

# Allometric Slopes and Independent Contrasts: A Comparative Test of Kleiber's Law in Primate Ranging Patterns

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**ABSTRACT:** At the most fundamental level, the size of an animal's home range is determined by its energy needs. In the absence of confounding variables, home range size should therefore scale with body mass according to Kleiber's exponent for metabolic rate of 0.75. Comparative studies in a wide range of taxa have failed to confirm this prediction: home range size has commonly been found to scale with an exponent significantly  $>0.75$ . We develop a comparative measure of metabolic needs that incorporates both mass-specific metabolic rate and social-group size. We test the prediction that home range size in primates scales isometrically with this measure when an appropriate linear model is applied to data corrected for phylogenetic bias. Analyses using species values as data points indicate an exponent consistent with Kleiber's law. This result is misleading, however, because ecological factors confound the analysis, and the slopes within some ecologically homogeneous taxa are steeper. Accordingly, in analyses based on independent contrasts with reduced major axis, slopes are significantly greater than predicted by Kleiber's law. We examine the effects of other variables, and we find that systematic variation in substrate use, home range overlap, and diet account for the steeper than expected relationship between home range size and metabolic needs based on Kleiber's law. We therefore conclude that the scaling of home range size is subject to Kleiber's law but in combination with other factors. These results emphasize that the study of allometry requires detailed attention to statistical models and control of confounding variables.

**Keywords:** home range size, primates, comparative methods, independent contrasts, allometry.

Comparative biologists have identified a number of relationships among ecological and life-history variables (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Harvey and Clutton-Brock 1985). Some of these patterns are so consistent that they have been called "laws." One example is Kleiber's law, which states that metabolic rate scales with body mass raised to the power of 0.75 ( $BMR = aM^{0.75}$ , where BMR is basal metabolic rate,  $M$  is body mass, and  $a$  is the allometric coefficient). Many studies across diverse taxa have demonstrated the consistency of Kleiber's law (Kleiber 1961; Schmidt-Nielsen 1975; McNab 1986; Harvey et al. 1991; Martin 1996; see also Smil 2000). As further evidence for the generality and power of this relationship, variables that are directly related to metabolic rate also scale according to Kleiber's law (e.g., airflow in the lungs: Peters 1983; surface area of the small intestine: Martin et al. 1985). A similar argument should also apply to the size of the area that supplies an animal's energy resources, that is, the size of its home range (Harestad and Bunnell 1979; Mace et al. 1983).

Home range size is expected to increase with body mass because larger-bodied organisms require more resources and thus a larger area in which to find these resources (McNab 1963). If the scaling of home range size is also directly related to metabolic rate, then home range size should scale with body mass raised to Kleiber's exponent of 0.75. While initial tests supported this prediction (McNab 1963), later research indicated otherwise: in a diverse array of species, the relationship between home range size and body mass scales with an exponent that significantly exceeds 0.75. For example, Milton and May (1976) found that, in primates, total home range scales with body mass raised to the 1.23 (see Calder 1984 for examples from other taxa). One potential reason for the steeper slope is that BMR is calculated in controlled laboratory conditions and therefore may not accurately reflect metabolic rate in field conditions. However, recent research determined that field metabolic rate scales with an exponent of 0.772 in mammals (least squares estimate based on phylogenetically independent contrasts in Nagy

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et al. 1999), suggesting that Kleiber's exponent of 0.75 is an appropriate prediction for the scaling of mammalian home range size. Moreover, alternative approaches that used estimates of energetic expenditure in free-living animals have also demonstrated steeper than expected slopes (e.g., measures of daily energy expenditure: Mace and Harvey 1983).

In this article, we reinvestigate the relationship between energetic needs and ranging patterns in primates. Our goals are twofold. First, we aim to understand home range size and its determinants. Metabolic needs determine ranging patterns at a fundamental level. Therefore, as we strive for a better understanding of the factors that determine home range size (e.g., Janson and Goldsmith 1995), the precise relationship between home range and body mass needs to be determined and its theoretical basis elucidated (e.g., Schoener 1968; Harestad and Bunnell 1979; Damuth 1981; Calder 1984). Compared to previous research on this subject (Clutton-Brock and Harvey 1977, 1984; Martin 1981; Mace et al. 1983), a better understanding of the scaling of home range size can be obtained by using new statistical models for determining allometric slopes (Rayner 1985; Harvey and Pagel 1991; Riska 1991). We focus on primates because this taxon has the most complete information available for the relevant variables, such as home range size, and these data on primate range size have expanded tremendously since previous comparative analyses. Furthermore, primates exhibit great social and ecological variability, and this variation provides a means to identify the factors responsible for the overall cross-species pattern and its particular deviations.

Second, we use this data set to explore the promise and pitfalls of calculating allometric slopes in a phylogenetic context, especially when using the method of independent contrasts (Felsenstein 1985; Harvey and Pagel 1991). Independent contrasts are standardized differences calculated between sister taxa at each node of a phylogeny. They are estimates of the evolutionary change in a variable since the divergence of the sister taxa from their common ancestor. Hence, independent contrasts make it possible to test for the occurrence of correlated evolution between two or more variables. What is perhaps not so widely appreciated is that contrasts analysis provides not only a means to test for the "presence" of an evolutionary relationship but also a means to assess its precise "form" (Harvey and Pagel 1991).

Previous analyses of home range scaling did not control fully for phylogenetic nonindependence because such methods were not available. Failure to incorporate phylogenetic information can lead to inaccurate statistical results, as demonstrated in previous comparative and computer simulation studies (e.g., Martins and Garland 1991; Garland et al. 1993; Purvis et al. 1994; Harvey and Ram-

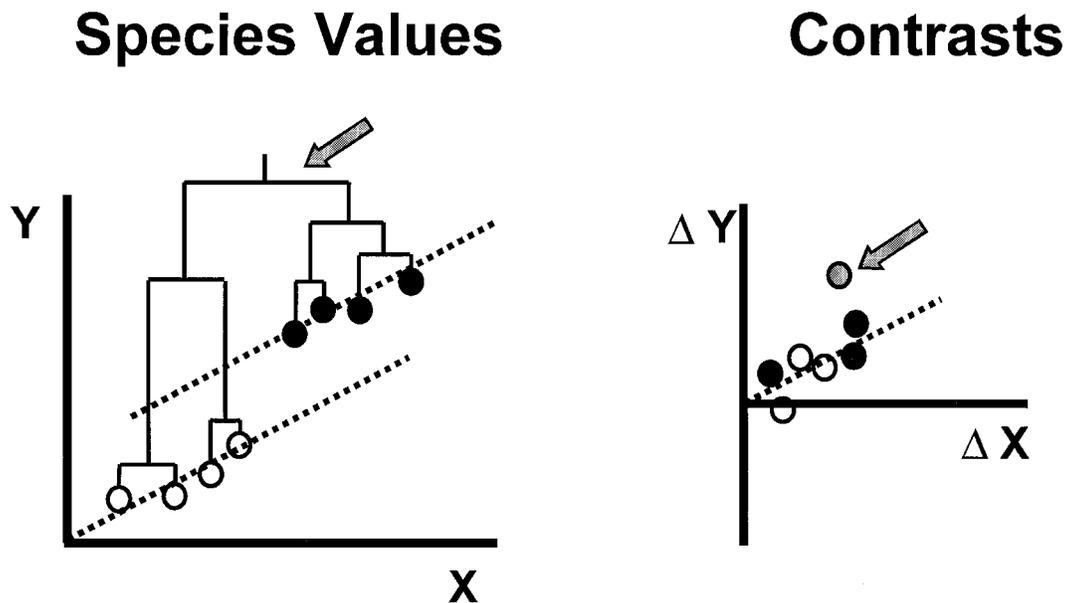
baut 1998; Purvis and Webster 1999). Allometric slopes calculated from species values may be particularly biased in the context of grade shifts. A grade shift occurs when a set of species shares a confounding character state through common ancestry that produces a shift in the relationship between the main variables with no change in their slope (fig. 1). In technical terms, the allometric exponent is the same in the two groups, but the allometric coefficient differs. In analysis of species data points, this grade separation can bias the slope estimate because multiple data points are treated incorrectly as independent. With the method of independent contrasts, however, only a single contrast is calculated for each grade shift, and this single data point will produce less bias than multiple data points in a species analysis (fig. 1). Hence, contrasts analysis may be more appropriate than species analysis when grade shifts exist, especially if the associated grade-shift contrasts can be identified and removed.

In the context of calculating allometric slopes using independent contrasts, we address two questions. First, what is the best line-fitting model to use with contrasts data? Although suggestions are available, most notably the structural relations model (Harvey and Pagel 1991), few studies have fully evaluated the difficulties of applying this line-fitting model to contrasts data (Berrigan et al. 1993). Other phylogeny-based methods, such as generalized least squares (GLS), are available and can take into account intraspecific variation (Martins and Hansen 1997), but the method of independent contrasts is the most widely used and best understood of existing methods and is functionally equivalent to GLS approaches (Garland et al. 1999; Garland and Ives 2000). Second, how do contrasts perform in the presence of grade shifts? Contradictory discussion of the effect of grade shifts in contrasts analysis can be found in the literature (e.g., Ridley 1989; Garland et al. 1993; Smith 1994; Martin 1996; Ricklefs and Starck 1996; Price 1997; Purvis and Webster 1999). Although some of these proposals (Smith 1994; Martin 1996) can be discredited based on the logic of contrasts above, additional research is needed on the use of contrasts when grade shifts occur. Our data allow us to examine these proposals empirically.

## Methods

### *Background and General Approach*

Most allometric analyses transform the variables by taking logarithms so that a straight-line relationship exists among the variables, and linear models can be used to assess their relationship. After logarithmic transformation, the expected relationship between home range size and body mass becomes  $\log R = \log a + 0.75 \log M$ , where  $R$  is



**Figure 1:** Independent contrasts and grade shifts. Different ecological niches are indicated by black and white data points that are shared through common descent. In this hypothetical case, the different niches represent a grade shift where the allometric exponent (slope) remains the same within grades, but the allometric coefficient (intercept) differs between them. In species analysis, phylogenetic clumps of data may therefore bias the estimated slope across all species. In the case presented here, the overall slope will be biased upward, but in other cases, it can be biased downward (i.e., when the grade is shifted “down” with mean increases along the  $X$ -axis). Contrasts represent evolutionary change, and so grade shifts between the different ecological categories should be represented by a larger than expected contrast in the branch linking the two subclades (shaded point indicated by arrow). This single outlier should have less of a biasing effect on the estimated slope than the many degrees of freedom in the species data. Furthermore, if these outliers are identified and removed, unbiased estimates of the true slope should be obtained. Felsenstein’s (1985) figure 7 provides a more extreme example in which analysis of species data produces a significant result when no underlying relationship exists; for another example based on real data see Garland et al. (1993).

home range size and  $M$  is body mass. In primates, however, sociality must be taken into account: the home range of a socially foraging organism reflects not just its own energetic requirements but the requirements of the entire foraging group (Milton and May 1976; Clutton-Brock and Harvey 1977). Furthermore, if larger-bodied primate species tend to live in larger social groups (Clutton-Brock and Harvey 1977), then sociality might account for the steeper than expected relationship between body mass and home range size. Yet, even when foraging group mass (the sum of body masses for all individuals in the group) has been used to incorporate sociality (Clutton-Brock and Harvey 1977, 1984), ranging area still exceeds expectations based on Kleiber’s law.

Martin (1981) pointed out that foraging group mass misrepresents the true “metabolic biomass” of the social group (see also Gittleman and Harvey 1982). This problem arises because the energetic needs of a social group will be the sum of the expected metabolic needs of its members, not the metabolic rate of its summed mass. Thus, a small-bodied species with the same total group foraging mass as a large-bodied species will require a larger ranging area

because the metabolic needs of the small-bodied group will be greater.

One way to include the effects of sociality is to use a measure of individual space, calculated as the inverse of population density. Research by Martin (1981) showed that this variable also scales with body mass greater than predicted by Kleiber’s law. Because this measure incorporates the total number of individuals in an area, it has the benefit of incorporating home range overlap (which may confound analyses if overlap with neighboring groups reduces the usable foraging area of the home range). However, population density estimates often include regions of nonproductive habitat and are thus sensitive to the total area used to calculate this variable. In addition, home range overlap itself is of interest, especially if overlap scales with body size (Damuth 1981; Calder 1984), yet home range overlap cannot be evaluated when it is subsumed into an individual space measure.

Individual space estimates have another problem in this context. The analysis is limited to using a single body mass estimate as the independent variable, yet individuals within a group differ in body mass. A weighted average of group

body masses might seem to correct this ambiguity. However, this solution leads to the problem noted above because a weighted average confounds the number of individuals with the metabolic rates of their differing masses (Martin 1981).

In this article, we therefore take an alternative approach that was identified by Martin (1981) and used by Gittleman and Harvey (1982) to examine patterns of home range size in carnivores. This alternative approach, which examines home range size relative to a derived measure of "group metabolic needs," has several advantages in this context. An index of group metabolic needs more fully incorporates variation in group composition and the metabolic rates of different age-sex classes within these groups. After logarithmic transformation, this approach also provides a linear, isometric prediction for the scaling of home range size. We calculated expected metabolic needs for a typical social group of each species based on the strong association between body mass and metabolic rate (i.e., Kleiber's law). Specifically, group metabolic need was calculated as the sum of the body masses ( $M$ ) for each of three age-sex classes (males, females, and immatures) raised to the 0.75 and multiplied by the number of individuals ( $n$ ) in that age-sex class, that is, group metabolic needs =  $\Sigma(nM^{0.75})$ . Thus, if Kleiber's exponent applies to primate ranging patterns, then a unit increase in group metabolic needs is expected to result in a unit increase in home range size, giving a predicted slope of 1 (see Gittleman and Harvey 1982). It is important to note that our aim is not to retest whether Kleiber's exponent for metabolic rate is correct, but rather to test whether this well-established scaling of BMR, which is similar to field metabolic rate (Nagy et al. 1999), can be used to understand the scaling of home range size.

#### Variables

We obtained information on group composition (number of males, females, and immatures) and home range size (ha) from the published literature. These data are available from the author on request and in the online edition of the *American Naturalist*. Body masses of males and females (kg, adult values) were obtained from Smith and Jungers (1997). Information on body mass is not usually available for more than just adult males and females, and so immature body mass is estimated as one-half of the mean of male and female body masses. We tested the sensitivity of our results to this estimate of immature body mass by repeating some analyses with immature body mass estimated as one-fourth and three-fourths of the average adult body mass (see also Harvey and Clutton-Brock 1981).

More detailed analyses were performed using a subset of taxa for which information could also be obtained on

diet (percentage of leaves), terrestrial activity (percentage of daily activity on the ground), and home range overlap (percentage of the focal group's home range that is used by at least one surrounding group, in some cases estimated from figures in published articles). Values for these variables were obtained from an unpublished comparative database and are available from the authors by request. These continuous measures provide greater statistical power than discrete measures, such as dichotomous categories of arboreal versus terrestrial substrate use. However, continuous measures are available for fewer species, whereas broad classifications of primate species into discrete categories of diet (folivore vs. nonfolivore) and substrate use (arboreal vs. terrestrial) provide larger samples. Other parameters of interest, such as activity pattern (diurnal vs. nocturnal) and habitat use (open vs. wooded), are only available as discrete variables. We therefore used discrete categories, updated from Nunn and van Schaik (in press), in analyses that examine slopes among broad ecological categories (e.g., folivores vs. frugivores or arboreal vs. terrestrial substrate use), but we used continuous measures in later tests that more accurately assess how socioecological variables affect the slope estimate.

Group composition of "solitary" nocturnal species is difficult to quantify because individuals of these species often sleep together during the day but then forage during the night in home ranges that overlap to varying degrees (see Bearder 1987). Similar problems are encountered with the orangutan (*Pongo pygmaeus*). In solitary species, male ranges usually overlap the ranges of one or more females; thus, we assumed that group composition in these species involves one male and one female. In addition, maturing offspring often inhabit their mother's home range (Bearder 1987). We therefore also assumed that home ranges in "solitary" species include one immature animal. Higher-level and fission-fusion primate societies, where foraging groups change composition over the day and coalesce with other groups, also pose a problem for estimating group composition (e.g., *Ateles* spp., *Papio hamadryas*, *Theropithecus gelada*, *Mandrillus* spp., *Pan* spp.). In this analysis, we are interested in the number of individuals that occupy a common foraging area. If this could not be determined for a species with a higher-level or fission-fusion organization, then it was excluded from the analysis.

The variables in question exhibit intraspecific variation. In order to assess the sensitivity of our analysis to variation in socioecological variables (especially group composition and home range size), three different data sets were used. First, we took values directly from a comparative database that includes most estimates of home range size and group composition that are available in the published literature (used in Nunn and van Schaik, in press). By using this database ("all data"), we maximized the number of species

and the amount of data going into the tests at the cost of including some estimates of home range size that did not have corresponding estimates of group composition, and vice versa. We also generated two additional data sets limited to particular studies within the larger database. Studies were included if a home range estimate could be linked directly to a group composition estimate. Thus, in a second test, we obtained values from long-term studies where information was available on both variables for the same social group, and when more than one value was available, we averaged these estimates to obtain a species value ("matched averages"). In a third test, we avoided taking averages by using as an estimate for each species a value taken from one study group ("single study"). Except for the sensitivity tests mentioned above, body masses of adults and immatures were held constant in all tests.

#### *Comparative Methods in Allometry*

Comparative methods have undergone a revolution since the 1980s. It is now widely accepted that species values may not be independent data points in a comparative test, and so phylogeny should be taken into account to assess the statistical significance of cross-species patterns (Harvey and Pagel 1991; Martins and Hansen 1996; Garland et al. 1999; cf. Gittleman et al. 1996; Abouheif 1999). We used the method of independent contrasts (Felsenstein 1985), as implemented by the computer program CAIC (Purvis and Rambaut 1995) and with the composite estimate of primate phylogeny provided by Purvis (1995). As noted above, contrasts are fully appropriate for determining allometric slopes (Harvey and Pagel 1991).

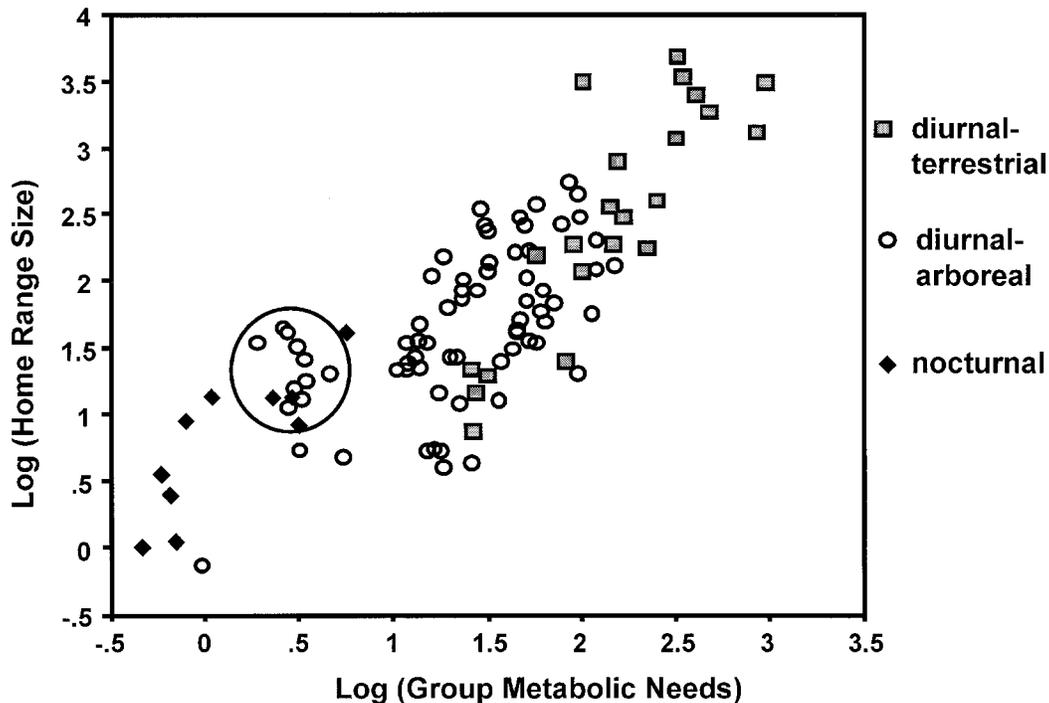
In the main analyses, we tested the assumptions of independent contrasts and transformed the data and branch lengths appropriately (Garland et al. 1992; Purvis and Rambaut 1995). These diagnostic checks and transformations have been shown to improve the statistical performance of contrasts in computer simulations (Diaz-Uriarte and Garland 1996, 1998). Specifically, we examined the regression of absolute values of contrasts on their standard deviations to ensure that the algorithm is properly scaling branch lengths (see Harvey and Pagel 1991; Garland et al. 1992; Purvis and Rambaut 1995). Logarithmic transformation of both the data (home range size and group metabolic needs) and branch lengths improved the fit of the contrasts to these statistical assumptions. We forced regressions and correlations through the origin using the formulae provided by Garland et al. (1992). Although we agree with Garland et al. (1992) that contrasts slopes should be forced through the origin, we also tested whether the unconstrained intercept differed significantly from zero, as nonzero intercepts may indicate a nonlinear relationship or other problems in interpreting contrasts

data (Harvey and Pagel 1991; Garland et al. 1992). In all cases, however, the intercept did not differ significantly from 0.

Because the intercept in contrasts analysis is constrained to go through the origin, standard ANCOVA approaches for testing elevation differences in allometry are meaningless for contrasts data (see Garland et al. 1993). Methods are available for estimating intercepts and for testing intercept differences (Garland et al. 1993). These tests generally have low statistical power, however, because in most cases, only one or a few degrees of freedom corresponding to evolutionary transitions between grades are available for statistical testing. We therefore avoid tests that rely on a few discrete transitions, such as phylogenetic ANCOVA; instead, we test particular hypotheses by using continuous measures (see "Variables" section). As pointed out by Garland et al. (1993), use of continuous measures generally provides greater statistical power in phylogenetic tests (see also Nunn 1999). This approach also avoids problems of dichotomizing what is often continuous underlying variation.

We examined contrasts plots to identify and to remove outliers, which were detected using mahalanobis distance methods in JMP (SAS Institute, Cary, N.C.). Our assumption is that outlying contrasts represent grade shifts that interfere with efforts to estimate the allometric slope (see fig. 1). In this context, however, it is important to note that grade shifts are not the only explanation for outliers in contrasts plots. If different field methods are used to estimate home range size in closely related species, for example, one likely result is a large home range contrast with little corresponding difference in group metabolic needs. The reason for this difference in the independent and dependent variables is that components of group metabolic needs (group composition and body masses) are generally more straightforward to quantify in the field, although both variables are subject to measurement error and intraspecific variation. In all of these cases, however, outliers are the result of factors that inappropriately bias the slope estimate and so their removal may be warranted.

We also investigated patterns using species data, that is, without controlling for phylogeny, to compare these results to those obtained with contrasts (Price 1997). In particular, a reduction in contrasts correlations, as compared to species correlations, may indicate the existence of grade shifts that are too subtle to be detected as outliers. Species plots also allow visual exploration of the data to identify potential grade shifts. With contrast plots, visual identification of grade shifts is more difficult because the intercept is removed and a grade shift shows up as a single outlier (see Garland et al. 1993).



**Figure 2:** Patterns across species using the “all data” data set. A slight curvilinear relationship exists owing to different ecological categories among the species. Patterns within ecological categories (three shown) appear to be steeper than patterns across the whole data set. Eight of the 10 “diurnal” circled values indicate small-bodied callitrichids that live in small groups (*Callithrix*, *Callimico*, and *Saguinus*, but not *Cebuella pygmaea*).

#### *Line-Fitting Models*

Our primary goal is to understand the precise scaling relationship between group metabolic needs and home range size. Least squares (LS) regression is the most widely used and readily available line-fitting technique. However, LS regression assumes that the independent  $X$  variable is measured without error. When this assumption is violated, LS estimates will consistently underestimate the true slope, and the magnitude of this error will increase with decreasing correlation between the variables (Harvey and Pagel 1991). Hence, if the true relationship between home range size and group metabolic needs is greater than expected by Kleiber’s law, LS analysis is less likely to reject correctly the prediction of a unit slope (see also Martin 1981). We predict a unit slope because a unit increase in group metabolic needs is expected to result in a unit increase in home range size, giving a slope of 1 (Martin 1981; Gittleman and Harvey 1992).

If the error variances of the independent and dependent variables are known, then calculations based on the structural relations model (SRM) provide unbiased slope estimates (Rayner 1985; Harvey and Pagel 1991). The critical variable in SRM is  $\lambda$ , which is the ratio of the error variance in  $Y$  to the error variance in  $X$ . In species analyses,  $\lambda$  can

be estimated from intraspecific variation in the two traits. Previous authors have suggested that these estimates of  $\lambda$  from the raw data can then be applied to contrasts data (Pagel and Harvey 1989; Harvey and Pagel 1991; Berrigan et al. 1993). We examined whether this is an appropriate means of estimating  $\lambda$  for contrasts data. We also investigated results based on reduced major axis (RMA), which is a special case of the SRM (see McArdle 1988; Harvey and Pagel 1991). For SRM calculations using species values, we used the value of  $\lambda$  calculated from all available intraspecific data points ( $=1.87$ ), and we assumed uncorrelated errors. All statistics were considered significant at  $P < .05$ .

## Results and Discussion

### *Species Analysis*

Across species, there is a strong association between group metabolic needs and home range size (fig. 2). LS slopes are  $<1$  but with confidence limits that enclose 1 (table 1). As expected, RMA analyses provide steeper slopes, but in all cases, the confidence intervals still enclose the predicted value of 1. Also, as expected based on values of  $\lambda$ , SRM slopes ( $\lambda = 1.87$ ) are intermediate to the LS estimates

Table 1: Regression slopes from species and contrasts analyses

	N	LS slope <sup>a</sup>	Confidence interval	RMA slope <sup>b</sup>	Confidence interval	SRM slope <sup>c</sup>	Correlation coefficient <sup>d</sup>
Nonphylogenetic:							
All data	107	.90	.77–1.02	1.11	.99–1.25	1.06	.81
Matched averaged	77	.86	.70–1.02	1.10	.95–1.27	1.03	.78
Single studies	77	.87	.71–1.04	1.13	.98–1.31	1.06	.77
Phylogenetic:							
All contrasts: <sup>e</sup>							
All data	91	1.06	.76–1.36	1.80	1.52–2.13	1.33	.59
Matched averaged	67	.84	.54–1.15	1.52	1.25–1.85	1.05	.61
Single studies	67	.84	.51–1.18	1.61	1.30–1.98	1.04	.52
Internal contrasts: <sup>e</sup>							
All data	29	1.10	.78–1.42	1.37	1.09–1.74	...	.80
Matched averaged	21	.94	.50–1.39	1.34	.96–1.87	...	.71
Single studies	21	.94	.46–1.42	1.40	.98–1.98	...	.67

<sup>a</sup> LS = least squares regression.

<sup>b</sup> RMA = reduced major axis. Confidence intervals are asymmetric around the estimated slope (see Clarke 1980; McArdle 1988).

<sup>c</sup> SRM = structural relations slope with  $\lambda = 1.87$  in nonphylogenetic analysis and 9.0 in phylogenetic analysis (because we are using a computer program, CAIC, that forces the  $X$ -variable to be positive; Purvis and Rambaut 1995). SRM slopes were not calculated for analyses of internal contrasts because the estimate of  $\lambda$  differs at these higher levels (see “Contrasts Analysis: SRM and RMA Slopes”), and there was no straightforward way to calculate this different estimate using the intraspecific data available.

<sup>d</sup> For contrasts, correlation and regression coefficients were calculated through the origin (see Garland et al. 1992).

<sup>e</sup> With outliers excluded (see text).

( $\lambda = \infty$ ) and RMA estimates ( $\lambda = 1.24, 1.21,$  and  $1.27$  for each of the data sets, respectively; see Harvey and Pagel 1991; Berrigan et al. 1993). Results are insensitive to the estimate of immature body mass as one-half of the average adult body mass (table 2). Results are also insensitive to estimates of group composition in solitary species: in species regressions that excluded solitary species, LS slopes ranged from 0.96 to 1.02 with confidence intervals that enclose one in each case.

Home range appears to scale nonlinearly with group metabolic needs even after logarithmic transformation (fig. 2). However, a polynomial regression increases the explained variance only slightly ( $r^2 = 0.68$  in a second-order polynomial regression vs. 0.65 in linear regression). Slopes are also steeper within some ecological subsets of the data, and a group of Neotropical primates have larger than expected home ranges for their metabolic needs (*Callithrix*, *Callimico*, and *Saguinus*; eight of the 10 “diurnal” data points circled in fig. 2). These members of the Callitrichidae are small bodied and live in small groups, and large home ranges in these taxa are consistent with their use of a narrow set of widely distributed resources (e.g., Terborgh 1983). In the context of allometric slopes based on species data points, these larger home ranges combined with low group metabolic needs bias the slope downward when this dietary specialization is ignored. This example therefore illustrates the biasing influence of grade shifts on non-phylogenetic allometric analyses.

Figure 2 reveals some other potential grade shifts, in-

cluding some slight differences between diurnal-terrestrial and diurnal-arboreal species. Figure 3 provides RMA slope estimates from species analyses within phylogenetic radiations and broad ecological categories. RMA slope estimates in these subsets of the data are  $>1$  and generally higher than those calculated across all species (a mean of 1.34 vs. 1.11 from table 1). However, seven of the 11 estimates in figure 3 have confidence intervals that still encompass the predicted value of 1. The lowest values for species slopes are for those ecological categories that lump the callitrichids with other species, as might be expected when this obvious grade shift is confounded with the allometric relationship in species analysis. For example, the callitrichids share with many other primates arboreal substrate use, a generally nonfolivorous diet and a closed environment, and slopes calculated within these ecological categories are the lowest of the slopes in the ecological categories in figure 3.

A number of confounding factors remain in these ecological subsets of the data (e.g., terrestrial primate species can live in open or wooded environments; see Nunn and van Schaik, in press). The interactions among these ecological factors, in addition to their dichotomous nature, make these confounding variables difficult to control in a multivariate context that also incorporates phylogeny (e.g., Garland et al. 1993). In a later section, we therefore perform phylogenetic tests using continuous measures of diet, home range overlap, and substrate use.

*Contrasts Analysis: LS Slopes*

If contrasts alleviate the confounding effect of grade shifts, then LS slopes should differ depending on whether they are calculated from species values or contrasts. However, in the whole data set, LS contrasts slopes are not markedly different from LS species slopes even after removal of outliers (tables 1, 2). The same is true for the ecological subsets of the data in a LS analysis, where none of the results are statistically different from 1 (not shown). In the analyses performed here, outliers are not particularly common, and the same outliers tend to be removed in different tests and subsets of the data. For example, only 10 different contrasts are excluded in the 12 tests that use the whole data set or phylogenetic-ecological subsets of the data (e.g., fig. 3).

Analysis of outliers reveals why the slopes are not strikingly different in LS contrasts analyses, as compared to LS slopes in species analyses. When observed values are regressed on expected values in a leverage plot, two types of outliers are detected: some outlying contrasts are within the 95% confidence intervals (type a outliers), while others are beyond these limits (type b outliers; see fig. 4). One justification for excluding type a outliers involves their higher leverage on the estimated slope. When the goal is to estimate the slope precisely, these outlying contrasts will have a greater influence on estimates of the regression line, as they fall within the confidence intervals on the regression line, but relatively far from most other data points (fig. 4). Type b outliers are more likely to represent the influence of grade shifts and other confounding variables, as shown in figure 1, because they fall outside the confidence intervals. These outliers will also tend to bias the fitted line, and their removal should therefore provide a more accurate slope estimate. Among the outlying contrasts removed in tests that use the whole data set or a phylogenetic-ecological subset of the data, four are type a and six are type b, but only one of the type b outliers falls below the line. Hence, the contrasts that are excluded (fig.

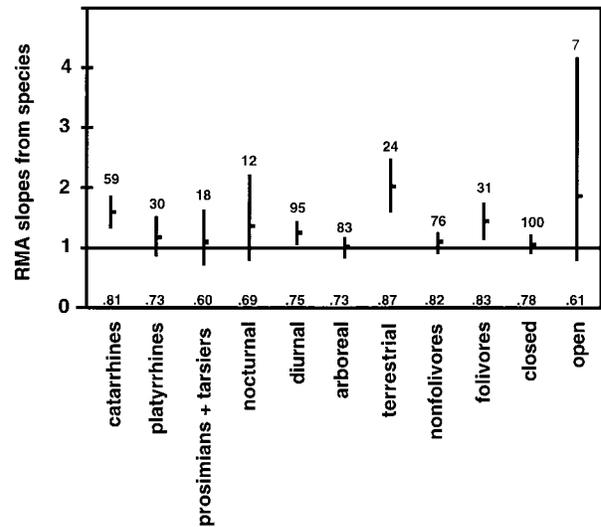


Figure 3: Reduced major axis (RMA) slopes from species data within phylogenetic radiations and ecological categories. Horizontal lines represent RMA slope estimates, while vertical bars indicate 95% confidence intervals. Sample sizes are provided above these lines, while correlation coefficients (forced through the origin) are provided along the X-axis.

4) do not lead to consistently steeper slopes, as had been expected based on slopes within phylogenetic and ecological subsets of the data (see fig. 3).

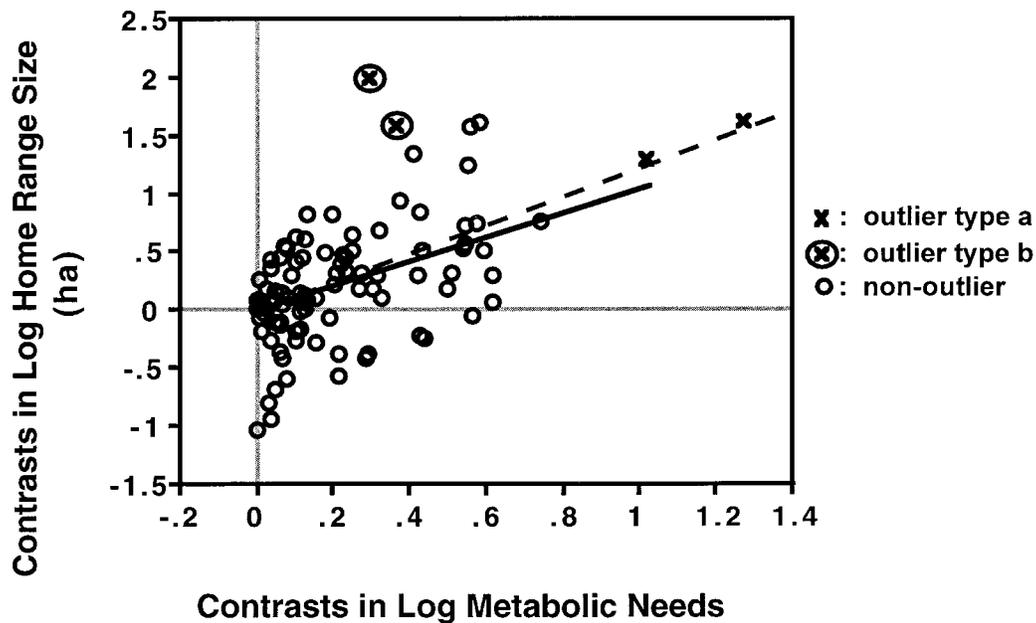
Least squares confidence intervals are much wider for contrasts and actually enclose those found in species analysis. Correlations are also markedly lower for contrasts than for species analysis (table 1). The lower correlations may indicate the existence of grade shifts through the effect of outliers that are too subtle to detect statistically. Two alternative explanations for the weaker correlations are possible, however. First, weaker correlations may result from violations of the Brownian motion model that underlies contrasts (see Price 1997; Abouheif 1998). We think

Table 2: Sensitivity of results to estimates of immature body mass

	1/4 average adult			1/2 average adult LS slope <sup>b</sup>	3/4 average adult		
	LS slope	Confidence intervals	N <sup>a</sup>		LS slope	Confidence intervals	N
Species values:							
All data	.91	.78–1.04	107	.90	.89	.76–1.02	107
Matched averaged	.87	.71–1.03	77	.86	.85	.70–1.01	77
Single studies	.88	.72–1.05	77	.87	.86	.70–1.03	77
Contrasts:							
All data	1.06	.76–1.36	91	1.06	1.05	.75–1.36	91
Matched averaged	.91	.58–1.23	66	.84	.80	.47–1.13	67
Single studies	.84	.51–1.18	67	.84	.84	.50–1.17	67

<sup>a</sup> Sample sizes differ in some contrasts analyses because different numbers of data points are excluded as outliers.

<sup>b</sup> From table 1.



**Figure 4:** Contrasts analysis using all species. Contrasts in log home range size plotted against contrasts in log group metabolic needs from the “all data” data set. Four outliers are indicated by x’s: two are type a, and two are type b (circled x’s). Outliers were identified as type a or b based on confidence intervals on a leverage plot (not shown). Solid line indicates least squares (LS) regression line with these outliers excluded ( $b = 1.06$  in table 1). Dashed line indicates the LS regression line that includes all contrasts and gives a steeper slope ( $b = 1.21$ ,  $F = 70.82$ ,  $n = 95$ ,  $P < .0001$ ).

this is unlikely, however, because we tested the assumptions of independent contrasts and transformed our data and branch lengths to meet these assumptions (Garland et al. 1992). Second, the weaker contrasts correlation may reflect greater error variance in the tips of the tree, where fewer “meaningful” contrasts are available because species within a genus are more similar in group metabolic needs and other variables. In such a case, contrast values may reflect measurement error to a greater extent (Ricklefs and Starck 1996; C. Janson, personal communication). We tested this possibility by examining only internal contrasts, that is, those calculated using reconstructed nodes higher in the tree. When using only internal contrasts, correlations are indeed higher, but the correlations remain slightly weaker than in analysis of species data points (table 1). Thus, grade shifts may explain the lower correlations in contrasts analysis, although possibly in combination with higher measurement error on the “tips” of the phylogeny.

#### *Contrasts Analysis: SRM and RMA Slopes*

As noted in “Methods,” previous authors have suggested that  $\lambda$  estimates calculated from raw data can be used in contrasts analyses (Pagel and Harvey 1989; Harvey and Pagel 1991; Berrigan et al. 1993). However, the error variance in the raw data need not equal the error variance

in contrasts (see Ricklefs and Starck 1996), and any difference in error variances could lead to incorrect SRM slope estimates. We investigated this issue by examining contrasts calculated using subsets of the intraspecific variation, as suggested for species values in Harvey and Pagel (1991).

We found that several difficulties arise when attempting to calculate  $\lambda$  from contrasts. First, the direction of subtraction is arbitrary for contrasts (see Garland et al. 1992), yet when using the approach for calculating  $\lambda$  in Harvey and Pagel (1991), different combinations of positive and negative contrasts, calculated for different populations of the same set of species, will give different estimates of the error variances. In particular, one commonly used computer program for calculating independent contrasts (CAIC; Purvis and Rambaut 1995) forces the independent  $X$  contrasts to be positive; when the differences between species are negligible, and therefore mainly due to error variance, this “positivizing” reduces the intraspecific variance in  $X$  contrasts relative to that in  $Y$  contrasts, giving a higher value of  $\lambda$ . We tested whether estimates of  $\lambda$  from species values equal those calculated from contrasts in CAIC by examining 12 primate species with data available for at least four different populations or groups. For the raw species data,  $\lambda$  was calculated using the variation in four of these intraspecific values following procedures in

Harvey and Pagel (1991). For contrasts,  $\lambda$  was calculated using the same basic approach, where intraspecific variation was based on four estimates of each contrast calculated using each intraspecific data point only once and entered in a random order. This gives an estimate of  $\lambda = 1.45$  for the species data, as compared to  $\lambda = 9.00$  for contrasts (the value of 1.87 used for species SRM slopes in table 1 was based on all the intraspecific data available). When  $X$  was not forced to be positive, the value of  $\lambda$  differed (e.g., a value of  $\lambda = 4.09$  was found in one case, but  $\lambda = 3.66$  under the next random assignment of contrast signs).

The nature of contrasts as species differences leads to another problem in calculating  $\lambda$  from contrasts data. The estimate of  $\lambda$  in contrasts depends not only on the population used to represent a single species, as in calculating  $\lambda$  for species regressions, but also on the populations used to represent other species in the sample. Thus, the population value chosen to represent one species will affect the value of other contrasts that use that value, including internal contrasts higher in the tree whose values are weighted averages of the tips of the phylogeny. While it is possible to estimate  $\lambda$  by calculating contrasts from all permutations of the intraspecific data, even relatively small numbers of intraspecific data points may require many calculations. A randomization procedure would be needed to deal with unequal numbers of intraspecific data points.

One final problem complicates calculation of  $\lambda$  for contrasts. As noted above, estimates of error variance from lower-level contrasts on the tips of the tree may be larger than internal contrasts (e.g., through measurement error; Ricklefs and Starck 1996; Purvis and Webster 1999; C. Janson, personal communication). Using the methods just outlined for calculating error variance of contrasts, we confirmed that error variance declines with increasing node age in our data set (Spearman's rank correlation between intraspecific variance in contrasts in group metabolic needs and the age of the contrasts' node,  $r_s = -0.84$ ,  $N = 11$ ,  $P = .001$ , and between intraspecific variance in contrasts in home range size and the age of the contrasts' node,  $r_s = -0.85$ ,  $N = 11$ ,  $P = .001$ ).

Results based on the SRM for contrasts are therefore inconclusive because of the arbitrariness and difficulty of calculating  $\lambda$ . LS along with major axis (MA) and RMA are all special cases of SRM (see Harvey and Pagel 1991) and therefore provide alternatives to this more general model. Of these, LS assumes that error variance in  $X$  is 0, which is clearly incorrect in our case because error likely exists for both body mass and group composition. Of the remaining methods, McArdle (1988) showed that RMA is superior to MA in simulations where  $\lambda$  was allowed to vary and was assumed unknown by the investigator. We therefore use RMA slopes, calculated through the origin

with the formulae in Garland et al. (1992). We provide some SRM slopes for comparison, but because of the uncertainties involved in calculating  $\lambda$ , we do not provide confidence limits for SRM slopes.

In contrast to the previous results, RMA slopes significantly exceed the predicted value of 1 in contrasts analysis (table 1). Not all slopes differ significantly from 1 when using only internal contrasts, but the predicted value of 1 is nearly outside the lower confidence limit in these cases (table 1). As expected based on estimates of  $\lambda$ , SRM slopes tend to be intermediate to LS and RMA estimates.

Reduced major axis slopes from contrasts in ecological subsets of the data are also significantly  $>1$  in all but one case (fig. 5), with the exception being species that live in open habitats where only five contrasts are available (giving wider confidence limits). Estimates were close to those in RMA analysis of all contrasts (1.80; table 1), which further suggests that compared to nonphylogenetic analyses, slope estimates based on contrasts are less sensitive to confounding effect of dietary and other grade shifts, such as the different ecological factors in figures 2 and 3. Moreover, the variability in contrasts RMA slopes was much lower than species RMA slopes, as indicated by lower coefficients of variation (CV) among slopes calculated for the different ecological niches (e.g., for the "all data" database: CV = 24.90 for species slopes, but 10.17 for contrasts

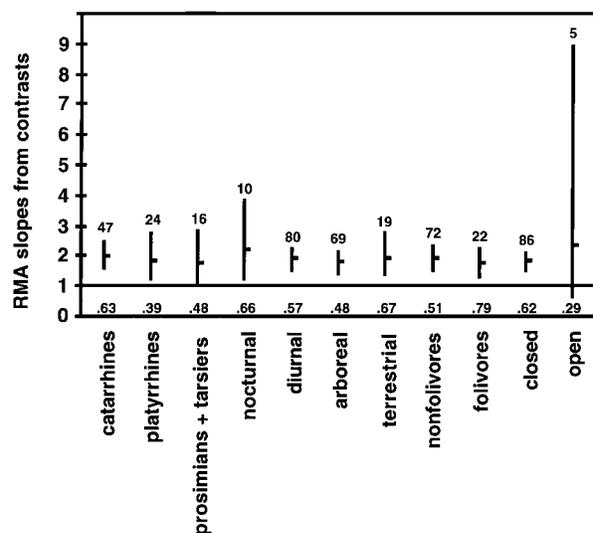


Figure 5: Reduced major axis (RMA) slopes calculated from contrasts within phylogenetic radiations and ecological categories. Horizontal lines represent RMA slope estimates, while vertical bars indicate 95% confidence intervals. Sample sizes are provided above these lines, while correlation coefficients (forced through the origin) are provided along the X-axis. Slope estimates are less heterogeneous than in species analysis (fig. 3) and cluster around the value of the RMA slope for contrasts in table 1 ( $\sim 1.80$ ).

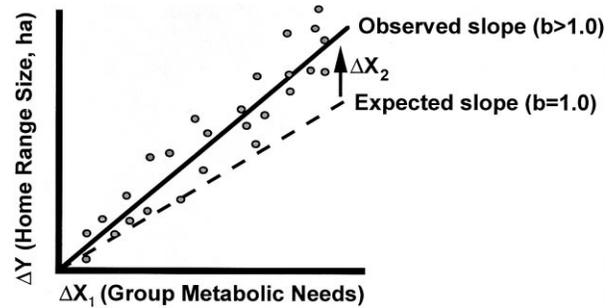
slopes). Because contrasts analysis should be less affected by confounding socioecological variables that are shared through common descent, the differences in slope estimates in species analysis (fig. 3) may not be meaningful.

#### Factors Leading to a Greater than Expected Slope

Based on RMA slope estimates from contrasts data, we conclude that home range size scales with group metabolic needs with a slope  $>1$ . Perhaps the most obvious explanation for the steeper slope is that one or more confounding variables cause increasingly larger home range size with increasing metabolic needs. For example, if terrestrial foraging increases the required ranging area (because of foraging in two rather than three spatial dimensions), and if the amount of terrestrial foraging also increases with body size (hence, with metabolic needs), this would result in a steeper than expected slope. Travel costs may lead to further increases in home range size in more terrestrial species because these costs decrease with body mass in terrestrial travel, but increase with body mass in the vertical travel more commonly associated with arboreal locomotion (Taylor et al. 1970; Schmidt-Nielsen 1984; Kram and Taylor 1990; see also Harvey and Clutton-Brock 1981; Rodman 1984).

A straightforward prediction is that deviations from the expected slope are positively correlated with the confounding variable in question. In addition to terrestriality (the percentage of time terrestrial), relevant variables on which we have data are home range overlap (percentage overlap with neighboring groups) and diet (the percentage of leaves in the diet). Increasing home range overlap may increase range size because more area is needed to compensate for shared use of the range (Milton and May 1976; Damuth 1981; Peters 1983). Diet may have an effect because folivores tend to have smaller home ranges than do species in other dietary categories, possibly as a result of a more dense leaf-based food supply compared to more widely distributed fruit resources (Milton and May 1976; Clutton-Brock and Harvey 1977).

To test the effects of these socioecological variables, we calculated deviations from expected home range size. Residuals were therefore calculated as the vertical deviation from home range size contrasts regressed on group metabolic needs contrasts, with the slope forced through the origin and set to a value of 1 (*dashed line*, fig. 6). We then tested whether contrasts in our continuous measures of substrate use, home range overlap and diet were positively correlated with these residuals. Because specific directional predictions were made, we used one-tailed statistical tests. To explore the independent effects of these variables on home range size, and to explore the role of outliers in our



**Figure 6:** Identifying reasons for the steeper than expected slope;  $\Delta X_1$  (contrasts in group metabolic needs) and  $\Delta X_2$  (contrasts in the percentage time terrestrial, home range overlap, or the percentage of leaves in diet) are expected independently to explain variation in  $\Delta Y$  (contrasts in home range size). To account for the steeper slope forced through the origin,  $\Delta X_2$  must also increase with  $\Delta X_1$ . An approach that avoids problems of collinearity in the independent variables is to test whether  $\Delta X_2$  accounts for significant variation in home range–size residuals based on the expected slope (i.e.,  $b = 1$ , *dashed line*). The regression of residual home range size on socioecological measures was not forced through the origin because the mean residual is expected to be positive. (Data points for this figure are hypothetical.)

bivariate analyses, we also performed multiple regression analyses.

Substrate use could explain the steeper slope if more terrestrial taxa have larger home ranges, predicting a positive association between the percentage of time terrestrial and residuals from a unit slope. In regression of unit-slope home range–size residuals on contrasts in the percentage of time terrestrial, the prediction is supported, but only when three outliers are removed (fig. 7A;  $b = 0.0085$ , one-tailed:  $F = 4.48$ ,  $df = 1, 31$ ,  $P = .021$ ; inclusion of outliers:  $b = 0.0034$ , one-tailed:  $F = 0.66$ ,  $df = 1, 34$ ,  $P = 0.21$ ).

To explain the steeper than expected slope, home range overlap is expected to correlate positively with home range residuals from a unit slope. In support of this prediction, contrasts in home range overlap explain significant variation in home range residuals (fig. 7B;  $b = 0.0057$ , one-tailed:  $F = 8.55$ ,  $df = 1, 42$ ,  $P = .0028$ ). Results remained significant after removal of two outlying contrasts ( $b = 0.0037$ , one-tailed:  $F = 3.13$ ,  $df = 1, 40$ ,  $P = .042$ ).

Finally, leaf-eating primates may require smaller home ranges if their food resources are more densely distributed than those of frugivores (Milton and May 1976; Clutton-Brock and Harvey 1977). To explain why the slope exceeds the predicted value of 1, the percentage of leaves in the diet should therefore be negatively correlated with residuals from the regression of home range size on group metabolic needs. In analyses based on independent contrasts, results approached significance in a one-tailed test

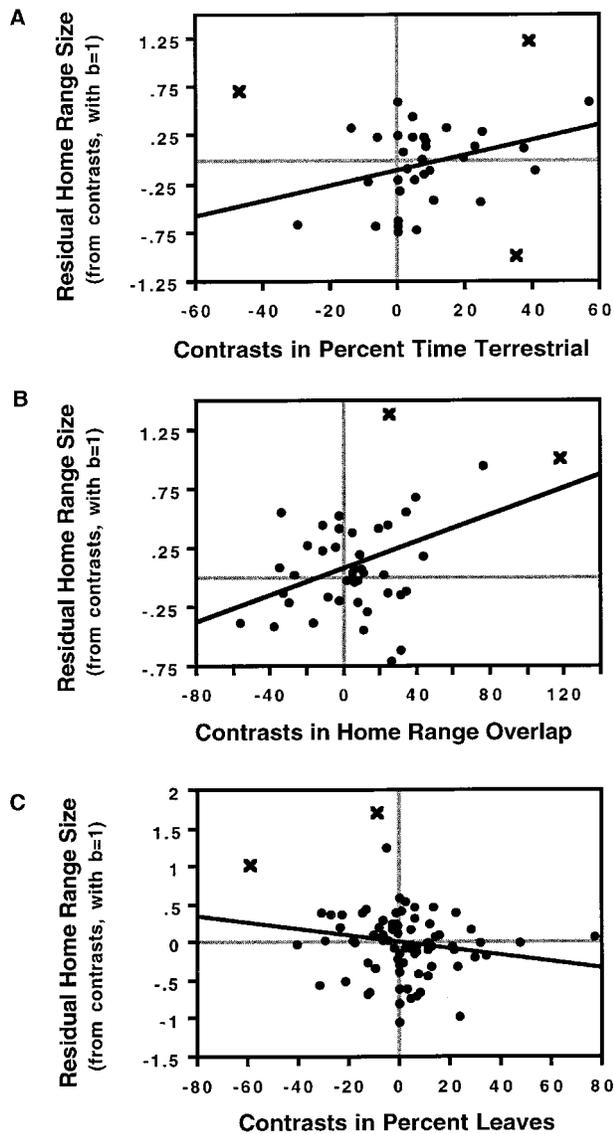


Figure 7: Factors accounting for residual home range size from a unit slope. Plots show contrasts, with outliers represented by X's. Regression lines do not include outliers for percentage time terrestrial (A) but do include outliers for home range overlap (B) and the percentage of leaves in the diet (C).

( $b = -0.0043$ ,  $F = 2.61$ ,  $df = 1, 76$ ,  $P = .055$ ). This result, however, was influenced by several outliers (fig. 7C), and removal of these contrasts produced a nonsignificant result ( $b = -0.0016$ , one-tailed:  $F = 0.47$ ,  $df = 1, 72$ ,  $P = .25$ ).

Diet, home range overlap, and terrestriality are not mutually exclusive as explanations for variance in home range size. Failure to include one of these variables may explain some outlying contrasts in the above analyses if these con-

trasts are heavily influenced by the unaccounted-for variable. We therefore entered all three socioecological variables, along with home range size and group metabolic needs, into CAIC (Purvis and Rambaut 1995) to identify a set of contrasts with information on all variables. This produced only 17 contrasts. No outliers exist in this small set of contrasts, but only the percent time terrestrial explains significant variance in home range-size residuals based on a unit slope in a one-tailed test ( $b = 0.015$ ,  $F = 3.32$ ,  $df = 1, 13$ ,  $P = .046$ ). The other variables, however, approached significance (percentage of leaves:  $b = -0.018$ ,  $F = 2.23$ ,  $df = 1, 13$ ,  $P = .08$ ; home range overlap:  $b = 0.0082$ ,  $F = 2.65$ ,  $df = 1, 13$ ,  $P = .064$ ). We increased statistical power by calculating all contrasts with information on percentage of leaves and home range overlap (but not percentage of time terrestrial). Using these 37 contrasts, both percentage of leaves and home range overlap are statistically significant in multiple regression analysis (percentage of leaves:  $b = -0.0068$ ,  $F = 3.12$ ,  $df = 1, 34$ ,  $P = .043$ ; home range overlap:  $b = 0.0056$ , one-tailed:  $F = 5.25$ ,  $df = 1, 34$ ,  $P = .014$ ).

In summary, the analyses suggest that socioecological variables involving substrate use, home range overlap, and diet contribute to variance in home range size. Future comparative research on home range size should examine several other hypotheses for the steeper slope, including possible correlations between group metabolic needs and interspecific competition, within-group competition, forest productivity (Harestad and Bunnell 1979), and seasonality of resources. Tests of the "locomotor efficiency hypothesis," regarding the possible linkage between travel costs and terrestrial locomotion, will also require data beyond those presently available.

## Conclusions

We conclude that home range size is subject to the scaling of metabolic rate but in combination with other socioecological factors. Compared to some previous research on the scaling of home range size in primates, however, the results presented here are not as clear cut in the finding of a steeper than expected slope (Clutton-Brock and Harvey 1977, 1984; Martin 1981; Mace et al. 1983). In fact, slopes only exceed predictions significantly when combining contrasts data with RMA line-fitting techniques. We therefore consider the appropriateness of each of these methods in what follows.

The allometric slope calculated from species values is equivalent to the slope calculated from contrasts (Harvey and Pagel 1991; Pagel 1993; Martin 1996). Independent contrasts is therefore appropriate for understanding the scaling relationship between two variables (Harvey and Pagel 1991). This is an important point because some

authors have argued against using independent contrasts in allometric studies (Smith 1994; Martin 1996).

In addition, previous simulation research has shown that results from contrasts analysis are less prone to greater than expected Type I and II error rates, as compared to results from species analysis (Martins and Garland 1991; Purvis et al. 1994; Díaz-Uriarte and Garland 1996, 1998; Harvey and Rambaut 1998). Contrasts are also less affected by grade shifts, especially when the goal is to estimate precisely an allometric slope (fig. 1; see also Felsenstein 1985; Ridley 1989; Garland et al. 1993; Price 1997; Purvis and Webster 1999). Thus, allometric slope estimates based on contrasts should be preferred to slope estimates based on species values.

In terms of line-fitting models, LS regression assumes no error variance in the independent variable. However, both of our variables, home range size and group metabolic needs, likely have nonzero error variances. When the error variances of the two variables are known, then the SRM should produce unbiased slope estimates. The structural relations model requires an estimate of  $\lambda$ , which is the ratio of the error variance in  $Y$  to the error variance in  $X$  (see Harvey and Pagel 1991). We found that estimating  $\lambda$  from contrasts has its challenges. The ratio of error variances is sensitive to the arbitrary signs of contrasts. Furthermore, it is not straightforward to use contrasts to calculate error variances because the error variances are sensitive to the values used to represent different species and to the level in the phylogeny at which contrasts are calculated. Error variances from the raw data are therefore unlikely to match error variances from contrasts (cf. Harvey and Pagel 1991).

Because it is not possible to calculate SRM slopes with contrasts data, we used RMA slope estimates (McArdle 1988). Reduced major axis allows for error variance in the independent variable and is appropriate for contrasts when the line is forced through the origin (Garland et al. 1992). Two assumptions of contrasts should be tested and the data transformed appropriately: the absolute value of contrasts should bear no statistical relationship to the square root of their branch lengths, and the intercept should not differ statistically from 0 (see Harvey and Pagel 1991; Garland et al. 1992; Purvis and Rambaut 1995; Díaz-Uriarte and Garland 1996, 1998).

Removal of outliers should also improve slope estimates, and we recommend careful graphical inspection of species and contrasts plots for outliers. Removal of outliers is appropriate in analyses of allometric slopes, as these outliers will have excess leverage on the slope (type a outliers) or may represent the presence of unaccounted-for grade shifts (type b outliers). In our analyses, however, fewer than expected type b contrasts were actually removed. It is possible that outlier contrasts are so plentiful or they

are only slightly “aberrant” that outlier analysis fails to detect them. This situation would be reflected in a lower contrasts correlation than species correlation, even after removing the outliers, as we found here. These conclusions may need to be tempered by the type of grade shift studied, of which there are actually two possibilities. In one type, the slope is biased upward in species analysis because the intercept is shifted up with an increase in the  $X$  variable (e.g., fig. 1). In the second type of grade shift, the slope is biased downward because the intercept is shifted down with an increase in  $X$ . In data sets involving many potentially confounding variables such as ours, a combination of both types will probably exist, yet documentation of grade shifts using phylogenetic methods can be difficult due to low statistical power, especially when using discrete variables (see Garland et al. 1993).

In conclusion, home range scales greater than expected based on consideration of Kleiber’s law alone. Although the value of the exponent used here could be too low, given that field metabolic rate was calculated using LS regression (Nagy et al. 1999), this cannot account for why other variables related to metabolic rate, such as airflow in the lungs and surface area of the intestines, scale according to Kleiber’s law (Peters 1983; Martin et al. 1985). Finally, our research further highlights the benefits of using contrasts to calculate allometric slopes. Issues concerning slope estimation from contrasts that deserve future attention include the use of different line-fitting methods with contrasts data and estimation of error variances for SRM, the effect of grade shifts on trait correlations, slope estimates and the coefficients of variation in slope estimates of subsets of the data, and use of outlier analyses with contrasts data.

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