

EVOLUTION OF SPECIES ASSEMBLAGES: EFFECTS OF ENERGETIC
CONSTRAINTS AND SPECIES DYNAMICS ON THE DIVERSIFICATION
OF THE NORTH AMERICAN AVIFAUNA

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One way to account for the diversity of living things is to derive the rules that govern the adaptive diversification of a taxonomically constrained biota within a geographical region. These rules, if they exist, should be reflected in patterns of attributes that represent the outcomes of a combination of ecological, biogeographical, and evolutionary processes. Species, the basic units that make up biotas, interact with their environment on a wide range of spatial and temporal scales. At one extreme, variation on large spatial and long temporal scales determines the biogeographical and evolutionary processes that shape the composition of the pool of species that historically have had access to a geographical region. At the other extreme, variation on small spatial scales and short time scales influences the dynamics of local populations of interacting species and determines the combinations of species that constitute local communities. The dynamics of processes at these two extremes are not independent: species cannot occur in local communities unless historical events have given them access to the region, and species do not remain in the pool unless they are able to maintain populations within local communities.

The characteristics of species that are found at any scale represent the outcome of ecological interactions and evolutionary changes within populations as well as the origination and extinction of species. At the large scale, relationships between species and their environment are mediated largely by the dynamics of evolutionary change both within and among species. Opportunities for colonization continually modify the composition of the species pool, and speciation, extinction, and evolutionary differentiation adjust the number and attributes of species to environmental conditions. On the small scale, the interactions of species with their environment are mediated by the dynamics of local populations.

To the extent that these evolutionary and ecological processes are general, we can expect them to be reflected in the attributes of species that constitute taxonomically and geographically defined biotas. In order to study these processes empirically, we must first select an assemblage of species that share a common

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geographical region and close taxonomic relationships. Then, we must select for analysis those traits that influence the species' ecological and evolutionary dynamics.

The present study focuses on the almost 400 species that make up the North American terrestrial avifauna. Although this fauna results from the separate invasion and proliferation of several different lineages on the North American continent, the attributes of its species should reflect the common evolutionary history of the monophyletic class Aves and the shared ecological conditions within temperate North America. We analyze four attributes of these species that should influence the structure and dynamics of this biota: individual body size, average local population density, area of geographical range, and trophic guild. Each variable reflects different aspects of the interactions between a bird species and its environment. Because of the ubiquity and importance of allometric scaling relationships, body size, better than any other single variable, describes the attributes of the lower-level units, the individual organisms that species comprise (Peters 1983; Calder 1984). Population density, averaged over many local sites, characterizes the intensity with which the total area inhabited by the species is populated by individuals. The area of the geographical range provides a measure of the breadth of tolerances and requirements of the individual units, and it characterizes the extent to which each species is able to use the total space available to the biota. Trophic guild provides a discrete, qualitative categorization of the types of resources used by the species.

There is precedence for analyzing population density, body size, and geographical-range size as important characteristics of species assemblages. Initial efforts focused on documenting empirically the frequency distributions of each of these variables among species and explaining them theoretically: body size (e.g., Hutchinson and MacArthur 1959; Van Valen 1974; May 1978); population density (e.g., Fisher et al. 1943; Williams 1944, 1953, 1964; Kendall 1948; Preston 1948, 1962; Brian 1953; Kerner 1957, 1959; MacArthur 1957); and area of geographical range (e.g., Willis 1922; Rapoport 1982). Additional insights into the factors affecting biotic diversity and composition have come from analyzing bivariate distributions of these variables among species: population density and body mass (e.g., Mohr 1940; Damuth 1981; Peters 1983; Peters and Wassenberg 1983; Calder 1984; Peters and Raelson 1984; Brown and Maurer 1986); area of geographical range and body mass (e.g., Brown 1981); and population density and geographical range (e.g., Hanski 1982*a,b*; Bock and Ricklefs 1983; Bock 1984; Brown 1984). Most efforts to explain the distributions of these attributes among species have been couched in terms of traditional models of population dynamics and natural selection, where the units of primary interest have been individuals within populations. Beginning with MacArthur and Wilson's (1967) attempt to explain the composition of insular biotas, however, numerous neontologists and paleontologists have begun to recognize the potential importance of processes that operate at the level of species within biotas in determining the body sizes, population densities, geographical ranges, trophic specializations, and other attributes of living and fossil organisms (see, e.g., Stanley 1975, 1979; Vrba 1980, 1983; Arnold

and Fistrup 1982; Fowler and MacMahon 1982; Gould 1982; Vrba and Eldredge 1984; Damuth 1985; Eldredge 1985).

THEORETICAL FRAMEWORK AND PREDICTIONS

The main objective of this paper is to propose a provisional set of rules that characterizes the adaptive response of a large biota of many species (the terrestrial avifauna of North America) to the limits imposed by biological constraints (in this case, the morphological, physiological, and behavioral attributes shared by the terrestrial birds), the large-scale environment (the North American continent with its limited space, resources, and other biotic and abiotic factors), and the dynamics of species origination and extinction. We develop these rules by considering species as the unit of interest and by examining the empirical patterns and underlying mechanisms in the relationships among the three variables that have been measured for each species: average population density where the species occurs, average adult body mass, and area of geographical range.

Consider the following general framework. Imagine a three-dimensional space formed by the log-transformed values of body mass, population density, and area of geographical range (fig. 1a). Each species of a large biota can be plotted as a point on this graph, such that the distribution of points reflects the dispersion of species with respect to the three variables. Some regions of the three-dimensional space defined by the graph contain no points because they represent impossible combinations of traits that are precluded by absolute constraints. Other regions contain only sparsely distributed points because they represent regions of species-phenotype space that have few resources, have only recently been colonized, or have a high probability of extinction. Still other regions contain densely distributed points because their attributes enable many species to exploit abundant resources. To clarify the relationships among these variables, we focus on two-dimensional representations in which the boundaries separating those regions containing points from those representing combinations of variables not possessed by species can be characterized more precisely.

We now make predictions about the distribution of species with respect to these pairwise combinations of variables, beginning with the relationship between population density and body size. First, we assume some minimum size of bird that is determined primarily by physiological constraints; however, different bird species that approach this minimum size can exhibit a wide range of population densities. Second, we hypothesize that the minimum population density reflects an increasing probability of extinction with decreasing population size. If I represents the total number of individuals in a species, N the average population density, and A the area of the geographical range, then $NA = I$, and $\log N + \log A = \log I$. We further assume that some minimum total population size, I_{\min} , is necessary for long-term persistence. Since $\log A$ tends to increase with increasing body mass, M (Brown 1981; see below), then the log of minimum population density, $\log N_{\min}$, should decrease with $\log M$. Third, we predict that maximum population density, N_{\max} , should also decrease with increasing body size. Because the space

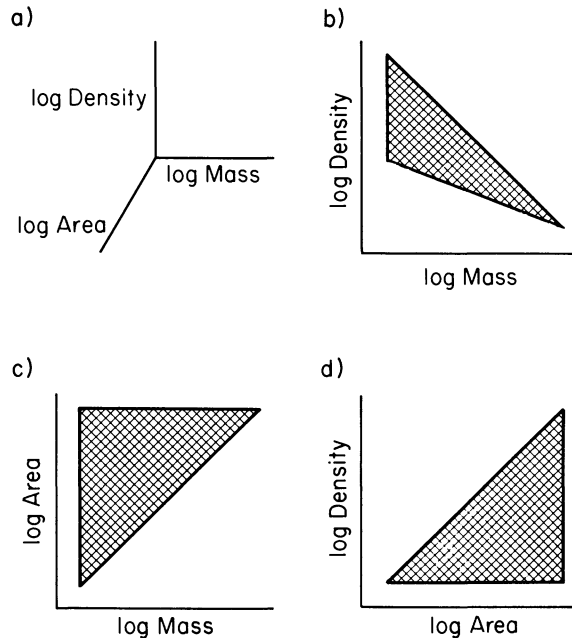


FIG. 1.—Predicted distributions of species with respect to three variables, individual body mass (M), average local population density (N), and area of geographical range (A). Conceptually, each species can be thought of as a point in three-dimensional space (a). Practically, the predicted relationships can be represented in two-dimensional plots (b–d), in which the combinations of variables expected to be possessed by species are delineated by the cross-hatched triangles. For the basis of these predictions, see the text.

and energy resources used by an individual organism are positive allometric functions of body mass, a fixed unit of space with its resources should support fewer large individuals than small individuals. Because the trade-off between population density and body mass should be steep (Damuth 1981 and Peters 1983 suggested that N scales as $M^{-1.0}$ to $M^{-0.75}$), we suggest that N_{\max} decreases more rapidly with increasing body size than N_{\min} . Thus, if on a log scale these boundaries are approximately linear, the relationship between $\log M$ and $\log N$ should be triangular, with the range and minimum and maximum densities all decreasing with increasing body size (fig. 1b).

Now consider the relationship between geographical range and body size. Two limits are straightforward: physiological constraints again set the minimum body mass; and the land area of the North American continent determines the maximal size of a geographical range. However, the minimal size of the geographical range should be related to body size (Brown 1981). Since species of large body size are constrained to have low population densities, such species with small geographical ranges should have a high probability of extinction because the total species population is small. Consequently, the minimal size of the geographic range should increase with body size (fig. 1c). These considerations imply that the

relationship between the log of the geographical-range size ($\log A$) and $\log M$ should be roughly triangular with few or no species of large body size having small geographical-range sizes (fig. 1c).

The relationship between population size and area of geographical range is predicted to be as follows. Species of large body size are limited to a small region of low density and large geographical-range size. Species of small body size vary much more in both geographical-range size and density; however, many factors should limit the population growth of the species restricted to small geographical ranges, and hence they should have lower average population densities than more widely distributed species (Brown 1984). Thus, the upper density maximum should increase with geographical-range size. These factors suggest a triangular relationship between $\log A$ and $\log N$, such that few species have small geographical ranges, and these species tend not to have high average population densities (fig. 1d).

We consider the predicted distributions of trophic guilds with respect to these variables only briefly because they seem straightforward consequences of dietary and energetic constraints. Nectarivores should be limited to small body sizes and perhaps also to low population densities (e.g., Brown et al. 1978), but they might exhibit a wide range of geographical-range sizes. Body sizes of obligate insectivores should be relatively small, those of omnivore-insectivores should be of an intermediate size, and those of herbivores and carnivores should be relatively large. Insectivores, omnivore-insectivores, and herbivores should exhibit a wide range of population densities and geographical-range sizes for their body sizes, whereas carnivores should be limited to relatively low densities and large ranges (Brown 1981).

METHODS

We obtained estimates of average population density from the Breeding Bird Survey (BBS) conducted by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service since 1968 (Bystrak 1981). Each year, birds are censused using standardized procedures along approximately 2000 BBS routes distributed across the North American continent north of the Mexican border. Each route consists of 50 census locations 0.8 km apart. At each location, observers count all birds detected during a 3-min period. Routes begin at 0.5 h before sunrise and are conducted during June of each year on a day with good weather conditions. Although the BBS data set has a number of problems (Bystrak 1981), no other long-term standardized censuses cover such a large geographical area for any other group of organisms. Thus, any limitations of the BBS must be weighed against the great value of these standardized estimates of population density. Any species-specific, observer-specific, or site-specific biases should average out over time and/or space, so that major trends in the entire data set (approximately 400 species) are not greatly biased.

Our estimate of population density was obtained by averaging the number of detections per route for each species over all routes on which it was recorded between 1968 and 1982. We assumed that this average is proportional to the actual

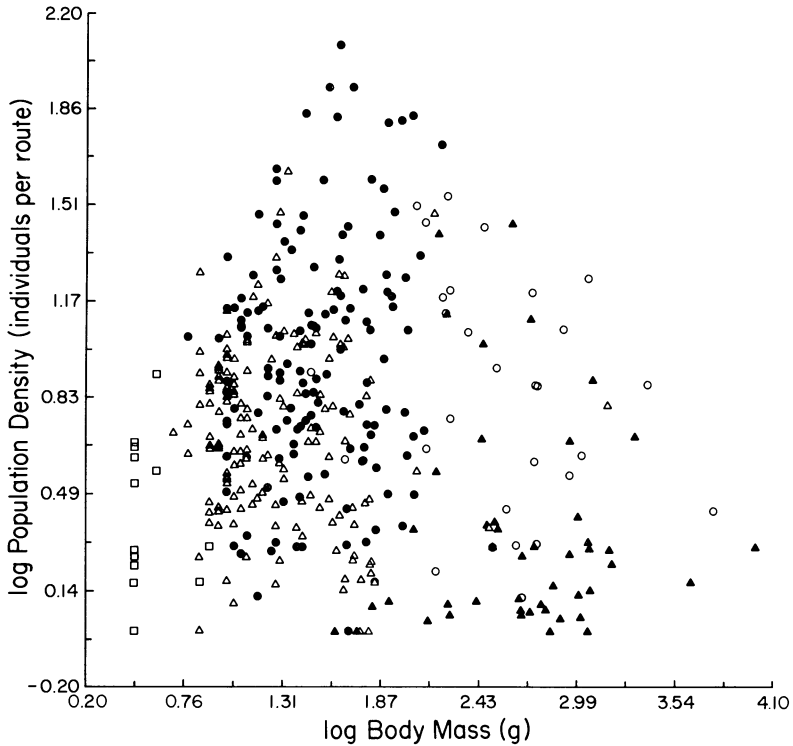


FIG. 2.—Relationship between $\log N$ (average local population density) and $\log M$ (individual body mass) for North American terrestrial bird species. Trophic guilds are depicted as follows: *open squares*, nectarivores; *open triangles*, insectivores; *open circles*, herbivores; *solid circles*, omnivore-insectivores; *solid triangles*, carnivores. Note that, contrary to our prediction, the points fall within a well-defined quadrilateral with a constant minimum density and a maximum density that is intermediate for the smallest birds, rises to a peak at an intermediate size, and then declines to the minimum with increasing body size.

average density (pairs per km^2) of each species. We obtained average adult body weights of all species from Dunning (1984), and sizes of breeding ranges by planimetry of unpublished breeding-range maps prepared by C. S. Robbins of the U.S. Fish and Wildlife Service. These range maps have since been published (Robbins et al. 1983). We measured any portion of the breeding range that extended across the Tropic of Cancer into northern Mexico, but not parts of the breeding ranges of the few species that extended farther south into the Neotropics or across the water gaps to Eurasia. We omitted from our analysis those species with breeding ranges largely in tropical America or Eurasia that occurred in only a small part of the continental United States, northern Mexico, or Canada.

We assigned each species to a trophic guild based on its most common food resources: carnivore, herbivore, omnivore-insectivore (those species that feed their young insects but consume substantial plant material outside the breeding season), insectivore, and nectarivore. These categories are broad enough that entire families could usually be assigned to a single category on the basis of

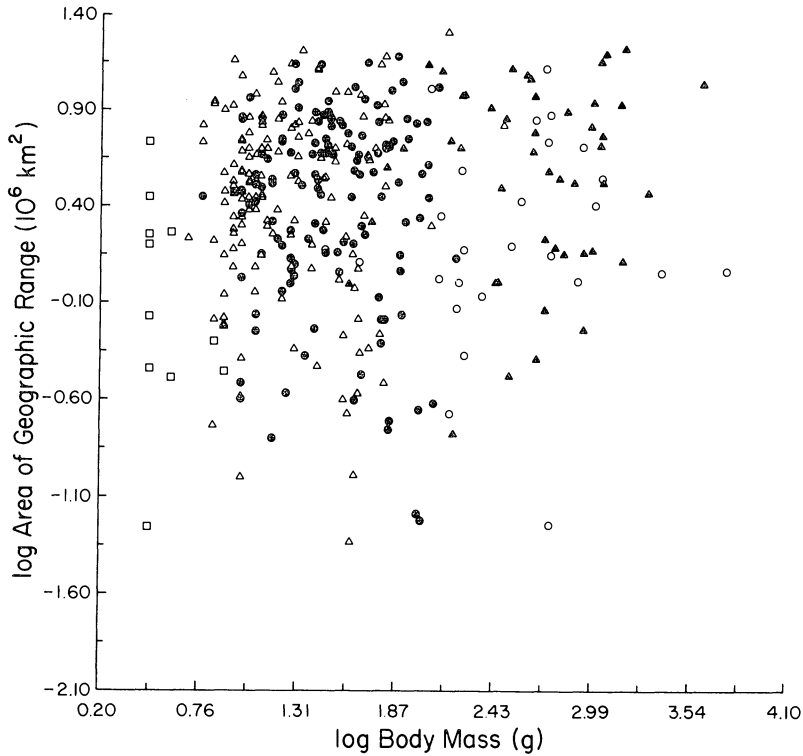


FIG. 3.—Relationship between $\log A$ (area of geographical range) and $\log M$ (individual body mass) for the land-bird species of North America. For an explanation of the symbols, see figure 2. Note that the points fall approximately within a triangle as predicted, but the lower boundary is not clearly defined.

general life history information. Bivariate plots of $\log N$, $\log M$, and $\log A$ were constructed. We were unable to obtain data for all variables for every species; we used all the values available for each pair of variables, hence the small differences in the number of points in figures 2–4. We used discriminant-function analysis to assess patterns of variation in $\log N$, $\log M$, and $\log A$ associated with differences among the trophic guilds. For the three log-transformed variables, we performed a four-group discriminant-function analysis, using all trophic guilds except nectarivores, which had many fewer species and a significantly different covariance matrix from that of the other groups.

RESULTS

Pairwise plots of log-transformed values of N , M , and A generally conformed to the hypothesized relationships among these variables (fig. 1), but with some conspicuous exceptions. $\log N$ did not attain its maximum for the smallest species as we anticipated (fig. 1*b*), but it was highest at a body weight in the range of 50–100 g, decreasing on either side (fig. 2). Moreover, minimum population

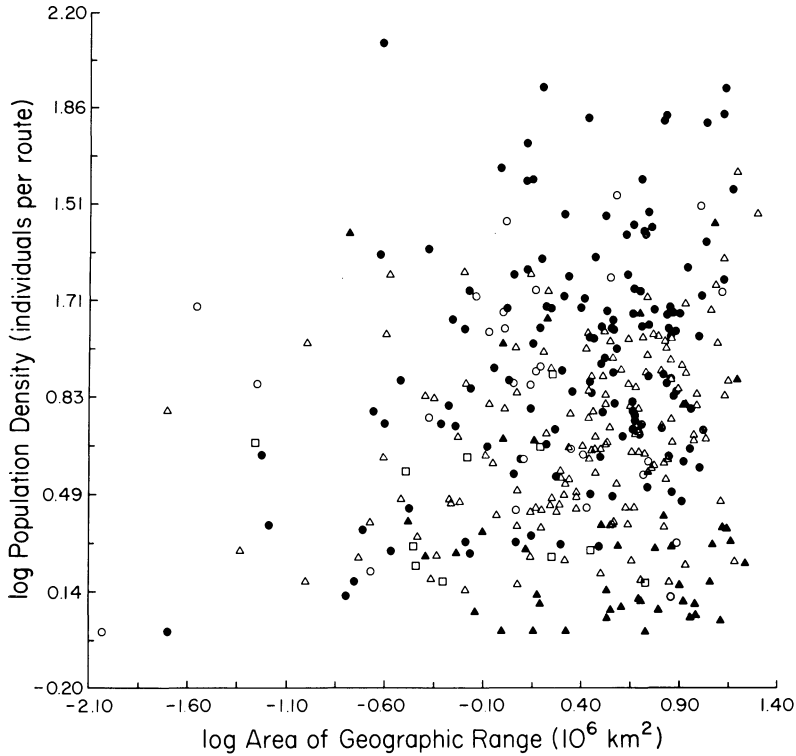


FIG. 4.—Relationship between $\log N$ (average local population density) and $\log A$ (area of geographical range) for the species of North American land birds. For an explanation of the symbols, see figure 2. Note that the points fall approximately within a triangle as predicted, but the upper boundary and the region near the origin are not clearly defined.

density did not decrease with increasing size, as we predicted, but was approximately constant, independent of size. Plots of $\log A$ against $\log M$ and of $\log N$ against $\log A$ (figs. 3 and 4, respectively) conformed quite closely to our predictions, but several of the boundaries defining the polygons enclosing the data points were not as clear-cut as those for the plot of $\log N$ against $\log M$. We also produced a three-dimensional plot of these log-transformed variables, but it is difficult to represent in a two-dimensional figure and is not presented here. It did, however, provide some additional information. The species of intermediate to large body sizes with the lowest population densities did not have small geographical ranges, whereas the species of small body size with the lowest population densities did not have large geographical ranges. The smallest geographical ranges occurred among species of small to intermediate body size and low to medium population densities, whereas the largest ranges (encompassing virtually the entire continent) were represented by species with almost all combinations of density and size except for low values of each.

The different trophic guilds tended to cluster in different parts of the two- and

three-dimensional plots, but there was extensive overlap (table 1; figs. 2–4). Herbivores generally had higher densities than carnivores of the same size, whereas omnivore-insectivores had higher densities than insectivores. The maximum span of geographical-range sizes occurred in small insectivorous species (fig. 3). All trophic groups overlapped extensively in geographical range, although for their body sizes carnivores appeared to have the largest ranges and herbivores the smallest (table 1). When $\log N$ was plotted against $\log A$, we observed only a few species that had both low densities and small geographical ranges (fig. 4). Carnivores conspicuously occupied a region of low densities coupled with large ranges, whereas the other four trophic groups were more widely dispersed. Differences in the positions of the four largest trophic groups (carnivores, herbivores, omnivore-insectivores, and insectivores) in the three-dimensional space were quantified by a discriminant analysis (table 1). The results imply that despite the substantial overlap, population density, body size, and geographical-range size form three relatively independent axes that can be used to characterize differences among the four trophic groups. Body size effectively distinguishes herbivores and carnivores from insect-eating species, and density effectively separates species that eat plant materials (herbivores and omnivore-insectivores) from species that eat exclusively animals. Geographical-range size appears to distinguish herbivores from the other three groups.

INTERPRETATION AND HYPOTHESES

Our analyses establish well-defined limits to the variation among species with respect to population density, body size, area of geographical range, and trophic status. We hypothesize that these limits reflect either absolute constraints on the attributes of species or differential extinction rates and/or differential origination rates of species possessing certain characteristics. The effects of these processes should be reflected in the distributions of points in the bivariate plots. On the one hand, absolute constraints should lead to sharp, well-defined boundaries delineating attributes possessed by species from impossible combinations of variables. On the other hand, characteristics of species that affect origination and extinction rates should result in boundaries that are neither abrupt nor absolute. These attributes interact with a spatially and temporally varying environment to cause a degree of uncertainty in the outcome of colonization, speciation, and extinction processes.

Some of the absolute constraints, such as the effect of the limited area of the North American continent on the maximum size of the geographical range (figs. 3, 4), are straightforward. Others, such as the apparent upper and lower limits on population density as a function of body size (fig. 2), which appears to be just as clearly delineated, have less obvious explanations.

A similar linear decline in the log of local population density with the log of increasing body mass in mammals has been explored by Damuth (1981). He hypothesized an exact trade-off between density and body size, such that the rate of decline in density as body size increased allowed populations of different species to use the same amount of energy. Damuth claimed that this relationship

TABLE 1
DISCRIMINANT ANALYSIS AND MEANS FOR FOUR TROPHIC GUILDS
OF NORTH AMERICAN TERRESTRIAL BIRDS

TROPIC GUILD	NO. OF SPECIES	DISCRIMINANT VARIABLE			log <i>N</i>	log <i>M</i>	log <i>A</i>
		1	2	3			
Group means							
Carnivore	53	3.00	-0.61	0.09	0.35	2.66	0.57
Herbivore	29	2.36	0.94	-0.26	0.86	2.54	0.24
Insectivore	154	-0.98	-0.44	-0.06	0.70	1.27	0.43
Omnivore- insectivore	144	-0.49	0.52	0.08	1.00	1.51	0.41
Canonical correlations							
log <i>N</i>		-0.21	0.90	0.39			
log <i>M</i>		0.98	0.20	0.03			
log <i>A</i>		0.03	-0.19	0.98			
Eigenvalues		2.16	0.30	0.01			
% variation explained		87.26	12.32	0.42			

NOTE.—Separation of the four groups on the first two discriminant variables implies that species eating at least some insects are confined to small body sizes, whereas species that eat substantial amounts of plant material attain higher population densities than carnivores or strict insectivores.

holds for all species within assemblages of mammals, but our analysis indicates that, at least in birds, this is a boundary condition, characteristic only of the highest-density species and only those above some threshold body size. We calculated the regression of log density on log body mass for those species that achieve maximum densities for a given weight and obtained the equation $N = cM^{-0.66}$. This is consistent with Damuth's hypothesis of equal energy use because the daily individual energy requirements of free-living birds and mammals scale as $M^{0.67}$ (Kendeigh et al. 1977; Walsberg 1983).

It is important to emphasize that our interpretation differs from Damuth's in one critical respect. Damuth's view implies that a constant amount of energy is available to each species and utilized by it within a taxonomically and geographically constrained assemblage, but the species allocate their energy to different numbers and sizes of individuals according to the strict trade-off. Our interpretation is that the maximum rate of energy intake that can be attained by species within a taxon is a constant, independent of body size above some threshold body mass. However, the trade-off between population density and body size that is responsible for this constant represents only an upper limit on the rate of energy use. Consequently, between the threshold and maximum body masses, a wide range of population densities can occur.

Figure 2 suggests that below the threshold body size (approximately 50–100 g in North American birds) lies another absolute constraint that results in decreasing maximum population densities of species as body size declines. The equation characterizing this boundary is approximately $N = cM^1$. Although we did not predict this boundary (fig. 1b), we suggest that it also implies some fundamental

energetic constraint. We hypothesize that below the threshold body size, the increasingly high energy requirements per unit of mass (which scale as approximately $M^{-0.33}$) as body size decreases requires that smaller species use more concentrated energy sources (see, e.g., Brown et al. 1978). The consequence of this limitation is that the density of usable resources declines with decreasing body size; thus, so does population density. Individuals of these small species probably are not dispersed uniformly over space; rather, we expect small birds to be restricted to local patches of habitat that are rich in the resources they require.

The apparent constancy of minimum population densities over the entire range of body sizes (the lower boundary in fig. 2) was not predicted a priori and calls for an explanation. It does not appear that this limit can be explained simply in terms of the effect resulting from the association of low total population size with a high probability of extinction, as we had conjectured. If this were the case, we would expect minimum population density to decrease with increasing body mass because species of large body size tend to have large geographical ranges. The trade-off between local density and geographical distribution should tend to maintain total population size and allow large birds to become locally rare without becoming extinct. But the fact that species of large birds apparently attain minimum densities that are no lower than those of some small birds suggests that an energetic constraint may again be involved. Since the minimum population density scales as M^0 and the rate of daily energy use per individual scales as $M^{0.67}$, the rate of total energy use by all individuals of these species per unit of area also scales as $M^{0.67}$. Since minimum energy use per species apparently scales with body mass with exactly the same exponent as energy use per individual, this suggests that the minimum population density is a consequence of a limit on the abilities of these species, independent of their body size, to extract usable energy from the environment.

It is important to recognize that the Breeding Bird Survey (BBS) censuses sample the environment at a standardized spatial scale, and therefore minimum population densities of different species may reflect different dispersions of individuals. We suspect that large, rare species are distributed in a relatively fine-grained manner, whereas small, rare species are clumped in patches of favorable habitat. Thus, the energy attenuation hypothesized above should have an effect on dispersion that scales with body size.

These energetic constraints, which appear to limit local population densities so rigidly, are of considerable interest in their own right. They must constitute some of the "allocation rules" that designate how the resources of a region are distributed among the resident species (Brown 1981). The implications of these energetic relationships will be addressed in a later paper.

The only diffuse, poorly defined boundaries that we observed appeared to be related to the minimum sizes of geographical ranges (figs. 3, 4). The minimum area of geographical range as a function of body size (the lower boundary in fig. 3) should reflect high extinction rates. Noting a similar diffuse boundary when the same variables were plotted for North American mammalian species, Brown (1981) attributed this effect of geographical-range size to increasing extinction rates as body size increases and total population size decreases. This interpreta-

tion is supported by the fact that many of the bird species (e.g., *Tympanuchus pallidicinctus*, *Dendroica chrysoparia*, and *Vermivora bachmanii*) along this boundary are currently considered either endangered or threatened with extinction.

At least two diffuse boundaries appear to characterize the relationship between population density and area of geographical range (fig. 4). The first of these characterizes the region of few species with low population densities and small geographical ranges. These species should be subject to high rates of extinction because they have low total populations. Many of these same species (e.g., *D. chrysoparia* and *Crotophaga ani*) appear along the lower boundary in figure 3. Colonizing species should tend to show similar combinations of these variables. In fact, the two points nearest the origin in figure 3 represent *Acridotheres cristatellus* and *Streptopelia risoria*, two introduced species that appear to be becoming established residents. The second diffuse boundary defines a region of increasing maximum density with increasing geographical range. We cannot imagine absolute constraints that would preclude species with small ranges from attaining high densities, but unusual environmental conditions would be required for species to exhibit this combination of attributes. Some species may be specialized to exploit the resources of highly productive but spatially restricted environments. These species are an exception to the generalization that high densities within a local site usually depend on the ability to exploit a wide range of resources and tolerate a wide range of conditions, so that local abundance is positively correlated with geographical distribution (Brown 1984). Perhaps the best example of such an exceptional species is *Agelaius tricolor*, an abundant species largely restricted to the highly productive marshes of the Central Valley of California.

The distribution of trophic guilds with respect to the pairwise combinations of variables is fairly straightforward. Two points warrant brief consideration. First, within guilds, the distribution of species with respect to certain variables is strictly limited. For example, both nectarivores and insectivores exhibit only a narrow range of body sizes, whereas carnivores are restricted to relatively large geographical ranges. These patterns were predicted a priori on the basis of trophic and energetic relationships, and additional explanations seem unnecessary. Second, and more interesting, when there is sufficient variation within a guild to permit resolution, it appears that the same qualitative patterns that characterize the entire avifauna in the bivariate plots (figs. 2–4) also apply to subsets of species that are even more similar in resource use. Thus, the same absolute biological constraints and origination and extinction processes that were hypothesized to determine the limits of variation for the avifauna as a whole can also be invoked to account for the qualitatively similar, but more restricted patterns of variation among species within the individual guilds.

We propose a model, based on the empirical patterns, for adaptive evolution of the North American terrestrial avifauna. The essentials of this model are illustrated in figure 5. For the present, the limits of variation in the species attributes can be characterized by polygons. The solid lines on some sides of these polygons reflect either intrinsic properties of the species that place absolute constraints on their structure and function or extrinsic environmental factors that have general

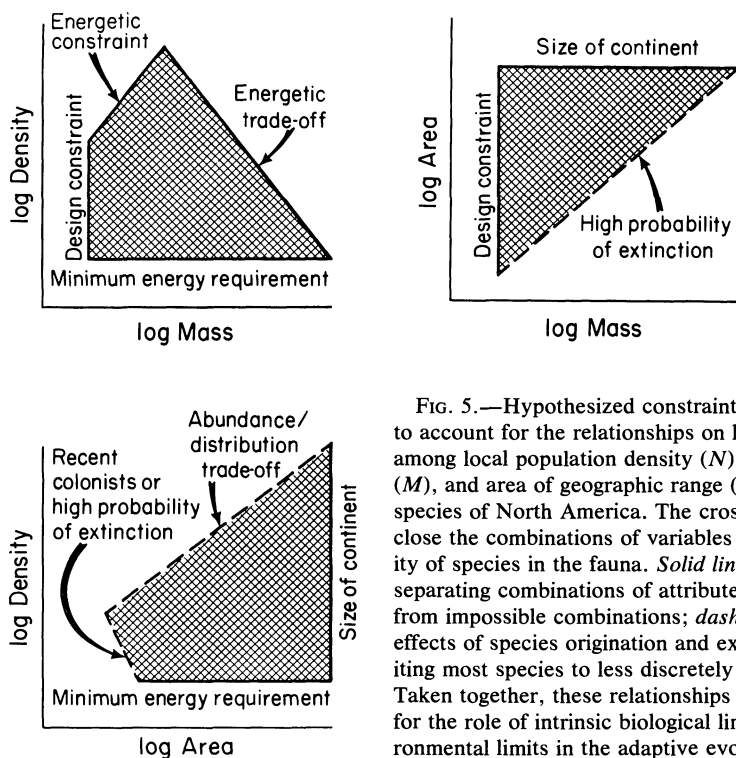


FIG. 5.—Hypothesized constraints and species dynamics to account for the relationships on log-transformed axes among local population density (N), individual body mass (M), and area of geographic range (A) for the land-bird species of North America. The cross-hatched polygons enclose the combinations of variables exhibited by the majority of species in the fauna. *Solid lines*, absolute constraints separating combinations of attributes possessed by species from impossible combinations; *dashed lines*, probabilistic effects of species origination and extinction processes limiting most species to less discretely defined boundaries. Taken together, these relationships provide an initial model for the role of intrinsic biological limits and extrinsic environmental limits in the adaptive evolution of the avifauna.

effects on all species. The dashed lines forming other sides of the polygons represent characteristics that interact with the environment in a more probabilistic way to affect the origination and extinction of species. Ultimately, it should be possible to develop a more sophisticated model that goes beyond this polygonal representation to account for the density with which the species units are distributed within the three-dimensional space defined by population density, body size, and area of geographical range.

DISCUSSION

The model presented above was developed to provide an ad hoc explanation for the static structure of the North American terrestrial avifauna. The model should be regarded as a hypothesis or, better, as a series of hypotheses about the processes that limit the adaptive differentiation of the bird species. The model can be evaluated by gathering additional and independent evidence about the energetic constraints and species dynamics that we have hypothesized. It may be possible to generalize the model from North American land birds to other biotas by making some simple quantitative and perhaps qualitative modifications. Our model can be thought of as characterizing the adaptive exploitation of resources available to a taxon within a geographical region. Since the partitioning of re-

sources among the species of any natural assemblage occurs within limits imposed largely by a combination of absolute energetic constraints and the dynamics of origination and extinction, we suggest that the patterns and processes may be general.

Our analysis supports the suggestions of recent authors (e.g., Allen and Starr 1982; Arnold and Fristrup 1982; Vrba and Eldredge 1984; Eldredge 1985; Maurer 1985; Salthe 1985) that it is productive to view the complex organization of biological systems as a nested hierarchy, with ecological communities and geographically and taxonomically limited biotas as important upper levels. Over geographical spatial scales and evolutionary temporal scales, species assemblages exhibit dynamic behavior that is not readily predictable from the properties of the individual organisms constituting the species populations. The patterns that we have documented appear to be in large part attributable to the dynamics of species origination and extinction, and these processes depend greatly on properties, such as population density and area of geographical range, that cannot even be defined at the individual-organism level of the hierarchy.

Our analysis also supports the recent claims of "macroevolutionists" (e.g., Eldredge and Gould 1972; Stanley 1975, 1979; Gould and Eldredge 1977; Eldredge and Cracraft 1980; Vrba 1980, 1983, 1984; Arnold and Fristrup 1982; Gould 1982; Vrba and Eldredge 1984) that a dynamic selective process, analogous in many ways to the natural selection of individual organisms within populations, operates at the level of species within biotas. The combinations of attributes possessed by species appear to be determined in part by how the species-level units interact with the environment to result in selective speciation, colonization, and extinction. We agree with Damuth (1985) that this concept of species selection is most useful when patterns are analyzed and hypotheses are tested within a limited geographical and environmental context so that the dynamic processes can be identified. We believe that it is also essential to evaluate the importance of taxon-specific evolutionary constraints; this will require accurate reconstruction and appropriate analyses of phylogenetic lineages, a point seemingly ignored by Damuth.

Although most of the current interest in macroevolutionary patterns and processes has been generated by paleontologists, the present study demonstrates the value of neontological data for developing and testing macroevolutionary hypotheses. Just as studies of the patterns of phenotypic variation in relation to environmental gradients continue to provide valuable insights into the adaptive evolution of individuals, so analogous studies of species characteristics in a large-scale environmental context can be expected to shed new light on the adaptive evolution of biotic diversity at the species level and above. Data from the fossil record will be required to provide essential information on kinds and rates of changes that have actually occurred in species and biotas over the long sweep of evolutionary time. However, since species dynamics are a consequence of interactions between the evolving units and their environment, it is equally important to incorporate the ecological perspective that can come only from analyses of contemporary biotas.

SUMMARY

Characteristics of the terrestrial avifauna of North America can be viewed as adaptations by a taxonomically, geographically, and ecologically defined assemblage of many species to the constraints imposed by its own biology and by the environment. We have identified distinctive patterns in the variation among species in population density, body size, area of geographical range, and trophic status.

The patterns observed in bivariate plots of log-transformed variables can be characterized provisionally in terms of polygons that enclose combinations of the variables exhibited by species. The sides of these polygons may be either abrupt or indistinct. We suggest that sharp, clear-cut boundaries separating combinations of characteristics that species possess from those combinations that are not observed in any species are the result of absolute constraints. As a trivial example, the maximum size of the geographical range is determined by the size of the continent. A more interesting example of an apparently absolute constraint is an energetic trade-off between maximum population density and body size. Boundaries separating combinations of characteristics that species possess from those not possessed can also be diffuse and relatively poorly defined. We suggest that such boundaries result from the probabilistic processes of origination and extinction, such that the number of species declines gradually across the boundary. An example is the increase in minimum area of geographical range with increasing body size, which is hypothesized to reflect the probability of extinction. We summarize our hypotheses to account for the observed patterns in a model for the adaptive evolution of the North American terrestrial avifauna. With appropriate modifications, a similar model could be developed for any biota.

Our analyses provide neontological evidence for the kinds of patterns observed in the fossil record and used by paleontologists to argue that a process analogous to natural selection at the level of individuals within populations operates at the level of species within biotas. It is useful to view certain attributes of contemporary species as the result of some combination of absolute constraints and the dynamics of speciation, colonization, and extinction processes.

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