VOL. 172, NO. 1 THE AMERICAN NATURALIST JULY 2008

Exploring Predictions of Abundance from Body Mass Using Hierarchical Comparative Approaches

Brian J. McGill[*]

Department of Biology, McGill University, Montreal, Quebec H1A 1B1, Canada

Submitted October 6, 2006; Accepted February 11, 2008; Electronically published May 27, 2008

ABSTRACT: Understanding and predicting how and why abundance varies is one of the central questions in ecology. One of the few consistent predictors of variation in abundance between species has been body mass, but the nature of this relationship has been contentious. Here I explore the relationship between body mass and abundance in birds of North America, using hierarchical partitioning of variance and regressions at taxonomic levels above the species. These analyses show that much variation in abundance is found across space, while a moderate amount of variation is found at the species/genus and also at the family/order level. However, body size and trophic level primarily vary at the family/order level, suggesting that mechanisms based on body size and energy should primarily explain only this moderate-sized, taxonomically conserved component of variation in abundance. Body size does explain more than 50% of the variation at this level (and almost 75% when trophic level is also included). This tighter relationship makes clear that energetic equivalence (slope $= -3/4$) sets an upper limit but does not describe the relationship between body mass and average abundance for birds of North America. Finally, I suggest that this hierarchical, multivariate approach should be used more often in macroecology.

Keywords: scale, energetic equivalence, Damuth's rule, mass-abundance.

An important question in ecology is what controls variation in abundance, and at least two textbooks (Krebs 1972; Andrewartha and Birch 1984) define it as the central question. Likewise, from an applied point of view, conservation has been defined as the "science of scarcity" (i.e., of low abundance; Soulé 1986). That abundance varies between species is indisputable. *Birds of North America* (Poole 2005) shows up to nearly seven orders of magnitude of variation in abundance between species (McGill 2006).

One approach to understanding this enormous variation in abundance between species is to identify traits that make a species abundant or rare (Rosenzweig and Lomolino 1997), but Murray et al. (2002) showed that dozens of studies have made little progress on this program. One of the few traits that has been consistently tied to abundance is body mass, which usually has a negative relationship (White et al. 2007). In a general sense, this almost has to be true—it seems obvious that there will be more mice than elephants in a field. At the other extreme of specificity is Damuth's (1981, 1987, 1991) energetic equivalence rule, which states that abundance N relates to body mass M according to $N \propto M^{-3/4}$, leading to the fact that the energetic requirement for an entire species, E_{species}, is constant between species: $E_{\text{species}} \propto N \times E_{\text{individual}} \propto M^{-3/4}M^{3/4} \propto M^0 \propto c$, assuming that individual energy requirements scales as $E_{\text{individual}} \propto M^{3/4}$ (Peters 1983; Calder 1984).

Support for the more specific energetic equivalence rule is mixed (Blackburn et al. 1993; Russo et al. 2003). Abundance clearly decreases with body mass, but it is unclear whether it decreases with a slope of $-3/4$ on a log-log scale (energetic equivalence rule) or something less steep (which would merely imply the weaker claim that mass affects abundance). Moreover, these regressions usually contain many orders of magnitude of variation in abundance for a given mass (i.e., large scatter) with concomitant low r^2 (often $r^2 < 0.15$). Figure 1 is typical; the regression is highly significant ($P < .0001$), the slope is negative (-0.39) but not close to $-3/4$, the r^2 is only 0.19, and there are 2.5 orders of magnitude of scatter about the line. It is hard to use such data to make definitive statements about the slope. A recent review of studies on mass-abundance relationships in birds (Russo et al. 2003) shows that this is typical for birds: average slope is -0.56, but the 95% confidence interval is (-1.54, 0.42) and the average r^2 is 0.147 (my summary of their table 1).

Why has ecology been unable to come to a clear res-

---

[*] E-mail: mail@brianmcgill.org.

Am. Nat. 2008. Vol. 172, pp. 88–101.
DOI: 10.1086/588044

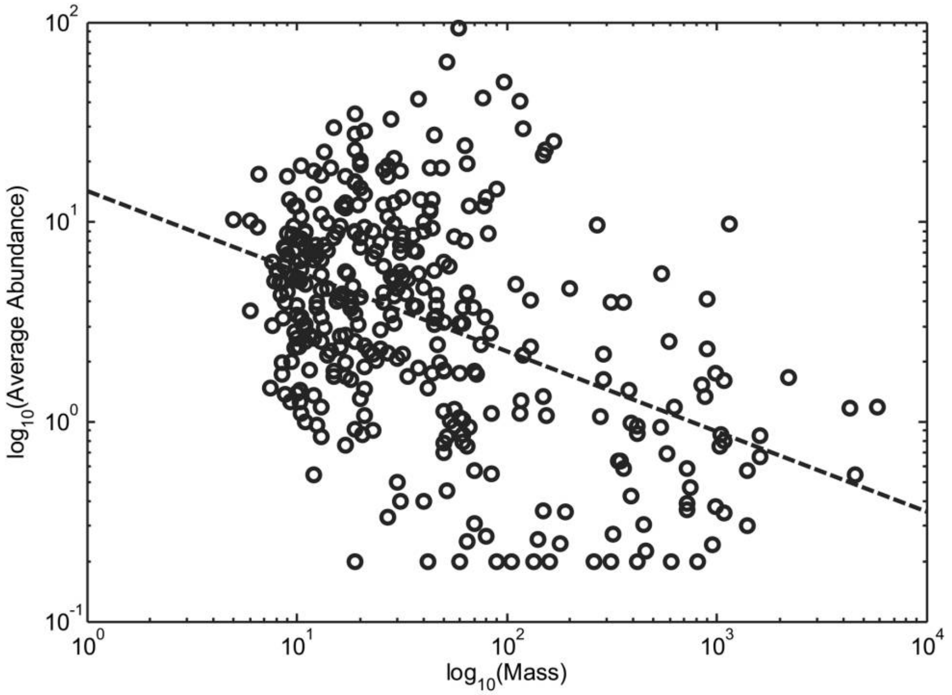

Figure 1: A typical example of the relationship of abundance to body mass. This figure is derived using the North American Breeding Bird Survey data described in "Methods" but analyzed at the level of species. It is similar to a figure first published by Brown and Maurer (1987). It is typical of the degree of scatter present when analyses are carried out at the species level.

olution of the nature of the mass-abundance relationship and whether energetic equivalence holds? I would suggest it is because there are a wide variety of causal factors implicated in abundance. Abundance is important, in no small part because it is highly integrative of the multitude of processes that affect an organism. Thus, many factors affect abundance, including competition, predation, parasitism and disease, resource availability, and climate (Newton 1998). Single-factor explanations (even with another integrative measure such as body mass) can hope to explain only a limited amount of the variance, a problem with which ecology struggles generally (Hilborn and Stearns 1982; Quinn and Dunham 1983). Unlike physics, which rarely deals with more than one or two forces simultaneously, ecology must make sense of situations where a half dozen or more forces have a significant impact on the outcome.

One way to deal with multiple causal factors is to build multivariate models. Toward this end, I propose a model based on the idea that the balance between energy availability and energy requirements must play a significant role in governing abundance (while still ignoring many other potentially important nonenergetic factors, such as species interactions):

$$\begin{aligned} N_i &\propto \frac{\text{energy accessible to species}}{\text{energy required by individual}} \\ &\propto \frac{\text{generalist}_i \times \text{trophic efficiency} \times \text{NPP}}{(M_i^{3/4})^z} \qquad (1) \\ &\propto \frac{\text{generalist}_i \times \varepsilon^{T_i}\text{NPP}}{M_i^{3/4z}}. \end{aligned}$$

Values that are subscripted by i are assumed to vary between species. The term "generalist$_i$" is used to measure the proportion (0–1) of resources at a specific trophic level that are used by a species. Because I do not have a good measurement for generalist$_i$ that is comparable across all species of birds, I treat it as a constant. The efficiency ε of transfer of energy between trophic levels (Lindeman 1942) is assumed to be a constant (often assumed to be about 10%; Whittaker 1975). This means that the energy available at a trophic level, T_i, can be described as ε^{T_i}. NPP stands for the net primary productivity. Because I use abundances aggregated across the entire continent, I treat NPP as a constant. The term M_i represents body mass, and the model assumes that energy requirements are well described by $M^{3/4}$ (Peters 1983;

Calder 1984; Brown et al. 2004; Savage et al. 2004). Although it has been suggested that birds may have a lower exponent for the metabolic relationship (Bennett and Harvey 1987), one recent comprehensive survey (Savage et al. 2004) suggests that 3/4 is the appropriate exponent for birds. Finally, the variable z is a measure of energetic equivalence; if $z = 1$, then energetic equivalence holds, with each species using the same amount of energy. If $z > 1$, then small species get a disproportionate share of energy, and vice versa. The model ignores many potential causal factors of abundance but still captures more of reality than the univariate mass-abundance relationship and is a reasonable attempt at framing a generally predictive rule that cuts across many species. Note that the energetic equivalence rule is a special case of equation (1), with $z = 1$, generalist $= c_1$, and NPP $= c_2$ both constant, with all species assumed to come from a single trophic level T (a common restriction in studies of energetic equivalence; Damuth 1987, 1991; Juanes 1986).

The inclusion of multiple explanatory variables in a predictive model is a step toward addressing the multicausality problem in predicting abundance, but there are many limits to multivariate regression, including an inability to resolve collinearity, to show causality rather than correlation, and the changing roles of variables with changing scales. A tool that allowed the matching up of specific independent variables with specific components of variation in the dependent variable ("abundance" in this model) would improve the power of multivariate regression. In particular, breaking variation in the dependent variable into evolutionarily conserved, evolutionarily labile, and ecologically variable ("across space" in this model) components could help elucidate mechanisms that drive abundance. Ecologists studying life histories (Stearns 1983; Bell 1989; Harvey and Pagel 1991 and references therein; Ricklefs and Nealen 1998) have long made use of taxonomically nested ANOVAs (partitioning variance among species within genera, genera within families, etc.) and performing correlations or regressions at different taxonomic levels as motivated by the variance partitioning results. For unknown reasons, macroecologists, including those studying the mass-abundance relationship, have tended to ignore these tools. Specifically, it has long been known that most of the variation in body mass occurs at the order level (e.g., Harvey and Pagel 1991, their tables 5.1, 5.2). Thus, only the variation in abundance at the order level can possibly be explainable by mass or the mechanism of energy requirements driven by metabolism driven by body mass, as assumed in the energetic equivalence hypothesis. But I know of no study that has quantified how much variation in abundance occurs. Variation in abundance at levels below order will likely be explained by factors other than mass.

In summary, I explore the predictive power of body size to explain abundance, starting from the assumption that many factors will contribute to abundance. To begin to isolate the role of body mass and to begin to approach a more mechanistic understanding, I (1) place body mass in a multivariate context by adding trophic level as an explanatory variable and (2) use hierarchical partitioning of variance. The importance of trophic level has long been recognized, as in work by Juanes (1986), Damuth (1987, 1991), and Jennings and Mackinson (2003), but Juanes and Damuth treated trophic level as a nuisance to be controlled for rather than as a potential explanatory factor. Similarly, the role of taxonomic scale has been recognized (Nee et al. 1991) but not placed into a partitioning of variance context.

Methods

Data

I used abundance data from the North American Breeding Bird Survey (BBS; Robbins et al. 1986; Patuxent Wildlife Research Center 2001). The BBS covers all of the continental United States and the lower portion of Canada. These data are gathered by volunteer observers, who sample more than 2,000 routes every year, counting individuals of every bird species seen or heard at 50 stops along a 25-mile (approximately 40 km) route. Since each route is the same length, I use birds counted per route as the measure of density (i.e., there is no need to standardize for area). I used data averaged over the 5-year period 1996–2000 to eliminate sampling noise and used only 1,401 routes that the administrators deemed to be high quality for all 5 years, based on criteria such as weather conditions and observer experience (for details, see McGill and Collins 2003). Thus, one abundance value (usually 0) was recorded for each species at each site.

For body mass, I used the mass estimates given in Sibley's (2000) *Guide to North American Birds*. In sexually dimorphic species, I used a geometric mean of the two sexes. For taxonomy, I used the American Ornithological Union taxonomy to assign an order, a family, and a genus to each species. Quantitative data on diet are not available for all species. Moreover, in birds, family is a reasonably good approximation of feeding guild and, hence, diet type. Thus, each species within a family was assumed to have the same trophic level. Trophic levels were assigned on a scale from 0 (eating only plant matter, such as seeds) through 1 (eating entirely insects) up to 2 (eating entirely vertebrates). Trophic levels were derived from Kauffman's (1996) *Lives of North American Birds*. Intermediate values were assigned based on the qualitative descriptions provided; for example, diet types of 0.25, 0.5, 0.75, and 0.9 were used, based on qualitative descriptions of the relative portions of insects and plant matter in the diet. Although these assignments of trophic level are inexact, they are approximately correct and are the best quantitative assignments available for a large assemblage of birds, to my knowledge. All assignments were done before the analysis, and no adjustments were made, so biases should not have occurred. Ultimately, inaccuracies serve as a source of noise and should lead to conservative results in the analyses where I am assessing predictive power (r^2) of trophic level. Finally, omnivores such as corvids and nectivores such as hummingbirds were not included in the analysis since it was unclear which trophic level to assign them to.

Families where all members were observed at fewer than 10 routes, where the diet was omnivorous or nectivorous (as discussed above), and where a majority of the member species are primarily aquatic were removed a priori. As a result, 374 species were classified into 164 genera, 37 families, and 10 orders. Ensuing analysis identified one serious shortcoming with these a priori selection criteria: I failed to account for the fact that seven families were monospecific within the BBS survey range. Had these families been monospecific globally, they might have merited inclusion, but an analysis of the monospecific families indicate that their role as single-species families was due entirely to the limits of the BBS geographical coverage. Thus, the seven monospecific families comprise bird families whose range barely extends into the BBS region (phainopepla, red-billed leiothrix), Eurasian families with a single species that has dispersed into or invaded North America with unusual outcomes often indicative of ecological release (European starling, horned lark, bushtit, brown creeper), and poorly observed nocturnal birds (Tytonidae). Removing the seven monospecific families matches the spirit of the analysis (capturing effects at higher taxonomic levels) and, more importantly, eliminates points that are clearly unrepresentatively sampled. Analyses were run with and without these seven monospecific families, and the results and their significance or nonsignificance were similar, with most of the relatively small difference being due to the single case of the European starling. The starling was enough of an outlier and unusual enough as an extremely successful invader that it arguably should be removed in any case. Therefore, all results are reported with the seven monospecific families removed, but this is technically a post hoc removal and is therefore reported here. Thus, in the end, results are reported for 367 species classified into 157 genera, 30 families, and 10 orders.

Hierarchical Partitioning of Variance. To explore the role of spatial and taxonomic scale, I fitted a nested one-way ANOVA model. I used log of abundance as the dependent variable versus different years to provide replicates nested within route nested within species within genus within family within order. By using years as the lowest level, not only year-to-year variation but also all other sources of error, such as measurement error, are attributed to the year level. In principle, a similar design could have been used, with route crossed with taxonomy rather than nested within taxonomy. However, there are an average of more than 70 species per route, so the measurements of different species on one route are largely independent of each other, the variation of abundance within a species across routes is clearly dominated by effects other than the average abundance of that route, and the route effect was considered uninteresting here (i.e., I wanted to look at species + species × route, which was the same as route nested within species, and not species + route + species × route, which would be obtained by crossing route with species), so I chose the nested design.

Each level was treated as random (Type II ANOVA). Several methods for calculating the variance components exist. They produce identical results for balanced designs, but unfortunately, they produce different answers for unbalanced data, such as the observational (and hence necessarily unbalanced) data used here. I examined two methods. The first was based on using REML (restricted maximum likelihood), as implemented in R, version 2.3.1 (R Development Core Team 2005), to estimate the model. I used the "lme" function in package "nlme" using default settings. I then used the "varcomp" function in the R package "ape" to estimate the variance components associated with each level with scaling turned on. Thus, a typical line of code was

$$\begin{gathered}\text{varcomp(lme(log (Abund)} \sim 1,\\ \text{random} =\sim 1|\text{Order/Family/Genus/Species},\\ \text{data} = \text{dataframe\_name),1).}\end{gathered} \tag{2}$$

The second method used classic sum of squares (SS) methods (Sokal and Rohlf 1981), using the calculation approach for unbalanced data suggested by Gower (1962) and implemented in MATLAB code available from me. This implementation was benchmarked against several published examples to ensure accuracy. Formal comparisons of the SS and REML methods (Swallow and Monahan 1984; Huber et al. 1994) generally find that both methods work well under most conditions. For my data, the results were qualitatively similar (large variances remained large, and small remained small), but there were notable quantitative differences. Overall, the REML method pushed more variance into species levels, while SS methods placed more variance in orders. Rank order of the sizes of the variance components remained the same between the two methods except when the species and order levels were very similar in magnitude. Then the aforementioned bias typically flipped the rank of the two roughly equal variance components. Since this article is not an analysis of calculation methods and the results were qualitatively similar, I report only the SS results, for two reasons. First, SS is an unbiased estimator, and second, the REML method was not able to run to completion (producing abortive errors) on my largest analysis (with 1.47 million records).

Analysis was also conducted with the year and route levels removed (leaving all error lumped into the species level). This was accomplished in two ways. First, the abundance for each species was averaged across every site where the species was observed (nonzero), giving an average abundance (AvgAbund). Second, the maximum observed abundance across any route for a given species was used, giving a maximum abundance (MaxAbund). Then, nested models were then fit with log abundance versus the hierarchy with route and year removed. Finally, the same techniques were used to analyze partitioning of variance in two presumed causal variables (mass, trophic level). Mass was available at the species level, and so log(mass) was analyzed for species within genera within families within orders. Trophic level did not vary within a family (by the method by which I obtained the data) and so was analyzed only as trophic level (untransformed continuous variable) by families within orders.

Regression at Guild Level. To further explore the role of taxonomic scale, I fitted equation (1) at the family level as follows. Trophic level was already assigned at the family level. Body mass for a family was calculated by taking a geometric average of the body mass of every species in the family. Abundance for the family was analyzed by taking the geometric average of either the average abundance or the maximum abundance for each species in the family as above. Taking the log of both sides of equation (1) leads to a linear equation in which

$$\begin{aligned}\log(N_i) &= T_i\log(\varepsilon) + \log(\mathrm{NPP}) + 3/4z\log(M_i)\\ &= b_0 + b_1T_i + b_2\log(M_i),\end{aligned}$$

thereby allowing standard multivariate ordinary least squares linear regression to be performed on abundance (average or maximum) versus mass or versus mass and trophic level. The log transform of mass and abundance also produced more normal distributions. A regression with only mass as an independent variable was also performed to obtain the best estimate of the slope of this relationship.

Hierarchical Reshuffling. It is well known that measures of explained variation (e.g., r^2) increase as the number of data points decreases (Zar 1999). Thus, the r^2 analysis performed on 30 families is expected to have a higher r^2 than the analysis on 367 species by statistical artifact alone; in other words, having 10 or more species averaged together to produce a single family-level data point reduces the noise. I tested for this possibility by using reshuffling. The previous section described regression analyses performed using the true taxonomic assignment of species to families. These analyses were repeated but using 1,000 regressions where species were randomly reshuffled into new families before aggregating the data up to family. Thus, every species was assigned randomly to a family without regard to taxonomy, and each family contained the same number of species as in the true taxonomy. Family-level values for mass, trophic level, and abundance were then recalculated according to this new reshuffled taxonomy as above. The r^2 value was calculated for each of these random reshufflings, and the true r^2 was compared with the median reshuffled r^2 for statistical significance by a one-sided t-test at the $\alpha = 0.05$ level. Thus, if the r^2 based on the real taxonomy was greater than the ninety-fifth percentile of the 1,000 reshufflings, then the true taxonomy was deemed to have a statistically significant effect on the predictive power of the model. Studies of mass-abundance relationships at the individual level (i.e., size spectra sensu White et al. 2007) also typically aggregate data points into bins based on body size. Although the focus here is on mass at the species level (i.e., species density relationships sensu White et al. 2007), an analysis of the effect of this type of aggregation was also performed by lumping species-level data into bins based on body size (the same number of bins as the number of families were created for comparison's sake).

Results

Hierarchical Partitioning of Variance

Table 1 contains the results of variance partitioning analysis. Very approximately, 80% is explained, of which half is explained by space within a species. Of the remaining half that is explained by taxonomy (i.e., species and higher groupings), roughly half (i.e., one-fourth) is explained by species/genus-level factors, and the balance is explained by order/family factors. The fact that the largest variance component by a substantial margin (37%) occurs within a species across space is especially surprising. The distinction between analyzing a body mass/density relation-

Table 1: Results of partitioning of variance analysis

Between	Within	Abundance % variance	Average abundance % variance	Maximum abundance % variance	Mass % variance	Trophic level % variance
Replicates /year	Routes	22.1	…	…	…	…
Routes	Species	37.1	…	…	…	…
Species	Genera	11.8	32.0	39.4	2.4	…
Genera	Family	6.5	14.5	12.2	9.1	…
Families	Order	8.0	2.1	1.7	6.1	12.4
Orders	Class	14.5	51.4	46.6	82.4	87.6
Total		100.0	100.0	100.0	100.0	100.0

Note: This table shows the percentage of variance in five variables (columns 3–7) explained by each level of taxonomic hierarchy that is relevant. Columns total to 100% except for rounding errors in the last decimal place. Variation between routes was analyzed only for abundance. Abundance was then reanalyzed with routes removed by an averaging and a maximum for abundance as described in “Hierarchical Partitioning of Variance” in “Methods.” Trophic level was coded at the family level and does not vary within families for this reason.

ship using local or ecological density (“route” in this model) versus regional/global densities was first discussed by Nee et al. (1991) and Damuth (1991) and has been identified as a critical causal factor in the varying results obtained (Blackburn and Gaston 1996). These results suggest exactly how much variance is to be found at the site level within a species and I hope will convince researchers of the importance of this issue (White et al. 2007). The variances of both mass and trophic levels are concentrated at the order level.

Regression at Guild Level

The regressions of abundance versus mass and diet aggregated to the family level are summarized in table 2 (also see fig. 2), which jointly shows that a 10-fold increase in mass leads to a 2.6-fold decrease in average abundance, while an increase of one trophic level results in a 2.2-fold decrease in average abundance. The 95% confidence interval (CI) for mass includes −0.75 for MaxAbund but excludes −0.75 for AvgAbund. The overall small effect of post hoc removal of monospecific families can be seen in the third row (with all seven monospecific families included) and the fourth row (just the European starling is removed but keeping the other six monospecific families in the analysis).

Since there is collinearity between diet and mass while the energetic equivalence rule (EER) hypothesis emphasizes the coefficient for mass, regressions with mass only were run as well as a regression with diet only (table 2, rows 5–7; also see fig. 3). So when analyzed separately, a 10-fold increase in mass leads to a 3.4-fold decrease in average abundance (or a 5.6-fold decrease in maximum abundance), while an increase of one trophic level results in a 3.3-fold decrease in abundance in birds. Interestingly, the slope for average abundance versus mass is close to −0.5 and has a 95% CI, which excludes the −0.75 predicted by the EER sensu strictu, but the slope for maximum abundance versus mass centers exactly on −0.75 to two decimal places, as predicted by the EER.

Table 2: Summary of regressions

Dependent variable ($\log_{10}$ transformed)	Intercept	Slope for $\log_{10}$(mass)	95% confidence interval for $\log_{10}$(mass)	Slope for trophic level	*P*	r^2	Families included
AvgAbund	1.44	−.416	(−.570, −.263)	−.339	1.1×10^{-8}	.74	>1 species
MaxAbund	2.60	−.599	(−.840, −.357)	−.415	1.9×10^{-9}	.68	>1 species
AvgAbund	1.37	−.275	(−.492, −.059)	−.473	4.0×10^{-6}	.518	All
AvgAbund	2.56	−.527	(−.759, −.296)	−.509	1.8×10^{-8}	.66	All except European starling
AvgAbund	1.36	−.5373	(−.715, −.359)	NA	1.1×10^{-6}	.58	>1 species
MaxAbund	2.49	−.75	(−1.00, −.49)	NA	2.1×10^{-6}	.56	>1 species
AvgAbund	.918	NA	NA	−.514	5.2×10^{-5}	.45	>1 species

Note: A series of regressions were performed at the family level with either average or maximum abundance (AvgAbund or MaxAbund, respectively) as the dependent variable and mass and/or trophic level as the independent variables. As described in the text, most regressions were reported excluding monospecific families, but two additional regressions are shown to substantiate the claim of the minimal impact of this issue on r^2. NA = not applicable because either only one calculation was done, meaning there is no 95% range, or else the comparison to random is not meaningful.

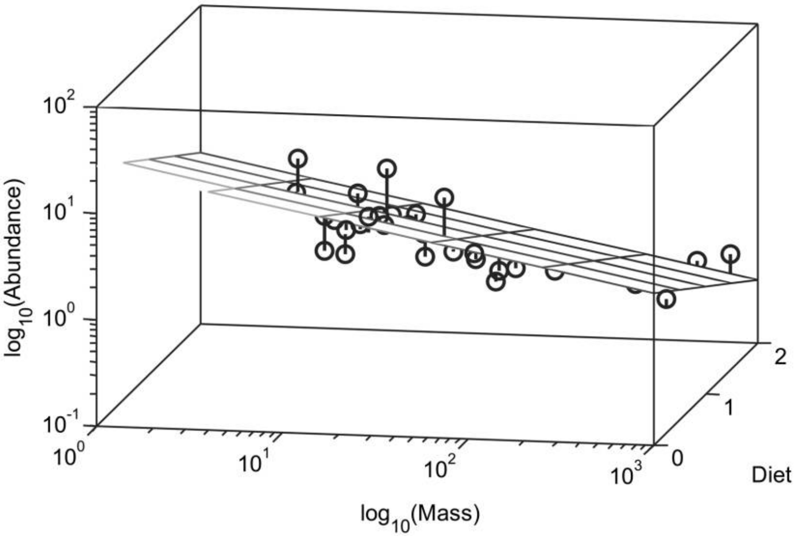

Figure 2: Effect of mass and diet on average abundance. Plot of the average abundance as a function of mass and diet (trophic level). Abundance and mass are log transformed while diet is not. The circles represent the actual values for families, while the lines indicate the residual relative to the least squares regression plane. Coefficients and *P* values are reported in table 2.

Hierarchical Reshuffling

The increases in r^2 from 0.19 for a species-level regression to a value of 0.58 for the regression of average abundance versus mass alone and up to 0.74 when trophic level is added seem like a strong confirmation that the energetic equivalence rule functions better at the feeding guild or higher taxonomic levels than it does at the species level. Visual inspection of the plots (fig. 1 vs. figs. 2, 3) also confirm a drastic decrease in scatter. However, as described in "Methods," further analysis is needed to confirm this in the context of aggregating data. The results of performing aggregations by bins based on mass of species or by random assignments (reshuffling) are reported in table 3 and figure 4. It is clear that the increase in r^2 when using actual families instead of random families is not only large but also larger than likely due to chance ($P = .007$ or .001, depending on whether trophic level is included). The actual taxonomic relations appear to play a significant role. On the other hand, the aggregation based on body size bins had little effect and seems likely to be the same as aggregations performed by chance. Overall, aggregation appears to have relatively little effect on r^2 unless it is using the true phylogenetic relationships.

Discussion

Nature of Mass-Abundance Relationship

With respect to the energetic equivalence rule ($z = 1$), I have shown for birds of North America that energetic equivalence is a constraint setting an upper limit on achievable abundance, but it is not an expectation. When maximum abundance is used as the measure, regression finds a slope nearly identical to 3/4 (i.e., $z = 1$). Although circumstantial, the extremely good match of the 3/4 exponent in the upper bound of abundance with the 3/4 exponent of metabolic allometry is strongly suggestive of a role of energy as a mechanism in this constraint. Moreover, there are other pieces of evidence suggestive of the role of energy relating to the intercepts between groups and other factors not studied here (reviewed in White et al. 2007). For every family, the maximum abundance found on the 3/4 line is approximately realized at some location. This is a stronger statement than the one by Blackburn et al. (1993), who, using quantile regression, showed only that the upper boundary sloped at $-3/4$ (implying that only a few species reach this envelope). However, the locations of maximum abundances for different guilds vary widely and more or less randomly across an area nearly the size of the North American continent. Thus, at no one point can we expect $N \propto M^{-3/4}$ within a single local community.

For within-community allometries, a more appropriate measure would be based on average abundances, which scales roughly as $N \propto M^{1/2}$ ($z < 1$). An exponent close to 1/2 has also been found for several aquatic groups (Cyr et al. 1997) and for subsets of birds (Juanes 1986; Russo et al. 2003; both find wide variation, but the average slope for each study was near 1/2). For these conditions, the EER sensu strictu is incorrect. Specifically, large organisms

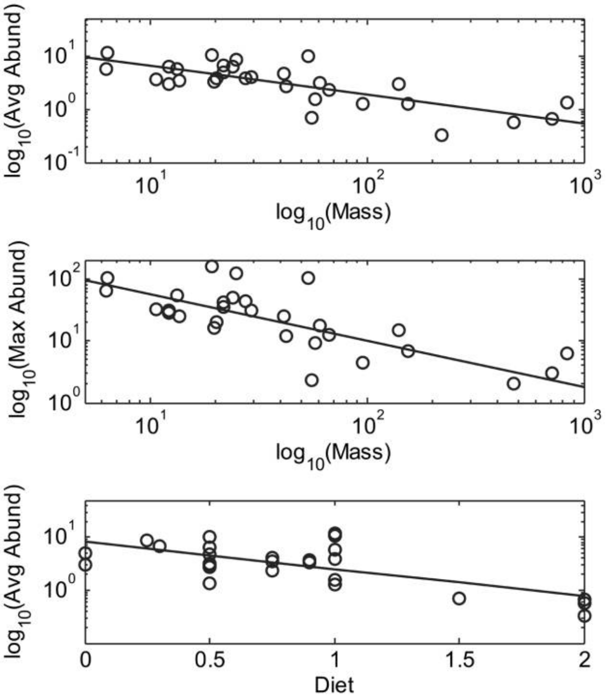

Figure 3: Effects of mass and diet individually on average and maximum abundance. Since mass and diet (trophic level) interact with each other, analysis was performed on single variables as well. All analyses are at the family level. *Top*, log average abundance versus log mass; *middle*, log maximum abundance versus log mass; *bottom*, log average abundance versus diet (untransformed). Coefficients and P values are reported in table 2.

are getting more than their share of energy available relative to their requirements, or big is better (Maurer and Brown 1988). A large number of hypotheses could explain this. One of many possible arguments based on energetic equivalence would be to suggest that birds are thermally constrained rather than resource constrained, which leads to $E \propto M^{-1/2}$ (Meehan et al. 2004) and hence $N \propto M^{1/2}$ under equivalence. Alternatively, there may in fact be an inherent inequality, whereby large animals do get a disproportionate amount (Maurer and Brown 1988; Russo et al. 2003) due to some inherent advantage, such as a broader diet (Wilson 1975; Cohen et al. 1993), faster movement (Calder 1984), or outright social/competitive dominance due to body size (Brown et al. 1994), which makes $z < 1$. It is unclear how much of the average mass-abundance relationship with an exponent 1/2 is driven by energetic factors relative to other factors, and it should not be taken as proven that this mass-abundance relationship is a result of energetic mechanisms.

Although this study is consistent with several earlier studies (as cited above), it disagrees with a few studies that have found a $-3/4$ exponent without using maximum abundances. Several of these (Enquist et al. 2001; Li 2002) share the axes of mass and abundance, but the points represent something other than species; they represent entirely different patterns, probably with different mechanisms (White et al. 2007), and are not directly comparable to the results here. There remains a handful of studies for mammals (Damuth 1981, 1987) and marine invertebrates (Marquet et al. 1990), where each data point represents a species, nonmaximum densities were used, and a slope of $-3/4$ was found. All of these studies used local rather than global abundances that were either (1) averaged across time or space, possibly causing the abundances to approximate maximum abundances because abundances occur on a log scale, which causes the largest abundance to dominate an arithmetic average, or (2) compiled from many studies, which means the compilations may be biased toward using maximum abundance because of a bias of field ecologists to study species where they are most abundant (White et al. 2007 and references therein). If true, these results would be consistent with my finding that maximum abundances show energetic equivalence. Alternatively, many studies show a wide range of exponents ranging from -0.5 to -1.1 (Juanes 1986; Marquet et al. 1995; Cyr et al. 1997; Russo et al. 2003), so it is also possible that these particular studies or groups were close to -0.75 by chance. If the methods used here (where analysis is performed at the family or order level and the scatter and resultant variability in estimates of the slopes are greatly reduced) are carried out in other taxonomic groups, then perhaps we will be able to make more precise statements in the future. On an opposite note, it appears that the claim that a plot of abundance versus mass produces a cloud that is better treated by quantile regression than a single line with a single slope (Maurer and Brown 1988; Cotgreave 1993; Marquet et al. 1995) also does not hold when a family-level analysis on global abundances is performed.

Interpretation of Partitioning of Variance

The partitioning of variance (table 1) found that of the explained variance in abundance, approximately one-half was across space within species, one-fourth was at low taxonomic levels (species or genera), and one-fourth was at high taxonomic levels. Most of the variance in mass and diet occurred at the order level. I propose that, given the hierarchical, nested nature of variance in both the dependent and the independent variables, the model of equation (1) can be best conceptualized as also occurring in a hierarchical fashion as shown in table 4. Due to limits in the availability of data, this article addresses only the cells in bold, and many additional energy-related or non-energy-related factors could be identified and placed into the framework. Only for those taxonomic levels at which a medium to high level of variation in a potential explanatory factor is found (table 4, fourth and sixth columns) is the factor likely to explain the corresponding variation in abundance (second column), and then the factor can explain just the amount of variation in abundance found at that level. In other words, important relationships are those within a single level where the variance is high (or at least medium) for both the dependent and the independent variable. This gives us an algorithm for identifying potentially important relationships.

The single largest component in variation in abundance occurs at the across-space-within-species level. This is unlikely to be explained by mass. Although the partitioning of variance of mass (table 1) did not have the level of individuals across space, other evidence suggests that variation in mass at this level is small. An informal evaluation of *Online Birds of North America* (Poole 2005) shows that variation in body mass within a site (for one gender) is usually on the order of 5%–10%, and maximum variation between sites (e.g., northern versus southern edges of the range) can reach 20%–30% (but is probably heavily biased toward reporting cases of the greatest variation). On the log abundance scale on which the variance partitioning was carried out, these are quite small amounts of variation, while abundance typically varies by two to three orders of magnitude within a species across its range (Brown et al. 1995; B. J. McGill, unpublished manuscript). One would have to hypothesize an extreme magnification of these small differences in mass to explain the large variations in abundance between sites. Lacking a specific hypothesis of a mechanism causing this magnification, it is more parsimonious to look elsewhere. Using the aforementioned algorithm suggests that variation in abundance between sites within a species is due to the energy availability factors (NPP; availability of particular categories of resources, such as seeds or leaf-eating insects; Korpimaki and Norrdahl 1991; Newton 1998; Karanth et al. 2004; Nilsen et al. 2005), energy requirement factors (variation in climate, with implications for factors such as thermoregulation), and possible unidentified non-energy-related factors (e.g., competition). Carbone and Gittleman (2002) have studied how prey availability interacts specifically with the mass-abundance relationship. Study of these nonbody size factors and the resulting intraspecific variation across space are the subject of separate research programs on home range sizes (Carbone et al. 2005). Study of the patterns

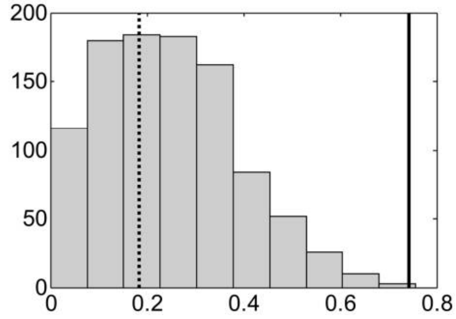

Figure 4: Hierarchical reshuffling results. A test of the effects of aggregation alone on r^2 values in regression versus the effect of using the actual taxonomy and the hypotheses that family is a more appropriate level of analysis. Bars give a histogram of r^2 values out of 1,000 reshufflings of taxonomic association. The solid vertical line represents the r^2 value for the true taxonomic hierarchy. The dotted vertical line indicates the r^2 found when aggregation was performed by body-size bins and was not significantly different from random aggregations. Note that it is in the far right tail and can be interpreted as being statistically significantly greater than the effect of aggregation alone.

Table 3: Predictive power based on different methods of aggregation

Aggregation mode	r^2	95% range for r^2	Percentile vs. random
Mass only:			
Species (no aggregation)	.19	NA	NA
Family/guild	.577	NA	.007
Mass bins	.183	NA	.372
Random	.152 (median)	(2.1×10^{-9}, .446)	NA
Mass + trophic level:			
Family/guild	.742	NA	.001
Mass bins	.1666	NA	.537
Random	.236 (median)	(3.1×10^{-4}, .514)	NA

Note: Species-level mass and average abundance were averaged across groups where the groups were determined by taxonomy (groups of families), by mass bins (groups of species similar in mass), or randomly (but with groups with the same number of species as the families). The random case was repeated 1,000 times. The r^2 values for a subset of the regressions reported in table 2 were then calculated. For the random case, the one-tailed range covering 95% of the cases is reported. For the deterministic family and mass bin cases, the percentile of the observed r^2 in the random cases is reported. This is analogous to a P value in that the increase in r^2 is due solely to the fact that an aggregation was performed.

Table 4: General framework for evaluating the mass-abundance relationship attributable to energetic mechanisms

Level	Variation in N (abundance)	Energy available		Energy required	
		Factors	Amount of variance	Factors	Amount of variance
Space within species	**High**	*Varying productivity (NPP)*	High	*Body size (M_i)*	Low
		Varying availability of specific resources	High	Varying climate (thermoregulation)	High
		Trophic level (T_i)	Low		
Species within genera/family	**Medium**	*Specialist/generalist* (*$generalist_i$*)	High	Life-history variation (reproductive allocation)	High
		Trophic level (T_i)	Low	***Body size* (M_i) *and metabolic rate***	**Low**
Family/order within class	**Medium**	***Trophic level* (T_i)**	**High**	***Body size***	**High**

Note: This table shows how spatial scale and taxonomic scale can be used to parse how much variation occurs at different scales and therefore which factors are likely contributors in the variation of abundance due to energy. The factors in italics are incorporated in equation (1) with the symbols given in parentheses. The factors in bold are specifically evaluated using the data and methods described in this article (and roughly parallel to table 1). Other factors are discussed with citations in "Interpretation of Partitioning of Variance." There is no correspondence between a row in the "Energy available" column and the corresponding row in the "Energy required" column.

and causes of variation in abundance within a species across space is also an active area of research (Lawton 1993; Brown et al. 1995; McGill and Collins 2003). In the end, spatial variation in abundance is probably largely independent of mass.

About one-fourth of the explained variation occurs at the species/genus level. Again the variation can be large; global abundance between confamilial species typically varies by a couple of orders of magnitude (Robbins et al. 1986; Gaston and Blackburn 2000). Mass proved to have relatively little variation between species within a family (only 11.5% of all variation in body size). As before, either body size (and its effect on energy requirements) is an unimportant factor in explaining variation in abundance at the species/genus level or else it is highly magnified through some unknown mechanism. Even congeneric species with similar masses and eating habits can have very different abundances (e.g., compare the very common yellow warbler *Dendroica petechia* and the very rare Kirtland's warbler *Dendroica kirtlandii*). It seems more likely that highly labile traits of high ecological importance—such as food or habitat specialist/generalist trade-offs, behavior, life history, competitive interactions, and so forth—determine the difference in abundance between species rather than mass-related processes. For the aforementioned species of warblers, the extreme variation in abundance is probably explained by the extreme difference in habitat specialization (15-year-old jack pine forests vs. most coniferous and deciduous forests).

The third level of variation in abundance is between higher taxonomic levels such as family and order, where about one-fourth of the explained variation in abundance occurs. In birds, these higher taxonomic levels serve as a good proxy for feeding guild and hence most of the variation in trophic level occurs here. The family/order levels are also where most (almost 90%) of the variation in body size occurs. Thus, both body size and trophic level are relatively conserved traits in the bird phylogeny. This suggests, by my algorithm, that an analysis of the mass-abundance relation is best performed at the family/order level. Mass alone (a possible measure of energy requirement) explains more than half the variation, and when mass is combined with trophic level (a measure of energy availability), the two explain about 75% of the variation in abundance at this higher taxonomic level. This improved explanatory power is not an artifact of aggregating the data (table 3; fig. 4). Thus, most of the mass-abundance relationship is a consequence of macroevolutionary processes at the family/order level (i.e., traits that are highly conserved in the phylogeny). The significant relationship observed at the species level (fig. 1) is merely a noisy shadow of the much tighter relationship at the family level (figs. 2, 3).

Toward the Use of an Enhanced Comparative Method in Macroecology

I have demonstrated that using multivariate models and hierarchical variance partitioning is useful in the context of understanding the mass-abundance relationship. Certainly these tools facilitate breaking out of the traditional but tiresome question of whether a theory is right or wrong, to move toward a more nuanced approach of asking what the relative importance is of different processes at different scales.

These same tools are likely to prove useful more generally in macroecology and ecology. The central issues in the mass-abundance relationship (the working of many processes across many scales) are in fact general issues in ecology. Variation is generally hierarchical and spread across a variety of scales (Bell 1989; Harvey and Pagel 1991; Chown 2001; Silvertown et al. 2001). Patterns and processes also change with scale (Brown and Maurer 1989; Levin 1992; Rosenzweig 1995; Schneider 2001; Russell et al. 2006). O'Neill (1979) calls this the "transmutation problem," where nonlinearity causes the outcomes of process to change across hierarchical aggregation. Likewise, all of ecology faces the fact that multiple factors almost always contribute to a single observed pattern (Hilborn and Stearns 1982; Quinn and Dunham 1983; Gaston and Blackburn 2000). This implies that ecology needs to develop novel methods to further its quest for understanding (Quinn and Dunham 1983).

The experimental method has had some success in teasing apart the relative role of multiple factors in some systems (Hairston 1989; Resetarits and Bernardo 1998; but see Møller and Jennions 2002). Experiments, however, are limited to small spatial and temporal scales (Maurer 1999). The larger scales have mostly needed to use comparative (primarily regression) approaches. While multiple regression has proven successful at identifying key variables and their relative importance (e.g., Rahbek and Graves 2001), I suggest that regression has not yet fully come to terms with collinearity among variables, multiple scales, the spatial and phylogenetic structure in which processes play out, or the need to identify not just correlation but mechanism. One solution is to develop more explicitly mechanistic multivariate models. Another is the use of partitioning of variance along hierarchies.

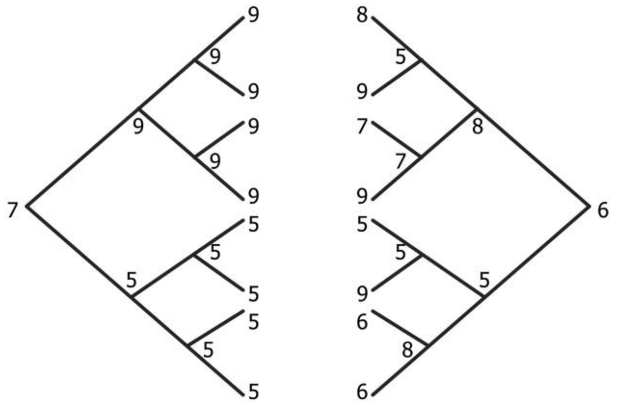

Figure 5: An example of why comparison at the species level is sometimes a bad idea. This figure shows two phylogenies, with the values of a phenotypic trait shown at each node. The phylogeny on the left is highly conserved, with only a single instance of change. It might represent something such as a trait associated with carnivory versus herbivory. The phylogeny on the right represents a trait that is extremely labile (in fact, the leaf numbers were generated by independent samples from a random-number generator). This might be a trait under sexual selection or perhaps an α trait such as hydrological niche (Silvertown et al. 2006*b*). Despite this, a comparative analysis done at the species level would conclude there is a good relationship between these two values (Pearson's $r = 0.59$, $r^2 = 0.34$), but with the full phylogeny it is clear that different processes must be invoked to explain the observed values at the tips and that any correlation must be purely coincidental. The highly conserved trait experiences strong constraints on change, evolved early in the radiation, and the ecology of these organisms is limited by this trait, while the labile trait experiences little constraint and is constantly evolving in response to the ecological context of the species. Hierarchical partitioning of variance would detect this situation. The phylogeny on the left would show all the variation concentrated at one level, while the phylogeny on the right would show equal variation at all levels.

The prevailing view remains that the species level is the only proper level for comparative analysis. Several attitudes need to change. Analysis of processes at the family level makes many uncomfortable since mass and energy use fundamentally are both processes and traits at the level of the individual. At its extreme, though, this logic prohibits the study of abundance at all (since abundance is a property only of a population or species) as well as the study of many other species properties, such as species ranges (e.g., Jablonski 2003; Hunt et al. 2005). Moreover, comparative analysis at the species level can lead to incorrect conclusions (fig. 5), and it is undeniable that traits and properties show variation throughout the entire phylogeny (Bell 1989; Silvertown et al. 1999; Webb et al. 2002), with the traits sometimes being labile and sometimes being conserved (fig. 5). Another frequent objection to analysis of higher taxonomic levels is the notion that species are a natural unit, while higher and lower taxonomic groups are arbitrary assessments of a taxonomist; however, even a well-known, rarely hybridizing group such as birds of North America sees frequent lumpings and splittings of species, giving lie to the notion that species are natural units. If we are to deal with the empirical reality that traits are phylogenetically conserved, we must adopt some tool, and the main alternative to using genera, families, and orders is to use actual phylogenies (Harvey and Pagel 1991; Webb et al. 2002), but these require significantly more data and still contain uncertainties and errors. To move forward, a choice must be made among imperfect choices. A final obstacle is the attitude that sees trait variation at higher taxonomic levels primarily as a source of nonindependence among species and therefore a nuisance to be removed (Harvey and Pagel 1991). While this can be important to address, it can also be an opportunity to treat this fact as a signal that is indicative of mechanism (fig. 5; table 4), as we have done here. In the end, analyzing causal processes at higher taxonomic levels will become more accepted if it proves useful over time.

These methods and changes in attitude are well established in other fields, such as the study of life-history variation (Harvey and Pagel 1991; Ricklefs and Nealen 1998), but they remain rare in macroecology. The few cases where they have been used in macroecology suggest that this approach may be fruitful. Kaspari (2001) found in ants that abundance of families was primarily driven by productivity but that abundance of genera was primarily driven by temperature. McGill and coworkers (2005) found that the constancy of community structure depended on an interaction between spatial and taxonomic scales. Russell and coworkers (2006) found that the relationship between local and regional richness depended heavily on spatial and taxonomic scale. Community ecology has also begun to move in this direction as well; several researchers (Ackerly et al. 2006; Silvertown et al. 2006*a*, 2006*b*; Ackerly and Cornwell 2007) have begun talking about α, β, and γ traits of species as traits that allow coexistence within a habitat (α), that adapt to a particular habitat (β), or that adapt to a particular region/climate (γ) and exploring whether α or γ traits are more conserved in a phylogeny. It is not inconceivable that this same partition might carry over to abundance with α traits affecting species-level variation in abundance and γ traits affecting order-level traits (presumably through body mass). If true, this would represent an important conceptual unification for ecology.

Summary

The evidence presented here suggests that body size can explain much of the variation in abundance that is highly conserved in the phylogeny (i.e., family/order level) but not much of the remaining variation in abundance. Moreover, for birds of North America, energetic equivalence sensu strictu serves only as an upper limit on abundance that is attained somewhere for every family but with larger species getting more than "their share" on average in a particular location. These conclusions were reached using multiple explanatory variables and partitioning these multiple variables hierarchically. I hope that this paradigm and approach continue to become more common in macroecology.

Acknowledgments

I thank B. Maurer and E. White for discussions of this work and the Natural Sciences and Engineering Research Council of Canada for funding this work. An anonymous reviewer provided helpful feedback on the manuscript.

Literature Cited

Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecology Letters 10: 135–145.

Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology 87:S50–S61.

Andrewartha, H. G., and L. C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago.

Bell, G. 1989. A comparative method. American Naturalist 133:553–571.

Bennett, P. M., and P. H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. Journal of Zoology 213:327–363.

Blackburn, T. M., and K. J. Gaston. 1996. Abundance-body size relationships: the area you census tells you more. Oikos 75:303–309.

Blackburn, T. M., V. K. Brown, B. M. Doube, J. J. D. Greenwood, J. H. Lawton, and N. E. Stork. 1993. The relationship between abundance and body size in natural animal assemblages. Journal of Animal Ecology 62:519–528.

Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. American Naturalist 130:1–17.

———. 1989. Macroecology: the division of food and space among species on continents. Science 243:1145–1150.

Brown, J. H., D. H. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 81:1771–1789.

Brown, J. S., B. P. Kotler, and W. A. Mitchell. 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. Ecology 75:2286–2300.

Calder, W. A. I. 1984. Size, function, and life history. Dover, Mineola, NY.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273–2276.

Carbone, C., G. Cowlishaw, N. J. B. Isaac, and J. M. Rowcliffe. 2005. How far do animals go? determinants of day range in mammals. American Naturalist 165:290–297.

Chown, S. L. 2001. Physiological variation in insects: hierarchical levels and implications. Journal of Insect Physiology 47:649.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldana. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62:67–78.

Cotgreave, P. 1993. The relationship between body size and population abundance in animals. Trends in Ecology & Evolution 8: 244–248.

Cyr, H., R. H. Peters, and J. A. Downing. 1997. Population density and community size structure: comparison of aquatic and terrestrial systems. Oikos 80:139–149.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699–700.

———. 1987. Interspecific allometry of population density in mammals and other animals; the independence of body mass and population energy use. Biological Journal of the Linnean Society 31: 193–246.

———. 1991. Of size and abundance. Nature 351:268–269.

Enquist, B. J., J. H. Brown, and G. B. West. 2001. Allometric scaling of plant energetics and population density. Nature 395:163–165.

Gaston, K. J., and T. M. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford.

Gower, J. C. 1962. Variance component estimation for unbalanced hierarchical classifications. Biometrics 18:537–542.

Hairston, N. G. 1989. Ecological experiments: purpose, design, and execution. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.

Hilborn, R., and S. C. Stearns. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. Acta Biotheoretica 31:145–164.

Huber, D. A., T. L. White, and G. R. Hodge. 1994. Variance component estimation techniques compared for two mating designs with forest genetic architecture through computer simulation. Theory of Applied Genetics 88:236–242.

Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes." American Naturalist 166:129–135.

Jablonski, D. 2003. Geographical range and speciation in fossil and living molluscs. Proceedings of the Royal Society B: Biological Sciences 270:401–406.

Jennings, S., and S. Mackinson. 2003. Abundance-body mass relationships in size-structured food webs. Ecology Letters 6:971–974.

Juanes, F. 1986. Population density and body size in birds. American Naturalist 128:921–929.

Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences of the USA 101:4854–4858.

Kaspari, M. 2001. Taxonomic level, trophic biology and the regulation of local abundance. Global Ecology and Biogeography 10:229–244.

Kauffman, K. 1996. Lives of North American birds. Houghton Mifflin, Boston.

Korpimaki, E., and K. Norrdahl. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. Ecology 72:814–826.

Krebs, C. J. 1972. Ecology. Harper & Row, New York.

Lawton, J. H. 1993. Range, population abundance and conservation. Trends in Ecology & Evolution 8:409–413.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Li, W. K. W. 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. Nature 419:154.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Marquet, P. A., S. A. Navarrete, and J. C. Castilla. 1990. Scaling population density to body size in rocky intertidal communities. Science 250:1125–1127.

———. 1995. Body size, population density and the energetic equivalence rule. Journal of Animal Ecology 64:325–332.

Maurer, B. A. 1999. Untangling ecological complexity. University of Chicago Press, Chicago.

Maurer, B. A., and J. H. Brown. 1988. Distribution of energy use and biomass among species of North American terrestrial birds. Ecology 69:1923–1932.

McGill, B., and C. Collins. 2003. A unified theory for macroecology based on spatial patterns of abundance. Evolutionary Ecology Research 5:469–492.

McGill, B. J. 2006. A renaissance in the study of abundance. Science 314:770–771.

McGill, B. J., E. A. Hadly, and B. A. Maurer. 2005. Community inertia of Quaternary small mammal assemblages in North America. Proceedings of the National Academy of Sciences of the USA 102: 16701–16706.

Meehan, T. D., W. Jetz, and J. H. Brown. 2004. Energetic determinants of abundance in winter landbird communities. Ecology Letters 7: 532–537.

Møller, A. P., and M. Jennions. 2002. How much variance can be explained by ecologists and evolutionary biologists? Oecologia (Berlin) 132:492–500.

Murray, B. R., P. H. Thrall, A. M. Gill, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27:291–310.

Nee, S., A. F. Read, J. J. D. Greenwood, and P. H. Harvey. 1991. The relationship between abundance and body size in British birds. Nature 351:312–313.

Newton, I. 1998. Population limitation in birds. Academic Press, London.

Nilsen, E. B., I. Herfindal, and J. D. C. Linnell. 2005. Can intraspecific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? Ecoscience 12:68–75.

O'Neill, R. V. 1979. Transmutations across hierarchical levels. Pages 59–78 in G. S. Innis and R. V. O'Neill, eds. Systems analysis of ecosystems. International Cooperative, Fairland, MD.

Patuxent Wildlife Research Center. 2001. Breeding bird survey FTP site: ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Poole, A. 2005. The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY. http://bna.birds.cornell.edu/BNA/.

Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. American Naturalist 122:602–617.

R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences of the USA 98:4534–4539.

Resetarits, W. J., Jr., and J. Bernardo. 1998. Experimental ecology: issues and perspectives. Oxford University Press, Oxford.

Ricklefs, R. E., and P. Nealen. 1998. Lineage-dependent rates of evolutionary diversification: analysis of bivariate ellipses. Functional Ecology 12:871–885.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965–1979. Resource Publication 157. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Rosenzweig, M. L., and M. V. Lomolino. 1997. Who gets the short bits of the broken stick? Pages 63–90 *in* W. E. Kunin and K. J. Gaston, eds. The biology of rarity: causes and consequences of rare-common differences. Chapman & Hall, London.

Russell, R., S. A. Wood, G. Allison, and B. A. Menge. 2006. Scale, environment, and trophic status: the context dependency of community saturation in rocky intertidal communities. American Naturalist 167:E158–E170.

Russo, S. E., S. K. Robinson, and J. Terborgh. 2003. Size-abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. American Naturalist 161:267–283.

Savage, V. M., J. F. Gillooly, W. H. Woodruff, G. B. West, A. P. Allen, B. J. Enquist, and J. H. Brown. 2004. The predominance of quarter-power scaling in biology. Functional Ecology 18:257–282.

Schneider, D. C. 2001. The rise of the concept of scale in ecology. BioScience 51:545–553.

Sibley, D. A. 2000. The Sibley guide to birds. Knopf, New York.

Silvertown, J., M. E. Dodd, D. J. G. Gowing, and J. O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Silvertown, J., M. Dodd, and D. Gowing. 2001. Phylogeny and the niche structure of meadow plant communities. Journal of Ecology 89:428–435.

Silvertown, J., K. McConway, D. Gowing, M. Dodd, M. F. Fay, J. A. Joseph, and K. Dolphin. 2006*a*. Absence of phylogenetic signal in the niche structure of meadow plant communities. Proceedings of the Royal Society B: Biological Sciences 273:39–44.

Silvertown, J., M. Dodd, D. Gowing, C. Lawson, and K. McConway. 2006*b*. Phylogeny and the hierarchical organization of plant diversity. Ecology 87:S39–S49.

Sokal, R. J., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York.

Soulé, M. E. 1986. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, MA.

Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41:173.

Swallow, W. H., and J. F. Monahan. 1984. Monte Carlo comparison of ANOVA, MIVQUE, REML, and ML estimators of variance components. Technometrics 26:47–57.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22:323–330.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan, New York.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. American Naturalist 109:769–784.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upton, NY.

Associate Editor: Kaustuv Roy
Editor: Michael C. Whitlock