and spatially. However, individual species do appear limited by fruit availability. For example, populations of Toque macaques (*Macaca sinica*; Dittus 1979) and vervets (*Cercopithecus aethiops*; Struhsaker 1973; Lee and Hauser 1998) show decreases in population density when food resources are reduced. In addition, gibbons are limited more by their fallback foods than by preferred foods or overall food availability (Marshall and Leighton 2006). Thus, for frugivorous primates, examining food availability across taxa is very difficult because choice of fallback foods and preferred fruits will likely differ greatly. Combining energetics data with food availability may improve interspecific analyses of population density and allow more detailed predictions of population densities across a wide range of taxa.

It is important to note that energy (food) availability is not the only possible constraint on primate population densities. Frugivore densities may be limited more by certain nutrient compositions in fruits instead of by overall levels of fruit availability (Butynski 1990; Rode *et al.* 2006). Thus, it may be extremely difficult to extend these findings to broader samples because different sites may have different mineral deficiencies.

Why Does BMR Vary?

Explaining why BMRs vary may ultimately help us understand why primate population densities vary. At its most fundamental level, BMR is the sum of tissue metabolic rates (Wang *et al.* 2001), and variation in BMRs across mammals is likely explained by differences in organ mass at a given body mass. For example, heart and kidney masses explain some of the intraspecific variation in BMR found in laboratory mice (Konarzewski and Diamond 1995). Variation in brain mass accounts

for a small proportion of variation in BMR in a large sample of mammals (i.e., ca. 5% of the variation in BMR [Isler and Van Schaik 2006]). Finally, variation in total body muscle mass accounts for variation in BMR across a broad sample of mammals (McNab 1978, 2000, 2007; Raichlen *et al.* 2010). These studies suggest that, combined, variation in organ mass likely explains differences in BMR among mammals, including primates.

Variation in organ mass and BMR appears to be tied to climate and thermoregulatory adaptations (Lovegrove 2000, 2003; Raichlen *et al.* 2010). BMR acts as a set point for body temperature regulation, suggesting that climate might play a strong role as a selection pressure for energy expenditures (McNab 2002; McNab and Morrison 1963; Schmidt-Nielsen 1997). The set point is relevant because endotherms maintain a constant body temperature across ambient air temperatures (Schmidt-Nielsen 1997), which means that heat production (e.g., metabolic rate), must be equal to heat loss in both hot and cold climates. A relatively low BMR provides a higher critical temperature in hot climates and allows taxa to reduce chances of overheating and dehydration (Careau *et al.* 2007). A higher BMR results in a lower critical temperature in cold climates (the lower limit, or set point of the thermoneutral zone; McNab and Morrison 1963; Schmidt-Nielsen 1997). In addition, a high BMR in cold climates may increase thermogenic capacity, which correlates highly with cold tolerance and will help compensate for heat loss (Careau *et al.* 2007; Swanson and Liknes 2006). Thus, BMR differences among taxa may reflect adaptations to variation in climates (Careau *et al.* 2007). Several researchers have found relationships between climatic variables and BMR. For example, small mammals living in habitats with high mean annual temperatures generally have low BMRs relative to body mass (Lovegrove 2000, 2003). This relationship between temperature and BMR has also been found in canids (Careau *et al.* 2007), *Peromyscus* (McNab and Morrison 1963; Mueller and Diamond 2001), and humans (Leonard *et al.* 2002; Snodgrass *et al.* 2005).

Although we might expect to see correlations between population density and climatic variables among primates, Harcourt (2000) did not find global relationships between latitude and population density among primates, suggesting that climate may not influence primate population densities in the same ways as other mammals (Lovegrove 2003). It is possible that latitude is too coarse a variable for studies of primate climatological adaptations because primates are by and large confined to a narrow latitudinal range in the tropics. More localized climatic data will provide a better assessment of whether thermoregulation influences primate population densities. Interestingly, altitude seems to affect primate population density (Byrne *et al.* 1993; Whiten *et al.* 1987; Yoshihiro *et al.* 1999), which may link temperature and abundance patterns. For example, *Macaca fuscata* live at lower densities in higher altitude forests (Yoshihiro *et al.* 1999), where mean annual temperatures are colder and thermoregulatory needs are likely higher. Although food availability plays a role in broad population density differences between low- and high-altitude groups, total fruit availability does not appear to explain differences in population density at all altitudes in this species (Hanya *et al.* 2004). Future studies examining more localized changes in temperature and climate across primate populations may find that metabolic adaptations for thermoregulation ultimately play a major role in determining patterns of primate abundance.

Conclusions

Though forest productivity clearly plays a role in patterns of primate population density, primate energetic needs correlate with local densities. All else being equal, primates with relatively low BMRs are able to pack more individuals into a given area, achieving high local densities. Increased efforts to obtain metabolic data (both BMR and TEE) tied to local climate and geography may help explain how and why energy requirements, and therefore population densities, vary among primates.

Understanding this variation is not trivial, since population density has been implicated in extinction risk and species richness (Isaac *et al.* 2005; Purvis *et al.* 2000). Relatively low population densities increase rarity, and as a byproduct, increase extinction risk (Purvis *et al.* 2000). In addition, population densities of primate taxa correlate with overall species richness (Isaac *et al.* 2005). Although the mechanisms behind this relationship are unclear, it is possible that reproductive conflicts lead to high rates of speciation when taxa are locally abundant (Gavrilets 2000).

The results of our study highlight the importance of energy expenditure in determining primate distribution patterns. Energy constraints at least partially determine the number of individuals in a given area, and future studies of primate communities may be improved by including metabolic measurements. We do not suggest that bioenergetics itself is the main determinant of population density, but that energy constraints combined with food availability will determine primate population densities. In the end, climatic conditions likely account for these interactions, and environmental differences among primate populations may be the ultimate cause of differences in population density. Finally, we suggest that a more complete understanding of bioenergetic constraints on population density requires collection of TEE from primates in the wild.

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