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DISTRIBUTION OF ENERGY USE AND BIOMASS AMONG SPECIES OF NORTH AMERICAN TERRESTRIAL BIRDS¹

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Abstract. The distribution of biomass and energy use among species with different body sizes provides an empirical basis for studying ecological processes that determine species diversity. Biomass and energy use distributions were determined for North American terrestrial birds from data on population density and body mass of 380 species and data on energy use obtained from the literature. Using these data, several hypotheses regarding the specific form of biomass (summed for all species in a body size category) and energy use distributions were evaluated.

Biomass continued to increase in successive log body mass intervals, but this was not due simply to increasing species numbers. Energy use initially increased in these same intervals but leveled off above a body mass of ≈ 80 g. Energy used by average populations of individual species was uniformly distributed between the lower and upper bounds of each log body mass interval. In addition, the upper boundaries on biomass and energy use for individual species paralleled closely the biomass and energy use distributions. Qualitatively similar patterns were obtained for plant- and animal-eating birds considered separately, and for birds in 14 arbitrarily defined subregions of the North American continent. There were important quantitative differences among energy use distributions for the 14 subregions. Subregions at lower latitudes had energy use distributions that were nearly an order of magnitude higher than those of regions at higher latitudes. These results imply that previous hypotheses to explain biomass and energy use distributions were not of sufficient generality to account for both similarities among distributions of very different systems (e.g., birds and aquatic plankton) and spatial variation among systems composed of similar species. A more general hypothesis should consider the importance of inherent physiological constraints on energy use and environmental limitations on energy availability. The processes that influence resource allocation in a large assemblage of many species may result in statistical patterns of energy use and biomass that tend to maximize ecological quantities analogous to entropy in statistical physical systems.

Key words: biomass; birds; body size; energetics; macroecology; resource allocation; species diversity; statistical distributions.

INTRODUCTION

The processes that underlie the generation and maintenance of species diversity are poorly understood (Brown 1981). One of the first theoretical attempts to deal with the constraints that govern the species composition of a large group of organisms was Hutchinson and MacArthur's (1959) suggestion that the number of species was a consequence of the sizes of different organisms and how size structure affected the division of resources in the environment. Large species were hypothesized to use the environment at a much larger scale, and hence could not divide resources into as many niches as smaller species. An extension of this approach would suggest that in order to understand the relationship between species diversity and the size

structure of a biota, it is important to describe the quantity of resources used by populations of species of different body sizes.

If Hutchinson and MacArthur's (1959) insights are applicable, then the distribution of energy use and biomass by populations of different-sized species should provide information on both the similarities among diverse biotas and the variation among similar biotas experiencing different environmental conditions. In studies of aquatic planktonic and benthic assemblages, results have shown that qualitatively repeatable distributions of biomass characterize logarithmically increasing body size classes (Sheldon and Parsons 1967, Sheldon et al. 1972, Sprules 1980, Schwinghamer 1981, Peters 1983a, Sprules et al. 1983, Warwick 1984, Strayer 1986). In addition, biomass distributions often vary in a predictable manner across environmental gradients (Sheldon et al. 1972, Sprules 1980, Sprules and Munawar 1986). The regularities in these distributions for aquatic organisms suggest that their application to terrestrial systems might elucidate some of the processes that determine diversity in terrestrial species

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assemblages. However, few studies have considered biomass distributions in terrestrial systems (but see Griffiths 1986).

Although biomass distributions have been the subject of many studies, distribution of energy use among species has received little attention. The relationship between body size and population density has been used to estimate the amount of energy used by populations of species that differ in size (Damuth 1981, Peters 1983*b*, Peters and Wassenberg 1983, Peters and Raelson 1984, Brown and Maurer 1986). Results of such analyses may be difficult to interpret, however, because there is wide variation around the allometric regressions used to characterize the relationship between body size and density both within and among different kinds of species assemblages (Brown and Maurer 1986; cf. Juanes 1986, Robinson and Redford 1986).

Harvey and Lawton (1986) suggested that it is important to study the relationship between the distribution of species among biomass categories and the amount of energy used by them. They argue that both of these phenomena are important and suggest specific testable hypotheses regarding the relationship between them.

In this paper we use data on biomass distributions and energy use in North American terrestrial birds to evaluate several hypotheses that have been advanced to explain the patterns of biomass distribution and energy use. Our choice of the large spatial scale, the North American continent, and a taxonomically defined group of organisms, birds, has important implications for the generality of our results and the applicability of the above hypotheses. By focusing on a continental scale we are ignoring for the moment the details of how energy is allocated within local communities. By using a large, but taxonomically defined, assemblage we are able to address how organisms subject to a common set of evolutionary constraints have diversified ecologically to exploit the energy resources available to them. We are aware that birds may interact in important ways with other organisms that are prey, predators, pathogens, competitors, or mutualists, and that ultimately it would be desirable to include all of these organisms in a general concept of how communities are organized. For the present, however, it is instructive to ask how energy resources are allocated on a continental scale among a group of organisms that are ecologically diverse but constrained by common ancestry to have generally similar morphology, physiology, and behavior.

HYPOTHESES

There are actually three related phenomena, each of which has generated hypotheses, that are relevant to the present study. The first, the species density distribution, is the number of species in successive logarithmic body size classes. The second, the biomass

distribution, depicts the total amount of organismal biomass contained in successive logarithmic body size classes. The third, the energy use distribution, is the total amount of energy used by organisms in successive size classes. In all cases, these distributions have been analyzed using the logarithm of body size, because energy use and related processes scale allometrically with body size (e.g., Peters 1983*b*, Calder 1984).

Several hypotheses have been developed that predict specific forms of these three distributions (e.g., species density distributions: Hutchinson and MacArthur 1959, May 1978, 1986; biomass distributions: Sheldon et al. 1972, Kerr 1974; energy use distributions: Damuth 1981, Harvey and Lawton 1986). Many of these hypotheses are of limited generality since they deal with specific systems (e.g., Kerr 1974). Nevertheless, each hypothesis is based on empirical patterns, and we can use these patterns to predict alternative forms of these distributions that might be expected for our data. Similarities and differences between our data and those from other systems may suggest useful generalities about the constraints and processes that influence resource allocation in diverse kinds of organisms and different kinds of environments.

Several studies have suggested that on a logarithmic scale species density distributions should be unimodal and right-skewed (i.e., with a longer tail to larger body size categories than to smaller size categories; Hutchinson and MacArthur 1959, May 1978, 1986). This pattern seems to be more prevalent in samples taken from a large geographic area than within individual communities, where distributions may be more symmetric.

Some work on aquatic systems has suggested that biomass distributions are essentially constant across logarithmic body size intervals (Sheldon et al. 1972, Kerr 1974), while others have documented a great deal of variability (e.g., Sprules 1980, Sprules and Munawar 1986, Strayer 1986). Sprules and Munawar (1986) found that in planktonic communities deviations from a constant biomass distribution could be related to differences in ecosystem productivity. Thus, equal biomass in successive size categories, which we call the equal biomass hypothesis below, can be considered a baseline against which observed distributions can be compared.

Damuth (1981) presented data on the allometric scaling of population density of herbivorous mammals and suggested that population energy use by individual species of large organisms was equal to population energy use by small species, because small organisms had sufficiently high population densities to compensate for lower metabolic rates (see also Van Valen 1973). This hypothesis, referred to as the equal energy use hypothesis below, predicts a specific form of the energy use distribution as derived in the methods section of this paper.

The equal energy use hypothesis differs from Harvey and Lawton's (1986) recent suggestion that energy used

by species of small body size will be greater than that for large organisms. They argue that even though individual species populations of small organisms might use less energy than species of large ones, there are sufficiently more species of small organisms to more than compensate for their lower energy use per species. We call this the species density compensation hypothesis.

METHODS

Tests of the hypotheses developed in the previous section require comprehensive data on densities, body sizes, and energy use in a large species assemblage. Since the data in this paper often span several orders of magnitude and there is the potential for nonlinear relationships among variables, all data were log transformed. For the rest of the paper, we take all logarithms (log) to be base 10 unless explicitly stated (e.g., ln indicates natural logarithms).

Data on population densities of North American land birds were obtained from the Breeding Bird Surveys (BBS), conducted by the United States Fish and Wildlife Service and the Canadian Fish and Wildlife Service. A detailed description of the BBS can be found in Robbins et al. (1986), and additional information on our use of these data is given in Brown and Maurer

TABLE 1. Species density distributions across nine arbitrarily defined logarithmic (base 10) mass classes for five trophic groups of birds found in North America and for the entire avifauna.

| Mass class | Lower bound (g) | Upper bound (g) | Trophic group* | | | | | All species |
|------------|-----------------|-----------------|----------------|----|-----|-----|----|-------------|
| | | | C | H | I | O | N | |
| 1 | | 6.3 | 0 | 0 | 3 | 1 | 11 | 15 |
| 2 | 6.3 | 13.1 | 0 | 0 | 68 | 21 | 2 | 91 |
| 3 | 13.1 | 27.3 | 0 | 0 | 35 | 41 | 0 | 76 |
| 4 | 27.3 | 57.5 | 2 | 2 | 33 | 38 | 0 | 75 |
| 5 | 57.5 | 120.2 | 3 | 1 | 11 | 35 | 0 | 50 |
| 6 | 120.2 | 251.8 | 6 | 9 | 1 | 3 | 0 | 19 |
| 7 | 251.8 | 526.0 | 14 | 5 | 1 | 0 | 0 | 20 |
| 8 | 526.0 | 1101.5 | 12 | 8 | 0 | 0 | 0 | 20 |
| 9 | 1101.5 | | 11 | 3 | 0 | 0 | 0 | 14 |
| Total | | | 48 | 28 | 152 | 139 | 13 | 380 |

* C = carnivore, H = herbivore, I = insectivore, O = omnivore, N = nectarivore.

(1987). We used the BBS data to estimate the average density of each species across the entire North American continent and within 14 arbitrarily defined geographic subdivisions (Fig. 1). The estimate of abundance, given as counts of individual birds per 40-km BBS route, is assumed to reflect the average population density at those sites where it occurred. Body masses for the species were obtained from Dunning (1984). From the data on density and biomass, we calculated population biomass (grams per route) as average density times body size.

Obtaining data on energy use by birds was more difficult. Initially, we reasoned that trophic status of an organism should influence its rate of energy use. We had previously (Brown and Maurer 1987) assigned 380 species of North American birds to one of five general trophic groups (Table 1). We used data assembled from the reviews of Walsberg (1983) and Nagy (1987) on daily energy use (kilojoules per day) to develop regressions of log energy use per individual on log body mass for each of the five trophic groups used in this study. Although somewhat different techniques were used to estimate daily energy use in the studies summarized in these two papers, they represent the best data currently available on metabolic rates of free-living birds. They are sufficiently detailed to give reasonable estimates for each trophic group. Regressions for each trophic group were used to estimate energy use per individual from the data on average body mass. The transformation from the log-log regression back to energy use causes the resulting value for energy use to be underestimated (Miller 1984). A correction factor for this bias (Sprugel 1983, Miller 1984) was estimated for each trophic group and used to obtain a corrected estimate of energy use per individual. This value was then multiplied by population density obtained from the BBS data set to estimate population energy use (kilojoules per day per route).

To obtain the biomass distribution, we summed all population biomasses from species in each of nine ar-



FIG. 1. Fourteen arbitrarily defined biogeographic regions for the North American continent. Regions were defined in order to have roughly the same area.

bitrarily defined logarithmic body mass class intervals (Table 1). We obtained the energy use distribution by summing population energy use estimates in each body mass class. Since the arbitrarily chosen location and width of the body size intervals might influence the final shape of the distributions, we applied the following procedure. We selected an interval of fixed width on a log scale with its lower bound equal to the biomass of the smallest species. We summed all population energy use values for all species in this interval and calculated the midpoint of the interval. This gave a value for log body size and a value for total energy use. We then moved the interval a small increment to the right and recalculated total energy use and the body size interval midpoint. We continued this procedure until the upper limit of the body size interval corresponded to the body size of the largest species. The curve defined by the midpoints and total energy use values thus obtained gave a smoothed estimate of the energy use distribution. Since this estimate was virtually identical to that obtained using the original body size intervals (see Results: Distribution of Biomass and Energy Use among Species; Fig. 4) this smoothing procedure was not repeated for any other analysis.

The equal energy use hypothesis predicts a specific form for the energy use distribution based on the number of species in the interval and the energy used by populations of each species. Since this hypothesis assumes that population energy use is the same regardless of body size, the total energy use in any size class is simply the number of species in that class multiplied by the constant population energy use per species. This independence of population energy use and body size is assumed to hold across all mass classes, so it is possible to estimate the constant of population energy use from data on population energy use and the number of species in each category. Let A be the constant population energy use assumed by the hypothesis, then the total energy used in the j^{th} body size category, E_j , is An_j , where n_j is the number of species in that interval. Since a log scale is being used we have $\log A + \log n_j$ as a predicted value, $\log \widehat{E}_j$. Using the principle of least squares, we want the value of $\log A$ that minimizes the sum of squared deviations of the predicted value of log energy use in the nine body size categories, $\log A + \log n_j$, from the observed value, $\log E_j$. If ss is the sum of squares, then,

$$ss = \sum (\log E_j - \log A - \log n_j)^2.$$

This value is minimized when

$$\log A = \frac{\sum \log E_j - \sum \log n_j}{9}.$$

Using this estimate of $\log A$ and the $\log n_j$ for each interval, we predicted the energy use distribution under the assumptions of the equal energy use hypothesis.

To estimate the variance of $\log E_j$, a Taylor series

expansion can be used to derive an asymptotic estimator (Kendall and Stuart 1977:246–250). An estimate of the variance of the mean of a sample is s^2/n . Now $\log E_j$ is a function of the mean population energy use (x_j), that is,

$$\log E_j = f(x_j) = \log n_j x_j,$$

so using the Taylor series method, this gives,

$$\text{var}(\log E_j) = (s_j^2/n_j)[f'(x_j)]^2,$$

where s_j^2 is the sample variance of population energy use among species in the j^{th} mass class. Since $f'(x_j) = 1/(x_j \ln 10)$,

$$\text{var}(\log E_j) = s_j^2/[n_j(x_j \ln 10)^2].$$

From this asymptotic estimate of the variance of $\log E_j$, it is possible to calculate asymptotic 95% confidence intervals around $\log E_j$, and compare them with the expected values predicted by the equal energy use hypothesis. In addition, the species density compensation hypothesis can be evaluated by observing whether the values for energy use decrease significantly in successively increasing mass classes. If not, this constitutes a rejection of that hypothesis.

Initial inspection of the data on population energy use suggested that log population energy use values for individual species of similar body size were distributed uniformly between minimum and maximum values. If this were true, then each successive species would obtain a constant proportion of the total energy left after species of higher energy use were subtracted from the initial total. Thus, population energy use within body size categories would follow a log-series rule. That is, energy use by each successively less abundant species would decrease by a constant proportion. To evaluate this hypothesis, we assumed, for each body mass category, a uniform distribution of energy use values for individual species between the observed maximum and minimum log population energy use values. The number of species in the class was drawn from a Poisson distribution with a mean equal to the observed number of species in the category. Species were then randomly chosen from the uniform distribution, and the summed energy use of these species determined. The mean and variance of summed energy use for 1000 such selections for each body mass category defined the energy use distribution. A second such distribution was similarly determined, except the number of species in a mass category was fixed as the observed number. The two simulated energy use distributions were then compared with the observed distribution.

RESULTS

Energy use regressions

With the exception of herbivores, allometric regressions for all trophic groups indicated that slopes and intercepts, as well as correction factors, were similar

TABLE 2. Results of regressions of log energy use (measured in kJ/d) on log body mass (measured in g) for predicting individual energy use for five trophic groups of North American birds based on daily energy use estimates given by Walsberg (1983) and Nagy (1987). All parameter estimates were significantly different from 0 at $P < .05$.

| Trophic group | No. species | Slope (b) | Intercept (a) | Residual MS | Correction factor |
|---------------|-------------|-----------|---------------|-------------|-------------------|
| Carnivores | 7 | 0.69 | 0.98 | 0.0173 | 1.05 |
| Herbivores | 7 | 1.14 | -0.36 | 0.0390 | 1.09 |
| Insectivores | 13 | 0.58 | 1.15 | 0.0129 | 1.03 |
| Omnivores | 9 | 0.65 | 1.05 | 0.0100 | 1.03 |
| Nectarivores | 7 | 0.60 | 1.15 | 0.0080 | 1.02 |
| All species | 43 | 0.59 | 1.13 | 0.0201 | 1.05 |

to the overall equation derived from all the data (Table 2).

The reason for the different results obtained from the herbivores was unclear. In the herbivore regression, diagnostic statistics for the regression indicated that the data point most influential in the regression was that for *Nucifraga caryocatactes*, a passerine herbivore. The estimate of daily energy use for this species was obtained under conditions of severe cold weather (see Walsberg 1983), hence, it may not be representative of typical energy use by an herbivore of its size (158 g). However, no improvement was obtained by leaving this species out of the herbivore regression. Three of the seven herbivorous species were desert-dwelling birds, and Nagy (1987) indicated that desert birds tend to have lower metabolic rates than other birds. This may have also biased the herbivore regression. With such small sample sizes (7–10 data points), most of the regressions can be expected to be of low precision, and hence, the overall equation may provide a better estimate of daily energy use than any of the separate regressions for trophic groups.

Distribution of biomass and energy use among species

The frequency distribution of species with respect to body size in the entire North American avifauna agreed qualitatively with the form predicted by Hutchinson and MacArthur (1959) (Fig. 2). The distribution is unimodal and skewed toward larger body size categories. However, within trophic groups there was less variation in body size, and the predicted structure is much less evident (Table 1). Herbivores and carnivores accounted for almost all species at the large end of the size spectrum, whereas insectivores, omnivores, and nectarivores predominated at the smaller end (Table 1).

The distribution of population biomasses for North American birds shows an increase with body size (Fig. 3). There is no increase in the species density distribution (Fig. 2), indicating that the pattern of biomass is not simply due to species numbers. In addition, average values of population biomass for individual

species increased with increasing body size. Therefore, we reject the equal biomass hypothesis for North American birds.

The energy use distribution increased up to ≈ 80 g then leveled off (Fig. 4). Again this pattern is not simply due to number of species per mass category (compare with Fig. 2). The smoothed estimate of the energy use distribution was nearly identical to the pattern described using only nine logarithmic intervals (Fig. 4).

A striking feature of biomass and energy use for individual species was that values fell within a well-defined tetrahedron on log-scaled axes (Figs. 3 and 4). For both energy use and biomass, the maximum values for individual species described two lines that were roughly parallel to the values obtained by summing across all species in each body size interval. For energy use but not biomass, the maximum for individual species leveled off above 80 g, i.e., the slope of this segment of the tetrahedron was ≈ 0 . The species with the lowest population energy use fell along a line with a slope of ≈ 0.67 , and those species with the lowest biomass fell along a line of slope ≈ 1 . The fourth side of the tetrahedron was determined by several species near the minimum size for a bird (≈ 3 g) that exhibited a range of values for population density and hence for energy use and biomass.

When the population energy use distribution observed for the North American continent was compared with the value predicted from the equal energy use hypothesis, it was apparent that this hypothesis gave poor predictions (Fig. 5). Energy use was greatly overestimated for the smaller species and significantly underestimated for larger species. Our data also do not support the predictions of the species density compensation hypothesis. Rather than decreasing continuously as this hypothesis predicts, the energy use distribution actually increases with body size initially then levels out (Fig. 5). The increase occurs even though the greatest number of species occurs in the small mass classes

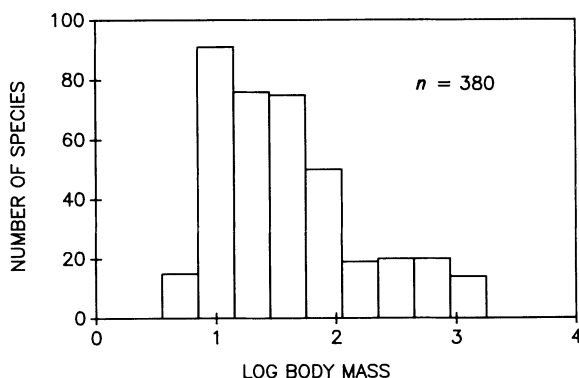


FIG. 2. The species density distribution for North American terrestrial birds. n = total number of species. Notice the rapid increase in species number with body size (measured in grams) in the first two body size intervals and the more gradual decline thereafter.

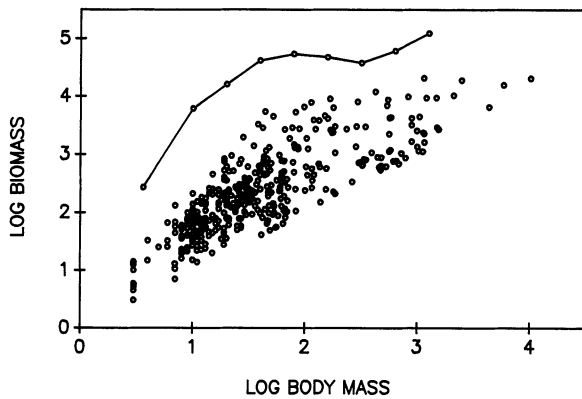


FIG. 3. Biomass distribution (○—○) measured in grams and population biomasses for individual species (measured in grams per route) of North American terrestrial birds. Overlapping (filled) circles represent multiple, similar values.

(Table 1, Fig. 2). Thus, we reject both the equal energy use and species density compensation hypotheses as explanations for the distribution of population energy use among North American land bird species (see also Brown and Maurer 1986).

The distribution of energy use values among species within a body size class corresponded closely to the uniform distributions generated using the log series assumption for energy allocation (Fig. 6). When the numbers of species in a mass class were not fixed, the variance around the distribution was slightly larger (Fig. 6), but otherwise the distributions were almost identical.

Variation of the distribution of energy use among species

The North American terrestrial avifauna consists of species that use very different energy sources. To assess whether the pattern of energy allocation varied among trophic groups, we divided the species into those that used primarily animal or primarily plant foods (Brown and Maurer 1987). We then repeated the above analysis and found that the distribution of energy use within these two groups was qualitatively similar to that for the entire avifauna (Fig. 7).

The energy use distributions within the 14 biogeographic regions in Fig. 1 were qualitatively similar to the pattern for the entire North American continent (Fig. 8; compare with Fig. 4). However, there were important quantitative differences among regions. The most striking was that maximum energy use per species and total energy use by all species in northern latitudes (i.e., regions 12, 13, and 14; Fig. 1) was nearly an order of magnitude less than in the southern regions (Fig. 8). In addition, fewer species occurred in the northern regions. This produced cumulative energy use distributions that were more irregular because of sampling error and were truncated at large or small body sizes relative to southern regions (Fig. 8). An analysis of

species shared among regions indicated that widely separated regions usually had <50% of their species in common, and that northern regions shared a larger proportion of their fauna with the southern regions than vice versa (B. A. Maurer and J. H. Brown, *personal observation*).

DISCUSSION

We have shown that the forms of biomass and energy use distributions predicted from several previous hypotheses are not supported by the observed distributions for North American birds. Our rejection of these hypotheses for birds is not due to the uniqueness of the system we studied. For example, biomass and assimilation (another estimate of energy use) distributions reported for a lacustrine zoobenthos are similar to those we show for birds (Strayer 1986), and the particular relationship between population density and body mass that is required by the equal energy use hypothesis does not appear to hold for many taxonomic groups (Brown and Maurer 1986). We suggest that the theories we have evaluated in this paper all share a common difficulty: they make too many simplifying assumptions to be applicable to most systems. These assumptions all have to do with the way that the distribution arises as a consequence of the properties of the units that are included in the distribution. For example, Kerr's (1974) derivation of the equal biomass distribution relies on assumed trophic relationships among successive body size classes. This may hold for a limited number of systems, but it is unlikely that it is applicable to continental-scale, taxonomically defined biotas, such as the North American avifauna. Although there is some predation by larger birds on smaller ones, this probably accounts for only a small fraction of the ecological relationships among size categories. Furthermore, since the system being studied

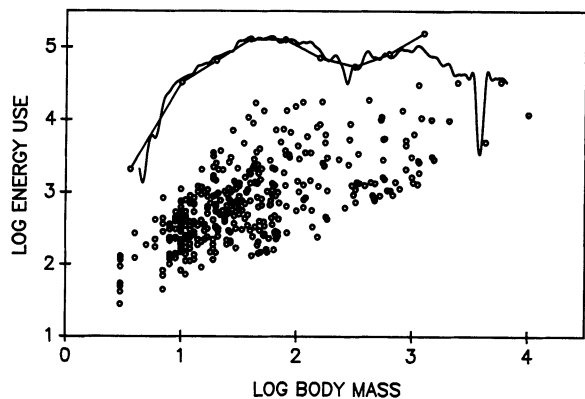


FIG. 4. Energy use distribution (○—○) and population energy use for individual species of North American terrestrial birds. Energy use is measured in kilojoules per day per route and body mass in grams. The smooth curve represents the energy use distribution obtained from the smoothing procedure described in Methods. Overlapping (filled) circles represent multiple, similar values.

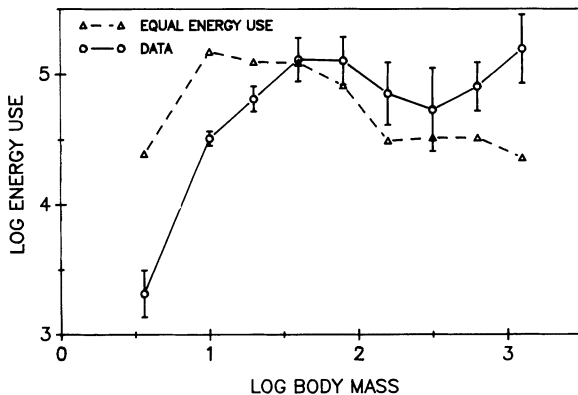


FIG. 5. Predicted form of the energy use distribution based on the equal energy use hypothesis and the observed energy use distribution for North American terrestrial birds. Energy use is measured in kilojoules per day per route and body mass in grams. Means and 95% confidence intervals are plotted.

is geographic in scale, it is unlikely that trophic interactions among birds will be of sufficient consistency in space and time to have a major impact on the distributions documented here for North American birds.

We suggest that previous hypotheses not only do not predict the patterns for birds and other systems well, but they do not account for spatial variation among similar systems. For example, Sprules (1980) documented that variation among biomass distributions of planktonic systems in several lakes could be associated with variation in the environment. We have shown here that energy use distributions of birds show systematic variation between geographic subregions. Presumably, more severe conditions at high latitudes result in lower total energy available, and these resources are divided among fewer species than farther south. There is little in the theories we considered here that would account for such variation in the system in response to environmental variation.

If the current theories are not sufficiently general to account for the properties of distributions of biomass and energy use, we suggest that these theories will be of limited usefulness in understanding the ultimate reasons for the widespread similarity in distributions observed in very different systems such as land birds, lacustrine plankton, and benthic organisms. Although we cannot yet offer a complete alternative hypothesis, we outline below what we feel are key elements of a general theory for population biomass and energy use distributions. This general theory is based on the early insights of Hutchinson and MacArthur's (1959) model for species size distributions.

A critical element of a general theory is what might be called a statistical approach (Brown 1984). By this we mean that the collection of organisms being studied can be viewed as a large number system, so that the properties of the aggregation of organisms (e.g., the energy use distribution) can be described as a statistical

consequence of the properties of the organisms. This was a key element of the Hutchinson-MacArthur model.

The second element of the theory consists of the set of constraints that determine the properties of the organisms and how they interact with their environment. The set of constraints can be divided into two different types. The first deals with the physiological processes by which organisms process energy. This set of constraints is similar to what Brown (1981) envisioned as allocation rules, in that they will determine how energy is used within and among species. It is clear that Hutchinson and MacArthur (1959) felt that the body sizes of individual organisms would have a profound effect on resource use. We suggest that allometric relationships describing physiological processes such as metabolism and reproductive effort will often provide information on the general nature of constraints on energy use (Peters 1983*b*, Calder 1984).

Our data on birds suggest that there are important regularities in the allocation of energy resources among species. First, recall that there was a well-defined tetrahedron described by the boundaries for population energy use by individual species. The boundaries determined by the species that use the most energy parallel the total energy used by all species (Fig. 4) on a log scale. This implies that the most abundant species in all body size categories use the same fraction of the total energy used by all species (≈ 0.1). Second, the density of species is greater in the smaller mass categories (Fig. 2), so that the average quantity of energy used by a small species is less than that used by a large species. The implication is that small species divide up the energy available to them into smaller units than

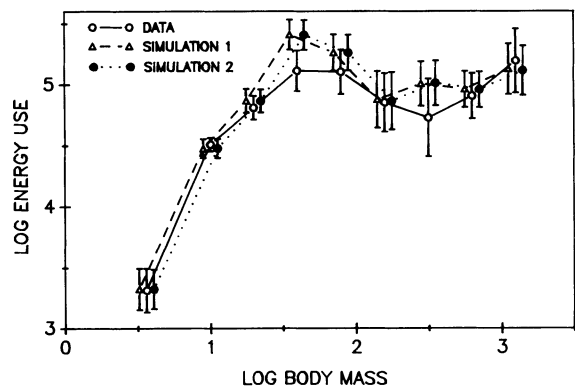


FIG. 6. Comparison of the observed energy use distribution for North American terrestrial birds with distributions obtained from simulations assuming a uniform distribution of log population energy use among species. Energy use is measured in kilojoules per day per route and body mass in grams. In simulation 1, species numbers for each body size interval were drawn at random from a Poisson distribution with a mean equal to the observed number of species in that interval. In simulation 2, species numbers were fixed as the observed number in each interval. Means and 95% confidence intervals are plotted.

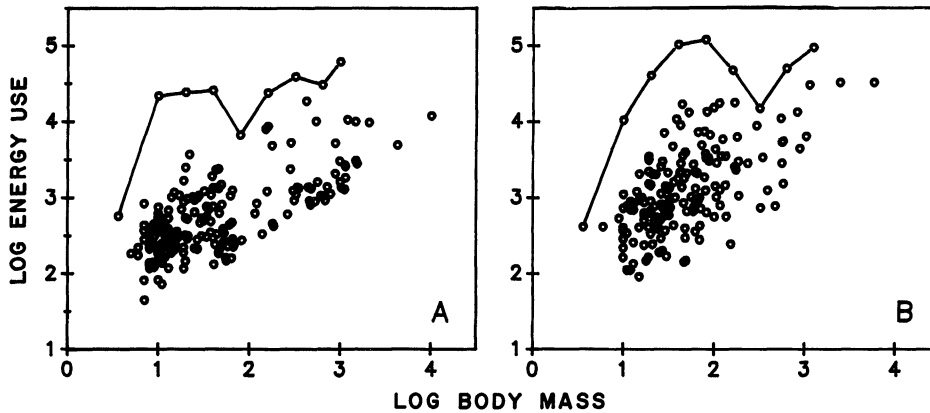


FIG. 7. Distribution of energy use (○—○) and population energy use for individual species for (A) animal- and (B) plant-eating birds considered separately for North American terrestrial birds. Energy use is measured in kilojoules per day per route and body mass in grams. Overlapping (filled) circles represent multiple, similar values.

large species, confirming Hutchinson and MacArthur's (1959) premise. Finally, within each category, the dispersion of population energy use by individual species on a log scale is not significantly different from a uniform distribution. Since a uniform distribution on a logarithmic scale is identical to a log-series distribution each successively rarer species within a size category should have a population energy use that is some constant fraction of the next most abundant species. This fraction varies significantly with body size. Thus the total energy used by a size class is subdivided in this fractional manner until the least abundant species obtains some minimal quantity. Since the lower boundary scales as $\approx \text{mass}^{0.67}$ (the same exponent as individual energy use), this suggests that population densities of the rarest species are limited by their abilities to obtain adequate energy resources.

Hutchinson and MacArthur (1959) indicated that the divisibility of resources in the environment was an important consideration in developing their model. We suggest that the second type of constraint important to the general theory we envision is imposed by the availability of resources in the environment. For example, variation in food quality, which would be differentially usable by species of different body sizes, would be such a constraint. These constraints, when fully elucidated, would explain why the properties of population energy use distributions vary with changes in the environment. Brown (1981) called such constraints capacity rules.

Given the two types of constraint described above, and a large number of organisms of similar type or function, the statistical expression of the interaction between allocation and capacity rules should be a characteristic distribution of population energy use among species, such as those described in this study. In much the same sense that statistical systems in physics can be said to be maximum entropy systems, we expect that distributions of energy use and biomass will be

found to maximize some analogous ecological quantity (Ulanowicz 1986, see also Brooks and Wiley 1986). Although the details of exactly how such ecological quantities are to be calculated for species assemblages have not yet been determined (but see Lurié et al. 1983, Lurié and Wagensberg 1983), we anticipate that they will provide a powerful phenomenological way of describing assemblages. This should eventually lead to powerful insights into the processes that determine the number and kinds of species that coexist within a site and the spatial and temporal variation in the composition of assemblages in response to a changing environment.

The theoretical approach that we have outlined above suggests that further efforts in investigating population biomass and energy use distributions should focus on describing the physiological constraints governing energy use by the organisms being studied and the availability of resources in the environment. Variation in population energy use and biomass distributions among different geographic regions, habitat types, and taxonomic groups may be especially valuable in identifying the important constraints. This large-scale approach to ecology, which we call "macroecology," should shed new light on the complexity of large-scale phenomena, and provide a paradigm for predictions regarding the properties of complex ecological systems. For example, the statistical approach we have described above and the data we have reported for birds allow us to predict that in large collections of organisms, relatively smooth, unimodal distributions of population energy use and biomass should result, while in smaller collections of organisms, sampling processes may cause the distributions to be multimodal (Fig. 8). Small collections of organisms may be the result of sampling a small part of a much larger system (e.g., for birds and small vertebrates a census plot of a few hectares) or a more complete sampling of a species-poor system (as for birds at high latitudes). As more data accumulate on

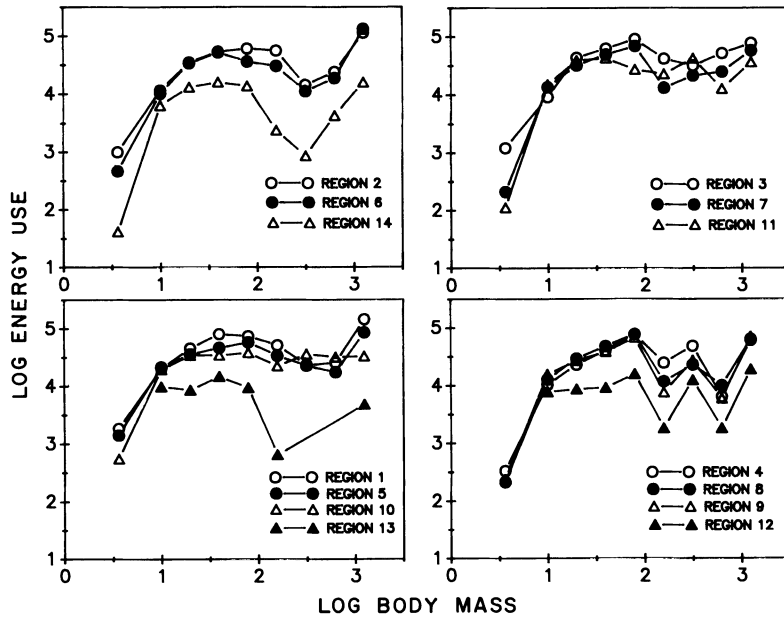


FIG. 8. Energy use distributions in each of the 14 biogeographic regions defined in Fig. 1. Note that regions at higher latitude (12, 13, and 14) have distributions nearly an order of magnitude lower than regions at lower latitudes. Energy use is measured in kilojoules per day per route and body mass in grams.

distributions of population energy use and biomass, a more complete knowledge of the constraints and processes that govern the allocation of energy among species should lead to a rigorous foundation for further progress in understanding spatial and temporal variation in the diversity and composition of ecological and biogeographic assemblages.

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