

## HOW DO SPECIES REALLY DIVIDE RESOURCES?

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*Submitted August 17, 1994; Revised September 28, 1995; Accepted October 10, 1995*

**Abstract.**—We show that the relationship between variance in population energy use and variance in species abundance depends critically on the model of causal relationships among metabolic rate, body size, and population density assumed, provided that they specify alternative paths of error propagation. It has been claimed that the allometric relationship between population density and body size indicates that species within communities use resources less equitably than would be inferred from a particular species abundance distribution. Our analysis of 41 local bird communities shows that this claim is supported only if it is assumed that both body size and metabolic rate are a consequence of population density. A more realistic model that assumes a causal role for body size as affecting metabolic rate and population density provides estimates of variance in population energy use that closely match the pattern of variance in population density. This implies that the apportionment of individuals and resources, among species, are equivalent processes.

The way in which resources are divided among species, within local communities and biotas, has long been recognized as a fundamental question in the study of evolutionary and ecological patterns (e.g., Hutchinson and MacArthur 1959; Schoener 1986; Brown and Maurer 1989; Lawton 1990). In particular, it has been suggested that the canonical lognormal distribution of species abundances (Preston, 1948, 1962*a*, 1962*b*; Sugihara 1980) is likely to result if niche apportionment among species involves the random, sequential division of a number of resources (Sugihara 1980). A particular species abundance distribution is said to be canonical when the variance of species' abundances is related to the number of species in the community according to a particular relationship (May 1975; Sugihara 1980, 1981). Sugihara (1980) has proposed an elegant plausible mechanism of hierarchical resource division that would lead to the observed canonical lognormal distribution of species abundance. Under Sugihara's model, interspecific patterns of resource division are inferred from the apportionment of individuals among species (species abundance) within natural communities. This logic has been criticized by Harvey and Godfray (1987) and, more recently, by Pagel et al. (1991). These authors point out that patterns of resource division may differ from those inferred from species abundance distributions, implying that a canonical lognormal species abundance distribution is not a necessary reflection of a canonical lognormal distribution of resource use. Stated in more general terms, this condi-

tion means that the apportionment of individuals and that of resources, among species, are not equivalent processes.

Harvey and Godfray (1987) begin by noting that species abundances are not independent of per capita resource requirements and that both abundance and resource requirements are allometric functions of body mass (e.g., Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Then, by using known allometric relationships among population density, metabolic rate, and body mass, they derive an expression for the variance in population energy use and compare it to the variance in population density. This article, and the articles that have inspired it (Harvey and Godfray 1987; Sugihara 1989; Pagel et al. 1991), are concerned directly with energy use and the variance in energy use. Nevertheless, it is considered that energy use is a surrogate measure for a broad class of resource. If we assume that the variance in population density was estimated from local communities with a canonical lognormal distribution of species abundance, then for energy use to be canonical lognormally distributed, its variance should be equal to the variance in population density. However, Harvey and Godfray (1987) conclude that the variance in energy use will be systematically lower than the canonical variance reported for population densities; the same holds for population biomass. This was taken as evidence that the distribution of energy and biomass would be more equitably distributed across species than predicted by the canonical relationship; a canonical lognormal distribution of resource use would not correspond to a canonical lognormal distribution of individuals under their model. Subsequently, Sugihara (1989, p. 459) suggested that in their derivation, Harvey and Godfray (1987) "underestimated the true variances" in energy use and biomass by ignoring the error terms in the allometric relationships relating population density, body mass, and metabolic rate. In addition, Sugihara (1989) presents empirical estimates for local communities that support the hypothesis of equal variance in both energy use and biomass as compared to population size. However, in a recent article Pagel et al. (1991) extend their allometric argument, improved by Sugihara's suggestions, and present further empirical evidence for 72 local communities of fish, mammals, birds, and diatoms. Their main conclusion is that depending on the specific slope of the relationship between population density and body size, resources in the community would be divided more equitably, less equitably, or about the same as would be inferred from the species abundance relationship. This discussion and the literature debate that led to it have assumed that a canonical lognormal distribution of abundances characterizes most communities. This is not a necessary condition for the validity of the main question addressed in this article: Are the apportionment of individuals and that of resources equivalent processes at the community level? Furthermore, no assumption of a lognormal distribution in either resource use or population density is used in the following analysis. This freedom from distributional assumptions allows us to comment on the possibility of canonical resource partitioning in communities without circular reasoning.

The principal demonstrations and points of this article are as follows. First, allometric relationships do make predictions as to the correlation between the variance in population density and the variance in energy use. Second, these

predictions depend critically on the assumed model of causal relationships among metabolic rate, body size, and population density. Third, the absence of covariation in the deviations from fitted allometric relationships between body size and metabolic rate, and between body size and population density, reduces the set of possible models to three: an "*n* causal" model in which population density influences body size, which in turn influences metabolic rate; a "*p* causal" model in which metabolic rate influences body size, which in turn influences population density; and an "*m* causal" model in which both metabolic rate and population density result from the influence of body size. Finally, the *m* causal and *p* causal models both predict that within communities, the variance in energy use will approximately equal the variance in population density. The *n* causal model does not make this prediction.

#### DETERMINING THE VARIANCE IN ENERGY USE

The energy use of most populations is unknown. Certainly, the within-community variance in energy use has never been directly measured. Workers in this field have relied on allometric relationships to estimate the energy use of species under consideration (Damuth 1981, 1987; Brown and Maurer 1986; Harvey and Godfray 1987; Maurer and Brown 1988; Sugihara 1989; Pagel et al. 1991). We recapitulate the development of the argument.

Population energy use (*E*) can be calculated as the product of individual metabolic rate (*P*) and population density (*N*). Both metabolic rate and population density are known to be related allometrically to body size (*M*) (Peters 1983; Calder 1984; Schmidt-Nielsen 1984) as

$$N = A_N M^{b_n} \quad (1)$$

and

$$P = A_P M^{b_p}. \quad (2)$$

The allometric exponent  $b_n$  in equation (3) is often taken to be  $-0.75$ , but empirical estimates range from  $-1.05$  to  $1.17$  (Pagel et al. 1991). Estimates of the exponent of metabolic rate as a function of body size,  $b_p$  in equation (4), cluster closely around  $0.75$  (SD =  $0.11$ ) (Peters 1983). The terms  $A_N$  and  $A_P$  are taxon-specific constants. Equations (3) and (4) represent relationships that are linear under logarithmic transformation, and they can be expressed equally well as

$$n = a_n + b_n m \quad (3)$$

and

$$p = a_p + b_p m, \quad (4)$$

where  $n$ ,  $p$ ,  $a_n$ , and  $a_p$  are  $\log_{10}(N)$ ,  $\log_{10}(P)$ ,  $\log_{10}(A_N)$ , and  $\log_{10}(A_P)$ , respectively. In equations (3) and (4) and below, we follow the convention that a lower-case variable is the  $\log_{10}$  transform of the corresponding uppercase variables. A comment on notation: in this article, we are following the conventions of Schmidt-

Nielsen (1984). Our variables  $M$ ,  $P$ ,  $E$ ,  $b_n$ , and  $b_p$  correspond to  $B$ ,  $E$ ,  $E'$ ,  $x$ , and  $y$  in Harvey and Godfray (1987), Sugihara (1989), and Pagel et al. (1991). We apologize for any confusion this causes readers of these articles.

The exponents  $b_n$  and  $b_p$  are generally estimated through linear regression of log-transformed variables. Thus, the log of energy use ( $e$ ) is given by

$$e = n + p = (a_n + b_n m) + (a_p + b_p m). \quad (5)$$

Since Harvey and Godfray (1987) are concerned with comparing the variance in population energy use to the variance in population density, they express metabolic rate as a function of population density. Rearranging equations (3) and (4) yields

$$e = k + \left(1 + \frac{b_p}{b_n}\right)n, \quad (6)$$

where  $k$  equals  $(a_p - a_n b_p / b_n)$ . Harvey and Godfray (1987) point out that if population densities ( $N$ ) are lognormally distributed, as has sometimes been observed (e.g., Preston 1962a, 1962b; Sugihara 1980), then  $e$  will be normally distributed with variance given by

$$V(e) = \left(1 + \frac{b_p}{b_n}\right)^2 V(n), \quad (7)$$

where  $V(\ )$  is the variance operator. However, as pointed out by Sugihara (1989), Harvey and Godfray (1987) assume in the derivation of equation (7) that deviations from the expectations given by equations (1) and (2) have no impact on  $V(e)$ . This assumption is not justified and may lead to greatly underestimated  $V(e)$ . Sugihara presents a formula for  $V(e)$  incorporating the effect of error in equations (1) and (2):

$$V(e) = \left(1 + \frac{b_p}{b_n}\right)^2 V(n) + V(d_p) + \left(\frac{b_p}{b_n}\right)^2 V(d_n), \quad (8)$$

where  $d_p$  and  $d_n$  are deviations from the expectations given by equations (3) and (4). Note that equation (8) differs from the one given by Sugihara (1989, eq. [4]) in two respects. First, we have absorbed the minus sign into the value of  $b_n$  (see the discussion of our eq. [1] above). Second, we correct a typographical error in the sign of  $V(d_n)$  (G. Sugihara, personal communication). It is noteworthy that equation (8) is derived under the assumption (explicit or implicit) that population density is the primary causal factor (see the appendix). That is, population density influences body size, which in turn influences metabolic rate and consequently population energy use (see fig. 1A). However, this is only one of a number of causal pathways linking population density, body size, and metabolic rate. Another, more reasonable set of causal pathways assumes that body size is the primary determinant of both population density and metabolic rate (Damuth 1981,

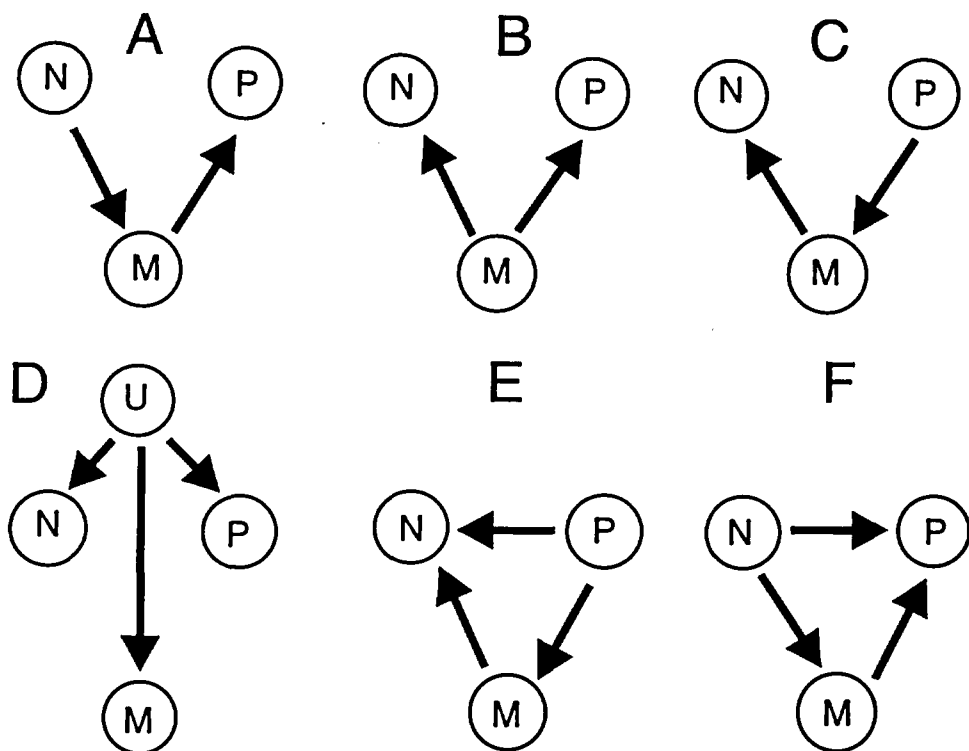


FIG. 1.—Graphic representation of alternative causal models of interaction among body size (*M*), population density (*N*), and metabolic rate (*P*): *A*, *n* causal model; *B*, *m* causal model; *C*, *p* causal model; and *D*, unknown causal model. Other possible alternatives are shown in *E* and *F*. See text for further details.

1987; Marquet et al. 1990) (see fig. 1*B*). If one assumes that body size is causal, one can derive a very different expression for  $V(e)$  (see the appendix):

$$V(e) = \left(1 + \frac{b_p}{b_n}\right)^2 [V(n) - V(d_n)] + V(d_n) + V(d_p). \quad (9)$$

In what follows, we refer to equations (8) and (9) as the *n* causal and *m* causal formulations, respectively.

A third possibility assumes that metabolic rate shapes body size, which then influences population density (see fig. 1*C*). This formulation (*p* causal; see the appendix) leads to the variance relationship given in equation (10):

$$V(e) = \left[ \frac{V(n) - \left(\frac{b_n}{b_p}\right)^2 V(d_p) - V(d_n)}{\left(\frac{b_n}{b_p}\right)^2} \right] \left(1 + \frac{b_n}{b_p}\right)^2 + \left(\frac{b_n}{b_p}\right)^2 V(d_p) + V(d_n). \quad (10)$$

Yet another possible set of pathways assumes that all three variables are affected by an unknown fourth variable (see fig. 1D). Interestingly, this condition yields an expression identical to equation (9). Equations (8), (9), and (10) demonstrate that the expected variance in  $\log_{10}(\text{energy use})$  depends critically on the causal model chosen as well as on the allometric relationships between body size and population density and between body size and metabolic rate. In the following, section we investigate consequences of the choice of each of these three causal pathways using empirical data for bird communities compiled by Brown and Maurer (1986).

Of course, the three models discussed above do not comprise an exhaustive list. Other more complex models such as those in figure 1 (E, F) are possible. However, these models imply a covariation in the errors of the two allometric regressions. Since we show below that this result does not occur, we will not pursue these models further in this article.

We have been speaking of causal models, which is not flying in the face of the dictum "Correlation does not imply causation." The models are not inferences from data but are scientific hypotheses. These hypotheses make predictions about the patterns of variation in energy use and population density. These predictions are testable, by field data on energy use.

#### VARIANCE IN ENERGY USE IN NATURAL COMMUNITIES: THREE CAUSAL MODELS

In order to empirically investigate the effect of each of the causal models described above on the estimation of the variance in population energy use, we use data on body size and population density for 41 local birds communities compiled by Brown and Maurer (1986). Body size estimates are from Dunning (1984). Population density estimates are from published reports of intensively surveyed bird communities. These studies were chosen by Brown and Maurer on the basis of soundness of density estimation methods, intensity of effort, and commitment to exhaustive surveying the entire avifauna (B. Maurer, personal communication). These data are the greater part of the 72 communities analyzed by Pagel et al. (1991). These authors report the regression statistics for each of the communities we analyze. However, the variances in energy use they calculate cannot be arrived at by application of their equation (2) to the variances in  $n(\log[N])$  and  $m(\log[B])$  that they report (see column  $\log E'$  in table 1 of Pagel et al. 1991).

In order to compute the variance in energy use, we need to estimate the error terms and allometric exponents relating body size to population density and metabolic rate. Previous analysis (Pagel et al. 1991) computed a lower-bound estimate for the variation in energy use by assuming no error variance (e.g.,  $V[d_n] = V[d_m] = 0$ ). We have undertaken to include these error terms. In the case of population density, variance in error terms and allometric exponents were obtained directly from the regressions computed for each community (data provided by B. Maurer). For metabolic rate, we estimate  $V[d_m] = 0.1142$  and  $b_p = 0.60$  as the mean squared error and the slope of the regression of  $\log_{10}(\text{body mass})$  against  $\log_{10}(\text{field metabolic rate})$  from data presented by Nagy (1987) for 50

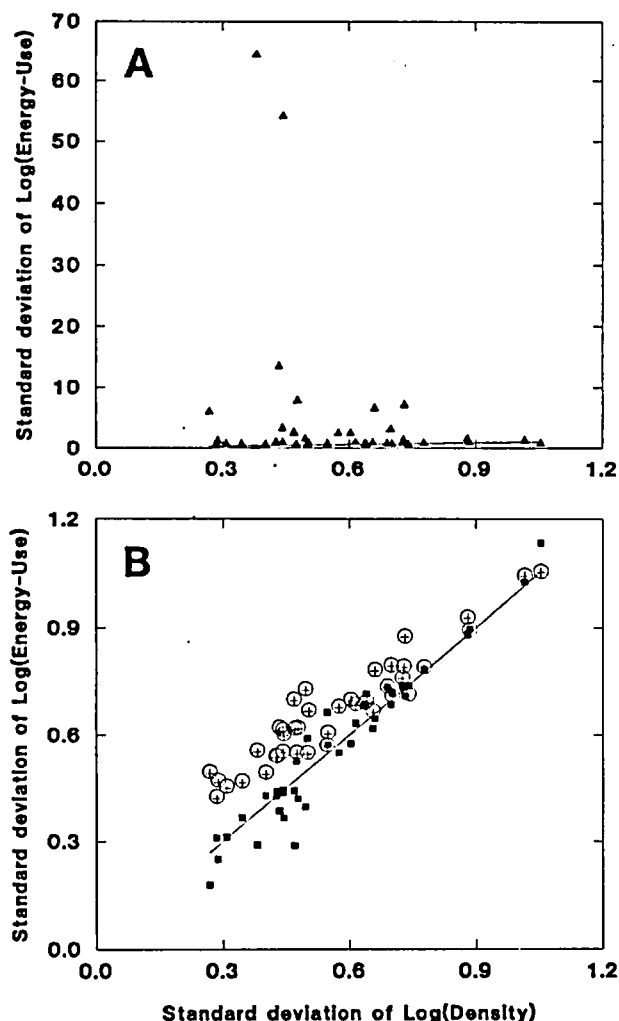


FIG. 2.—The relationship between the standard deviation of energy use and the standard deviation of population density for 41 bird local communities. *A*, Solid triangles are standard deviation in population energy use calculated under the  $n$  causal model. *B*, Circles are estimates of the standard deviation in population energy use derived from the  $m$  causal model, pluses are the estimates of the  $m$  causal bias-corrected model, and solid squares are the estimates derived from the  $p$  causal model. The solid line is a reference line of slope one. See text for further details.

species of birds. Figure 2 shows the relationship between variance in population energy use and variance in population density. Interestingly, the  $n$  causal model (fig. 2A) provides an estimation of variance in energy use that poorly matches the observed variance in population density. Further, there is a negative covariance between energy use and population density under this model. In contrast, the  $m$  causal, the bias-corrected  $m$  causal (see below), and the  $p$  causal models provide

estimates of the variance in energy use that closely match the observed pattern of variation in population density (fig. 2B). All show a positive relationship between estimated variance in energy use and population density. We would caution against overinterpreting figure 2A. Since the allometric exponents  $b_n$  and  $b_p$  are not known exactly but are estimated with error, all three models are functions of ratio statistics. Error can propagate explosively through such models, particularly when the denominator is near zero. The allometric exponent in the relationship of population density to body size,  $b_n$ , is the most poorly estimated quantity used in this study. Because the allometric exponent  $b_n$  enters into the three models in different ways, error in the estimate of  $b_n$  will affect the estimate of the variance in energy use differently. We have performed a simple analysis of the sensitivity of the results from the three models to error in the estimation of  $b_n$ . This was accomplished by recalculating the standard deviation for each community and model using  $b_n$  values randomly drawn from the sampling distribution of the slope parameter in the regression used to estimate  $b_n$  for that community. Our measure of sensitivity was the interquartile distance of the resulting predictions of the standard deviation in energy use. The interquartile distance is the difference between the values at the seventy-fifth and twenty-fifth percentiles. It is a standard nonparametric measure of variation and was used here because the distributions of the three models were skewed to some degree. For normally distributed data, the interquartile distance is approximately 1.34 SD.

The  $n$  causal model is very sensitive to error in  $b_n$  and particularly so for low standard deviations in population density. Regressing interquartile distance of the predicted standard deviation in energy use against the standard deviation in population density yields an intercept of 2.047 and a slope of  $-0.898$ . The  $p$  causal model is also moderately sensitive to error in  $b_n$  (interquartile distance intercept = 1.127 and slope = 0.091). In contrast, the  $m$  causal model is quite insensitive to error in  $b_n$  (interquartile distance intercept = 0.07 and slope = 0.002). Pagel et al. (1991) have suggested that in local communities, particular values of the allometric scaling parameter  $b_n$  for the relationship between population density and body size have a strong effect on within-community resource subdivision. The above analysis indicates that this is very true for the  $n$  causal model used in Pagel et al. (1991) but not true under the  $m$  causal model.

#### VALIDATION OF STATISTICAL ASSUMPTIONS

Equations (8), (9), and (10) are all derived on the bases of two assumptions. First, body size is assumed to have been measured without error. Second, all error terms are assumed to be uncorrelated. We investigate here the validity of these assumptions.

Measurement error in  $\log_{10}(\text{body mass})$  is crudely estimated by comparing, for a set of species, literature reports of body size from different sources. We subtracted the value  $\log_{10}(\text{body mass})$  for each species in one data set from its value in the other data set. If the two data sets are independent, measurement error variance can be estimated as one-half the variance of the differences between the two data sets. The error we arrive at is the error in the estimate of the  $\log_{10}(\text{body$



mass) for the species as a whole and includes inter- and intrapopulation variation and physical measurement error.

We used the compilations of bird masses found in Terborgh et al. (1990) and Dunning (1993). We eliminated the listings in Dunning derived from Terborgh et al. or one of their sources and those species in Dunning whose weights are explicitly recorded as coming from a single sex. This approach left a total of 176 species with independent estimates of body size in the two compilations.  $\log_{10}$  (body size) measurement error variance was estimated as a remarkably tiny 0.0019  $\log_{10}$  units. An appropriate pair of mammal data sets were also available. These were used to make a second estimate measurement error in reported body mass independent of the bird data. We used the compilations of Damuth (1987) and Brown and Nicoletto (1991). These lists share 113 species. This analysis yielded a measurement error variance estimate of 0.0086. Both of these estimates are quite close to the estimate of 0.0052 arrived at by Pagel and Harvey (1988), which was based on within-population sampling variability in 23 species. Riska (1991) points out that Pagel and Harvey's method will underestimate errors in the assessment of species body mass because it ignores interpopulation variability.

It is interesting to see whether the small amount of measurement error that we estimate is sufficient to bias our conclusions in any important fashion. If the variance in measurement errors in the predictor variable has been estimated from data external to the data set under consideration (as in this case), it is quite straightforward to correct the biases in the estimated parameters of a regression. We apply the following formulas (Madansky 1959) to correct the biases of all reported regressions used in the calculations of the variance in energy use. In a regression of  $z$  on the predictor variable  $w$ , the bias-corrected parameter estimates are given by

$$\beta_c = \frac{\beta V(w)}{V(w) - V(d_w)}, \quad (11)$$

$$I_c = \bar{w} - \beta_c \bar{z}, \quad (12)$$

and

$$\text{MSE}_c = \frac{1 - R_{wz}^2 V(w)}{[V(w) - V(d_w)]V(z)}, \quad (13)$$

where  $\beta_c$ ,  $I_c$ , and  $\text{MSE}_c$  are the bias-corrected slope intercept and mean-square error of the regression;  $V(d_w)$  is the measurement error variance in the predictor variable  $w$ . In our case, the predictor variable is  $\log$  (body weight) with measurement error variance as discussed above.

These formulas are unbiased. However, as with all bias correction techniques for regression, they can give erratic predictions if sample size is small and  $V(d_w)$  is a large portion of  $V(w)$  (Riggs et al. 1978). Neither of these problems occurs in our data, so equations (11)–(13) are adequate for our purposes. Figure 2B shows a plot of our estimates of  $V(e)$  versus  $V(n)$  for the  $m$  causal and  $b$  causal models. The estimates of  $V(e)$  for the  $m$  causal model are plotted twice. In the first set based on the allometric relationships (eq. [3] and [4]) and calculated

assuming no measurement error in  $m$ , the points are plotted as open circles. The second set of estimates, plotted as pluses, incorporates the effects of bias correction in the parameters  $b_n$  and  $b_p$  using equation (11). In figure 2B, we have used the largest of our three estimates of the measurement error for body size. Inspection of the figure (fig. 2B) indicates that measurement error on the order estimated will have only a minuscule effect on our estimates of  $V(e)$ . Thus, as Pagel and Harvey (1988) point out, measurement error in body size should have only a minimal effect on the estimation of allometric relationships unless the total variation in body size among the organisms studied is small. A problem with measurement error is most likely to occur when studying very closely related species (see Pagel and Harvey 1988, fig. 1).

The primary assumption of the models discussed in this article is that the errors in the regressions relating metabolic rate to body mass and population density to body mass are uncorrelated. If this assumption is not adequately met, then much more complicated forms of analysis must be undertaken (Fuller 1987). As in our estimate of the magnitude of measurement error in  $\log_{10}(\text{body mass})$ , we have been unable to locate appropriate data to measure the covariance in these errors for bird species. Again we have had to rely on mammal data. We have assembled data on body mass (Damuth 1987), population density (Damuth 1987), and basal metabolic rate (Elgar and Harvey 1987; McNab 1988) for 141 species of mammals. Using this data, we have regressed both  $\log_{10}(\text{population density})$  and  $\log_{10}(\text{metabolic rate})$  on  $\log_{10}(\text{body mass})$ . The covariance in the residuals of these two regressions was  $-0.000108$  (NS,  $P > .5$ ). Thus, at least in mammals, ignoring the covariance in errors is valid.

#### DISCUSSION

Allometric thought has traditionally been preoccupied with central patterns and with finding fit and has not been concerned with scatter (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Harvey and Godfray 1987). However, several lines of evidence underscore the need for explicit consideration of scatter in discussing allometric relationships. Riska (1991) points out that the scatter in allometric relationships is not all measurement error and that a portion of the "error variance" is due to real differences of species from predictions resulting from their individual evolutionary histories (see also Pagel and Harvey 1988; Harvey and Pagel 1991). In a similar vein, Brown and Maurer (1987, 1989), in discussing the relationship among population density, geographic range, and body size, point out the ecological and evolutionary importance of scatter confined within a conspicuous region or "constraint envelope." Brown et al. (1993) show that under close examination, a number of allometric relationships are not simple straight lines but in fact change direction around a body mass of 100 g (see also McNab 1983). Apparently, these changes had not been previously noted because the deviations were assumed to be simply "scatter." The same is true for the relationship between body size and population energy use. It has been shown (Marquet et al. 1995) that although under algebraic manipulation the allometric relationships between body size and population density and between body size and metabolic

rate in herbivorous mammals predicts that the expected energy use of species should be independent of body mass ( $M^{+0.75} \cdot M^{-0.75} = M^0$ ), this does not mean that all species use equal amounts of energy as predicted by the "energetic equivalence rule" (Damuth 1981, 1987; Nee et al. 1991*a*, 1991*b*). This is because the error associated with equations (1) and (2) causes energy use to vary dramatically among species. In particular, maximum population energy use is an increasing function of body size for small mammals (less than 100 g).

Sugihara (1989) introduced scatter into the allometric discussion of the relationship of variation in population density and variation in energy use. Our work confirms the importance of that insight and extends it by showing that once error is present, the way causality among variables is modeled matters. Different causal models determine different paths for the propagation of errors, hence affecting the value of  $V(e)$ . This raises the following questions: What are the possible causal relationships among the variables? How do different models of interaction affect our predictions? Without error, all three of the causal models we have discussed (fig. 2) collapse to the same predictions. We have shown that the causal relationships among variables have a strong effect on how scatter or error propagates through the system (see also Riska 1991). In contrast, the more traditional statistical concerns of measurement error in body size and covariance in errors (Harvey and Pagel 1988, 1991) seem to have only minor influence on our estimates of the variance in energy use in the communities studied here.

Which of the causal models best describes the real world? We have no way of deciding this objectively using the data that we have analyzed in this article. However, models *e* and *f* can be eliminated because of the lack of correlation of errors. Furthermore, we do not feel that it makes much sense either ecologically or evolutionarily to claim, as in the *n* causal model, that body size and metabolic rate are consequences of population density or, as in the *p* causal model, that body size and population density are a consequence of metabolic rate. One line of evidence might favor the *m* causal model. Figure 2 of Sugihara (1989) plots the standard deviation of  $\ln(\text{energy use})$  against the standard deviation of  $\ln(\text{population density})$ . This figure demonstrates a relationship that most closely matches that expected under our *m* causal model. Although energy use was not directly measured in this article, the methods used to estimate it are independent of the estimation we used here. The putative causal role of body size is in agreement with a large body of theory and empirical relationships that envisions body size as a fundamental trait linking different aspects of the physiology, ecology, and evolution of species (e.g., Damuth 1981; Peters 1983; Calder 1984; Brown and Maurer 1986; LaBarbera 1989; Lawton 1990; McKinney 1990; Brown et al. 1993).

If either the *m* causal or the *p* causal model describes the real world, then it is clear that the variance in species energy use,  $V(e)$ , closely tracks the variance in population density,  $V(n)$  (fig. 2*B*), whereas this is not the case under the *n* causal model. These relationships in no way depend on the assumption of a canonical lognormal distribution of species abundance. Furthermore, because this work does not depend on any assumptions about canonicity, this work could be used, without tautology, to draw conclusions about the canonicity of energy use. Should a researcher find that, in a community of interest, population densities

are canonically distributed, that researcher could reasonably infer that energy use is also canonically distributed. However, testing for canonicity is a difficult problem, which at this time is unresolved (Dennis and Patil 1988).

The existence of a nearly proportional relationship between the variance in energy use and the variance in population density, as indicated by the  $m$  causal model, suggests that species abundance distributions are good indicators of the way species divide resources within communities. Stated in more general terms, this means that the apportionment of individuals and resources, among species, are equivalent processes. This observation supports the biological interpretation of the hierarchical resource subdivision model proposed by Sugihara (1980).

#### ACKNOWLEDGMENTS

We thank B. Maurer for kindly providing the bird community data. J. Brown, T. Case, B. Dennis, B. Holt, M. Hooten, D. Kelt, S. Lele, B. Maurer, G. Sugihara, and G. Wilkinson provided helpful discussion and commented on the manuscript. M.L.T. was partially supported through National Science Foundation (NSF) grants BSR-8821458 and DEB 9411770 and U.S. Environmental Protection Agency Cooperative Agreement CR-820086. P.A.M. was partially supported through NSF grant INT-9223313.

#### APPENDIX

##### DERIVATION OF VARIANCE RELATIONSHIPS

##### $n$ CAUSAL MODEL

We begin with the empirically observed relationships between  $m$  and  $n$  and between  $m$  and  $p$ :

$$n = a_n + b_n m + d_n \quad (\text{A1})$$

and

$$p = a_p + b_p m + d_p. \quad (\text{A2})$$

Equations (A1) and (A2) are equations (3) and (4) including an error term. The  $n$  causal relationship assumes that  $n$  is the causal variable. Rearranging equation (A1), we can express  $m$  in terms of  $n$  as

$$m = \frac{n - a_n - d_n}{b_n}. \quad (\text{A3})$$

Substituting equation (A3) into equation (A2) yields

$$p = a_p + b_p \left( \frac{n - a_n - d_n}{b_n} \right) + d_p. \quad (\text{A4})$$

The  $\log_{10}$  of population energy use,  $e$ , can be calculated as the sum of  $n + p$ :

$$e = n + p = \left( 1 + \frac{b_p}{b_n} \right) n + a_p - \left( \frac{b_p}{b_n} \right) a_n - \left( \frac{b_p}{b_n} \right) d_n + d_p. \quad (\text{A5})$$

Recalling that the variance of a sum of independent random variables is the sum of the variances, that the variance of a constant is zero, and that the variance of a constant times a random variable is the constant squared times the variance of the random variable, we can easily see from equation (A5) that the variance in  $e$  is given by

$$V(e) = \left(1 + \frac{b_p}{b_n}\right)^2 V(n) + \left(\frac{b_p}{b_n}\right)^2 V(d_n) + V(d_p). \quad (\text{A6})$$

#### $p$ CAUSAL MODEL

Express  $m$ ,  $n$ , and  $e$  in terms of  $p$ :

$$m = \frac{p - a_p - d_p}{b_p}, \quad (\text{A7})$$

$$n = a_n + \frac{b_n}{b_p} (p - a_p - d_p) + d_n, \quad (\text{A8})$$

and

$$e = n + p = a_n + \frac{b_n}{b_p} (p - a_p - d_p) + d_n + p. \quad (\text{A9})$$

The variance in  $e$  in terms of the variance in  $p$  is given by

$$V(e) = V(p) \left(1 + \frac{b_n}{b_p}\right)^2 + \left(\frac{b_n}{b_p}\right)^2 V(d_p) + V(d_n). \quad (\text{A10})$$

For the purposes of this article,  $V(e)$  needs to be expressed in terms of  $V(n)$ , not  $V(p)$ . From equation (A8), we can see that

$$V(n) = \left(\frac{b_n}{b_p}\right)^2 V(p) + \left(\frac{b_n}{b_p}\right)^2 V(d_p) + V(d_n); \quad (\text{A11})$$

rearranging, we also see that

$$V(p) = \frac{V(n) - \left(\frac{b_n}{b_p}\right)^2 V(d_p) - V(d_n)}{\left(\frac{b_n}{b_p}\right)^2}. \quad (\text{A12})$$

Substituting equation (A12) into equation (A10) yields

$$V(e) = \left[ \frac{V(n) - \left(\frac{b_n}{b_p}\right)^2 V(d_p) - V(d_n)}{\left(\frac{b_n}{b_p}\right)^2} \right] \left(1 + \frac{b_n}{b_p}\right)^2 + \left(\frac{b_n}{b_p}\right)^2 V(d_p) + V(d_n). \quad (\text{A13})$$

#### $m$ CAUSAL MODEL

From equations (A1) and (A2),

$$e = n + p = a_n + b_n m + d_n + a_p + b_p m + d_p, \quad (\text{A14})$$

$$V(e) = (b_n + b_p)^2 V(m) + V(d_n) + V(d_p), \quad (\text{A15})$$

and

$$V(n) = b_n^2 V(m) + V(d_n). \quad (\text{A16})$$

Rearranging equation (A16),

$$V(m) = \frac{V(n) - V(d_n)}{b_n^2}. \quad (\text{A17})$$

Substituting equation (A17) into equation (A15) yields

$$V(e) = \left(1 + \frac{b_p}{b_n}\right)^2 [V(n) - V(d_n)] + V(d_n) + V(d_p). \quad (\text{A18})$$

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*Associate Editor: John Pastor*

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