Studies in Avian Biology No. 6:513–521, 1981.

SCALE PROBLEMS IN AVIAN CENSUSING

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ABSTRACT.—Bird populations and their habitats are not static, but vary in space and time on several scales of resolution. This variation is not smooth and continuous, but changes as a function of scale. The operation of biological processes is thus scale-dependent, and investigations conducted at one scale cannot evaluate the effects of processes that are most important at other scales; they may in fact produce misleading results. The patterns of habitat occupancy of breeding birds that are discerned by analyses spanning different spatial scales are different, for example, as are the factors that account for variations in bird community diversity. Temporal variations in population densities at local scales may also complicate the interpretation of bird-habitat associations, especially if populations do not completely pack the available habitat. Further, such temporal variations increase the likelihood that single samplings of densities will be incorrect and that patterns revealed by collections of such single censuses may be false. These problems are most severe in "quick and easy" studies that are conducted on ill-defined spatial scales and utilize single samplings of populations in time, but they beset carefully designed investigations as well. Only by recognizing that ecological processes operate with different intensities at different scales of space and time, and then attempting to match the scale of censusing or habitat evaluation with the scale(s) of operation of these processes, can we hope to derive a correct understanding of the patterns of nature.

Censuses of avian populations or evaluations of their habitat affinities can be conducted and analyzed on a variety of scales in space and time. Variations in population densities, for example, have been considered on spatial scales ranging from entire continents (e.g., Bock et al. 1977, 1978) to differences between areas within the same square kilometer (e.g., Wiens 1973, Wiens and Dyer 1975), and patterns of change in avian community diversity have been examined at local (Wiens and Rotenberry, In press a), regional (Rotenberry 1978), or continental scales (Schall and Pianka 1978, Short 1979). Similarly, patterns of avian habitat associations have been investigated at within-territory scales (Wiens 1969), over regions within the same general habitat type (Smith 1977), on continental, between-biome scales (e.g., Pitelka 1941), or by comparisons of the same habitat type on different continents (Cody 1975). In the temporal dimension, studies of habitat change may concentrate on seasonal patterns, successional transformations over decades or centuries, or large-scale changes in geological time. Populations may fluctuate in size over short time scales as consequences of reproduction, overwinter mortality, and emigration, follow multiyear cycles of abundance, or, over centuries, exhibit explosive expansions or decline to extinction.

It is thus possible to examine populations or habitat associations at several spatial or temporal scales of resolution. There is no "best" scale at which to operate; questions asked at one scale are inherently no better or worse than questions focused on some other scale (although some scales of resolution may yield answers more readily than others). It is just as legitimate, for example, to ask what factors contribute to yearly variations in the number of territories contained in a small plot in uniform habitat as it is to inquire what determines why the abundance of a species varies throughout its range, or how species are assembled into communities of different sizes in different biogeographic regions. The scale at which one asks questions, of course, dictates the scale at which one gathers information to answer the questions: broad surveys of continental abundance patterns, for example, are unlikely to provide information that will illuminate the dynamics of local populations.

Unfortunately, the spatial or temporal scale at which studies are conducted seems most often to be determined as a matter of convenience—whatever seems sufficient within the logistical constraints. A few local plots in various habitat types may be surveyed, for example, and the results then unhesitatingly generalized beyond the scale of space and time that has actually been sampled. The revealed patterns of population densities, habitat associations, and other local population phenomena are expected to hold over a much larger universe, so long as the basic conditions are relatively similar. We assume a scale-independent uniformitarianism in evolutionary and ecological processes. This approach, of drawing samples (censuses, vegetation surveys, etc.) in some unbiased fashion from a larger universe to determine what patterns exist, and then inferring that these patterns characterize the universe as a whole, is of course central to modern scientific methodology. So long as the samples are truly representative of the larger universe, this procedure is justified. However, if different processes operate to influence populations or communities at different scales, then the type of explanation

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that is appropriate at one scale may be quite inappropriate at another (Schopf 1979).

Consider, for example, patterns of variation in species diversity over a spectrum of spatial scales. Diversity generally increases as the geographic scale considered becomes larger, but the factors contributing to this increase are not the same at all scales (Cody 1975). At a local level, a certain *point diversity* level results from degree of overlap among the territories of different species occupying points within a plot. At a somewhat larger spatial scale, *α-diversity* measures the variety of species present in a given habitat. Variations in α-diversity thus are more a consequence of the suitability of conditions in different habitat types to different numbers of species than of the degree of territorial overlap among individuals of those species. As the geographic scale is expanded still further, however, habitats of different types will be included in the larger area. This habitat interspersion prompts a further increase in diversity (*β-diversity*) due to the addition of species restricted to only some of the habitat types. Finally, because similar habitats in different biogeographic regions may support different species for historical reasons, expansion of the geographic scale to include such regions results in a further change in diversity, this due to geographic species replacements (*γ-diversity*).

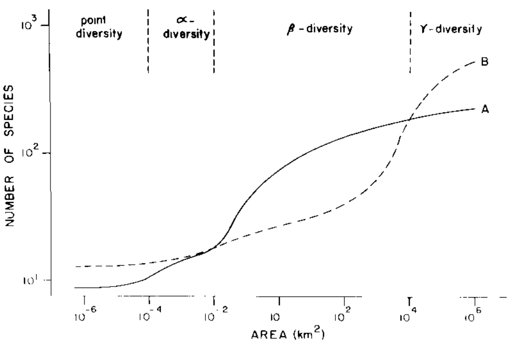

FIGURE 1. Changes in diversity as a function of increasing scale of geographical area surveyed. The two lines depict two different scenarios of diversity change, and demonstrate how different factors may affect diversity at different spatial scales. See text for explanation.

To see how the operation of different forces affecting diversity varies at different spatial scales, consider the two hypothetical patterns shown in Figure 1. In A, small-scale point diversity is relatively low, perhaps because some of the species are interspecifically territorial or because population densities are so low that individual territories of the different species are widely scattered. When one considers a somewhat larger area containing a single habitat type, however, diversity increases somewhat, as collectively several species are capable of occupying the habitat type (α-diversity). With further increases in scale, diversity rises dramatically, a consequence of the varied mosaic of habitat types in this landscape (as in a rural New England countryside) and the addition of new species characteristic of each of the habitat types (β-diversity). Finally, this region may be one that has undergone little biogeographic fragmentation, and thus as one encounters similar habitat types anywhere in the region, the species present are about the same—γ-diversity adds rather little to the overall diversity. In B, on the other hand, point diversity is initially relatively high, as nearly all of the species present in a local plot cover the entire plot and overlap completely with one another. Within-habitat (α) diversity is not much greater, because nearly all of the species that can occupy the habitat type occur at any point within that habitat. The α-diversity of B, however, is greater than that of A, perhaps reflecting a greater development of vertical vegetation profile. This habitat type may be rather widespread and unbroken over a fairly large geographic area; if that is the case, the accumulation of additional species with increasing area as a consequence of habitat interspersion (β-diversity) will be slow. At some larger geographic scale, however, areas of similar habitat that have a different biogeographic history (as a result, for example, of repeated fragmentation during glacial periods) differ in constituent species, and γ-diversity adds significantly to the overall species diversity.

The point of this exercise is to show that, because there are discontinuities in the operation or effectiveness of different processes affecting species diversity at different scales, extending interpretations of patterns revealed at any one scale uniformly to other scales is likely to produce incorrect conclusions and erroneous predictions. In the remainder of this paper, I wish to illustrate some additional problems associated with considering bird populations and communities at different scales in space and time, drawing from our studies in grassland and shrubsteppe systems. I can offer no definitive solutions to these problems, but by pointing them out I hope to foster greater care in the design and interpretation of avian surveys.

SCALE PROBLEMS IN SPACE

An example of the sort of contradictory results that can emerge from consideration of a question at different spatial scales comes from our attempts to define the patterns of habitat associations of grassland and shrubsteppe birds. In a "continental" scale analysis, we examined the patterns of correlation between the distribution and abundances of breeding bird species and a variety of habitat features over a series of sites ranging from tallgrass prairies in the eastern Great Plains to arid *Artemisia*-dominated shrubsteppes in the northwestern Great Basin (Rotenberry and Wiens, In press). At this scale of analysis, several bird species characteristic of tallgrass prairies (Dickcissels, *Spiza americana*; Grasshopper Sparrows, *Ammodramus savannarum*; Upland Sandpipers, *Bartramia longicauda*; Eastern Meadowlarks, *Sturnella magna*) exhibited strong correlations with single or multivariate measures of habitat structures. Another set of species (Sage Sparrows, *Amphispiza belli*; Sage Thrashers, *Oreoscoptes montanus*; Brewer's Sparrows, *Spizella breweri*), whose distributions are more or less restricted to the western shrubsteppe, was strongly associated with other features of habitat physiognomy. Several species that are widespread through the area we considered (most notably Western Meadowlarks, *Sturnella neglecta*), however, displayed *no* patterns of correlation with any of the habitat features that we measured. When we considered the habitat relationships of many of these same species at a more regional scale, restricting our study to shrubsteppe sites in the northwestern Great Basin (Wiens and Rotenberry 1981b), different patterns emerged. Here the species that are generally widespread through the shrubsteppe (Sage Sparrow, Sage Thrasher, Brewer's Sparrow) showed few significant correlations with variations in the structural configuration of the habitat, even though they had exhibited many clear correlations in the continental-scale analysis. On the other hand, species whose centers of abundance and distribution lie more in the steppe regions to the east, such as Western Meadowlarks, were strongly correlated with variations in several features of habitat physiognomy at this regional scale.

The patterns of habitat associations that emerged at these different scales of resolution were thus inconsistent and to some degree contradictory. Why? We have suggested (Wiens and Rotenberry 1981b) that these species are distributed among habitats over this grassland-shrubsteppe gradient more or less independently of one another, each following the dictates of its own habitat preferences and adaptations. The result is that species differ in the extent of their distribution over the habitat gradient: some species, such as Dickcissels or Sage Sparrows, occur over only a restricted portion of the gradient, while others, such as Western Meadowlarks, may encompass much of the spectrum of habitat conditions within their distribution (Fig. 2). When one surveys most of the gradient, as we did in our continental analysis, those species whose distributions cover only a restricted portion of the gradient will be likely to exhibit significant correlations, while the broadly distributed species will be more likely to vary in abundance independently of position on the gradient and thus produce few if any significant correlations. In a more restricted survey, such as our regional analysis in the shrubsteppe, only a portion of the habitat gradient is included. Here species distributed over most of the spectrum of conditions sampled (e.g., Sage Sparrows) reveal few clear associations with habitat features, while those occupying only a portion of the sampled gradient (e.g., Western Meadowlarks) do produce significant correlations and apparent patterns of habitat relationships. Obviously, neither of these scales of geographic resolution is "best" for studying the habitat relationships of these species, and in fact it is rather uncertain what the most appropriate scale of study might be for assessing the habitat affinities of the entire assemblage of bird species. It is clear, however, that our interpretation of habitat patterns among these birds is rather sensitive to the scale at which sampling and analysis are conducted.

Similar inconsistencies emerge if we consider an avian community attribute such as species diversity on several spatial scales. The diversity of an avifauna is a function of both the number of species present (its *richness*) and the equitability of the relative abundances of those species (*evenness*) (MacArthur 1965). When diversity is considered at a geographic scale including a wide range of habitat types in the northwestern U.S.A. (Washington, Oregon, and Idaho), the variations in diversity seem to be primarily a consequence of variations in evenness rather than richness (Rotenberry 1978). Within the shrubsteppe habitat type of this region, however, diversity variations may be associated with changes in either evenness or richness (Rotenberry and Wiens 1978). If the geographic scale is reduced still further, to include just a collection of locations in a restricted portion of this shrubsteppe habitat type, the variations in species diversity emerge as being a consequence primarily of differences in species richness (Wiens and Robenberry 1981b). Finally, at a local scale of resolution the variations in diversity of breeding birds among different study plots at a single shrubsteppe location in southeastern Washington are almost entirely related to differences in evenness, as nearly all of the plots contain the same three species (Wiens and Rotenberry, In press a). The factors that influence species richness and evenness, and thus the sorts of interpretations that one can place upon their variations, are complex (e.g., Rotenberry and Wiens 1980a), but it is nonetheless clear that unitary interpretations of variations in diversity without consideration of the spatial scale of the analysis are likely to be inaccurate.

SCALE PROBLEMS IN TIME

Population densities of breeding birds in local plots in many habitat types vary from year to year, often substantially (e.g., Wiens and Dyer 1975, Wiens and Rotenberry, In press a, Myers and Pitelka MS). Such variations complicate attempts to test ecological theories that assume equilibrium (Wiens 1977), although this complication is often circumvented by suggesting that the density variations represent close tracking of environmental conditions so as to maintain a shifting equilibrium between populations and their resources (e.g., Cody, In press). Whether population variations in local plots are largely independent of proximate local conditions or represent fine-tuned responses to variations in local conditions, the fact remains that such populations are not static through time, and this poses problems to analyses of avian distribution and abundance or habitat associations (see O'Connor 1981).

As an example of such temporal complications, we may again consider the patterns of habitat associations of breeding shrubsteppe birds (Wiens and Rotenberry 1981b). Bird populations and habitat features were measured at 14 locations during each of three years, so temporal as well as spatial patterns in bird-habitat associations could be analyzed. During the duration of this study, precipitation regimes varied from extremely dry to unusually wet. These variations were reflected in yearly changes in vegetational physiognomy, especially the coverage and stature of grasses and forbs, at the study locations. Despite these obvious habitat changes, the abundances of bird species over the region as a whole did not vary significantly between years, and variations in abundances were generally uncorrelated with annual variations in vegetation structure. The study sites were consistent from year to year in their relationships to one another as defined by overall habitat physiognomy, but varied independently of one another with respect to their bird populations. The strong patterns of yearly variation in habitat structure were thus not linked to variations in bird abundances and species occurrences and were independent as well of yearly dynamics of bird communities in nearby locations.

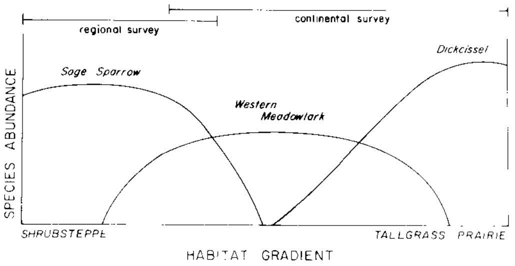

FIGURE 2. A schematic diagram of the distribution of three species along a habitat gradient from shrubsteppe through shortgrass and mixed-grass prairie to tallgrass prairie. The horizontal lines at the top indicate the span of the habitat gradient included in the regional and continental surveys described in the text.

These results argue in support of the view that populations may often vary independently of local conditions rather than tracking them closely, but how and why might this occur? We have sought a partial explanation of these variations by drawing an analogy with a checkerboard (Wiens and Dyer 1975, Rotenberry and Wiens 1980b). In this "checkerboard model" an area within a local habitat is represented by a checkerboard with walled edges. Checkers on this board represent the territories of individuals of a species. An area of, say, nine squares may represent a 10-ha study plot, within which populations are censused by counting the number of territories (checkers) or portions of territories included within the plot boundaries. The redistribution of individuals in the population resulting from migration and reestablishment of territories the following spring is simulated by shaking the checkerboard; this annual redistribution of territories is thus considered as a random process, subject to the constraint that territories may not overlap. We thus assume no site tenacity to previous breeding territories, and as well assume that territory size is fixed among all individuals within a population. Finally, we assume for simplicity that the number of checkers (individual territories) on the board as a whole remains unchanged from year to year. Altering these assumptions would in most cases only accentuate the conclusions we draw from the model. These conclusions may also apply in a general way to less mobile organisms, although the time scale of spatial rearrangement in the population will be much longer and the patterns will be more strongly influenced by reproduction and mortality than by individual movement.

If the available habitat in the region represented by the board is densely packed with individual territories (Fig. 3A), the process of yearly redistribution of individuals causes rela-

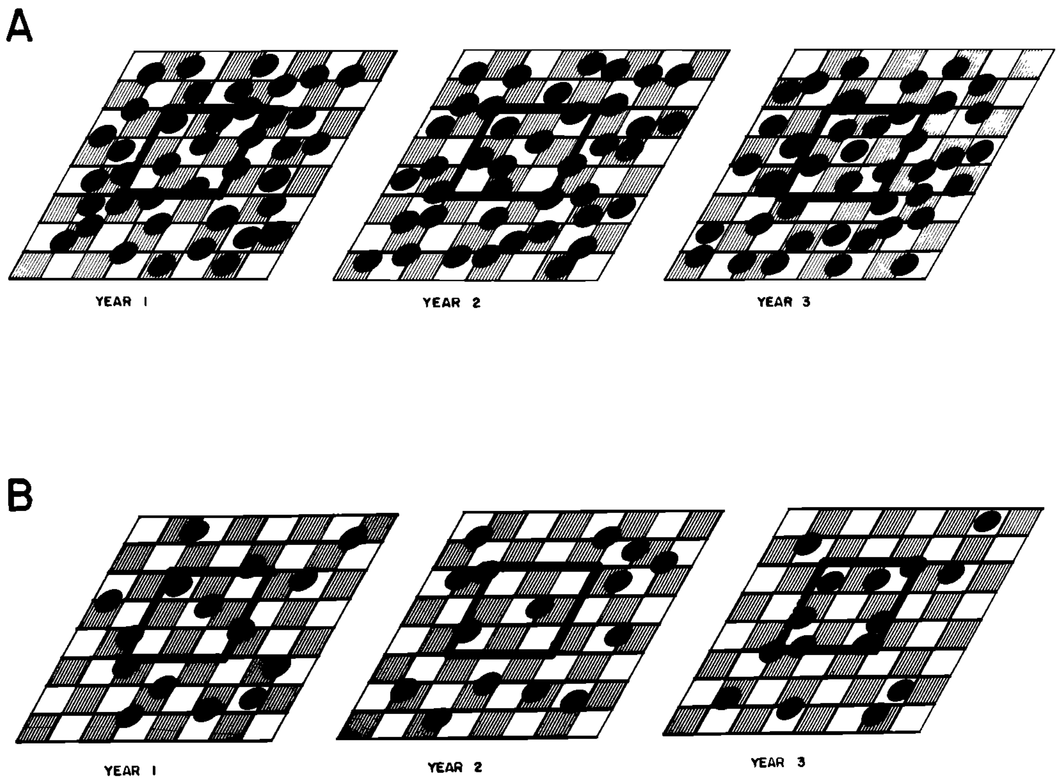

FIGURE 3. The "checkerboard model." Part A represents the distribution of territories of a species (= checkers) in a nearly saturated habitat (densely-packed board), while Part B depicts the dispersion of territories in a sparsely packed habitat. The habitat is assumed to be uniform, and thus the squares on the board do *not* represent habitat patches of different types. The solid line encompasses a sample plot established in the area depicted by the board as a whole and censused over three successive years. In A the number of territories included within the census plot (and thus our estimate of density) varies little between years, but in B there is substantial yearly variation in the census estimates, despite the fact that the total number of checkers on the board remains constant.

tively little change in the values recorded in the census of the smaller nine-square plot. If the board (habitat) is sparsely packed, on the other hand, the annual redistribution of individuals may produce substantial variations in the number of individuals occurring within the nine-square plot, and thus censused (Fig. 3B). In the latter situation, we will record substantial year-to-year variations in local density which, because the redistribution process is random, will be independent of any annual changes in the habitat, and which also will be likely to vary independently of yearly density changes in nearby plots in the same habitat. This, of course, is what we find in our shrubsteppe locations. It is also likely to be characteristic of endangered species, thus complicating efforts to define their true dynamics or habitat associations.

In a sense, this model demonstrates the close interplay between temporal and spatial scales in population censusing, for the considerable yearly variation recorded in plot censuses on the sparsely packed board, despite the actual constancy of the population occupying the board as a whole, indicates that the sample plot is too small. Had we used a plot the size of the entire board, our portrayal of population sizes would have been accurate. (This would be appropriate, of course, only if our initial questions were asked at a scale commensurate with that of the entire board.) On the densely packed board, on the other hand, a plot the size of nine squares is much more likely to provide a reasonably accurate estimate of population size and dynamics. Thus, the spatial scale at which such populations should be censused is at least partially a function of the degree to which individuals pack or saturate the available habitat. This observation may account for the general neglect of censusing methodology or census area size in much of the bird census work that has been aimed at testing ecological theory. Because this approach often presumes that populations are at equilibrium levels, saturating the available habitats, there seems little need for large survey plots, or indeed for much concern about sampling design at all. That habitats are in fact saturated (i.e., that populations are at "carrying capacity") is more often an unfounded assertion than a demonstrated fact, and indeed one might expect populations in many habitats to be below saturation levels frequently, especially in variable environments (Wiens 1977). If this is so, the spatial scale at which such populations should be censused is uncertain, and temporal changes in abundance recorded in censuses may be more apparent than real.

Real populations do change through time, however. Despite this, a good deal of the recent work in avian community ecology and population or habitat management follows the approach of conducting short surveys of a number of locations and then examining the collection of surveys for patterns, from which predictions or management policies are derived. Usually each location is surveyed only once (e.g., Cody 1968, 1974, 1978; Diamond 1972, 1975a; Terborgh and Faaborg 1980). It is thus implicitly assumed that a single census of a location provides an accurate statement of what is "normal" there, and that additional censuses would yield much the same results. The patterns that emerge from analyses of collections of such single surveys are, of course, considered to be accurate and real as well. Temporal variations in populations or habitats at any scale are thus ignored, perhaps because the underlying assumption that habitats are saturated and the ecological systems are in equilibrium generates confidence that the approach is robust.

Perhaps it is. Perhaps the patterns that emerge from analyses of such single-sample surveys are so reliable that the small amount of "noise" generated by temporal variation does not matter. To explore this possibility, I have conducted a rather simple exercise using censuses of breeding bird populations obtained in our work in North American grasslands; here I present just one example from the larger series of analyses that I conducted (Wiens 1981b). I had available 40 censuses taken at eight study locations; each location was censused for at least 2 years (usually 3 or 4), and in some cases two or three census plots were established in close proximity at a location. I used these values to test the hypothesis that the gradient of increasing annual precipitation among the eight locations should be accompanied by an increase in the total biomass of breeding birds of all species combined: more resources should support more avian biomass (Wiens 1974). This suggestion was tested in two different ways. In one, values for (a) the entire set of 40 censuses and (b) means for each location, averaged from all censuses taken there, were used to determine the "true" relation between total biomass and annual precipitation, using simple correlation procedures. The second test asked what sort of relationships might have been obtained had only a single census been taken in each location. To determine this, a single total biomass value was randomly selected for each location from the set of censuses actually taken there, and the correlation coefficient (r) between total biomass at the eight sites and annual precipitation calculated. A series of 200 iterations of this random census selection procedure yielded a frequency distribution of values of r. These portray the probability that a given value of r would be obtained by randomly drawing single censuses from the array actually available for each location.

The values for all 40 censuses considered together indicate that total biomass does indeed increase significantly with increasing annual precipitation ($r = 0.40$, $P = 0.01$), and a similar relationship is obtained when values for each site are averaged and then compared ($r = 0.75$, $P = 0.03$). The correlation coefficients for the randomly generated single-sample surveys cover a wide range of values (Fig. 4). Given the variation in total biomass at each of the locations, the probability that a set of single censuses would have detected a statistically significant positive relationship with annual precipitation is 0.185. Most sets of single-sample surveys would thus fail to demonstrate the "true" relationship, leading one to conclude (perhaps erroneously) that no such pattern exists in this system. Of course with single values for each location rather than an array of censuses, sample size is reduced from 40 to 8, and substantially larger values of r are required to demonstrate statistically significant relationships. Given a set of single samples from a relatively small number of locations, one might well be tempted to ignore statistical significance levels altogether and instead seek "biologically meaningful" trends. It is apparent from Figure 4 that single-sample surveys could easily provide a rather broad range of positive or negative trends, about which apparently logical biological explanations could then be developed. This suggests that the danger of drawing false conclusions from data obtained from a series of locations that are sampled only once is

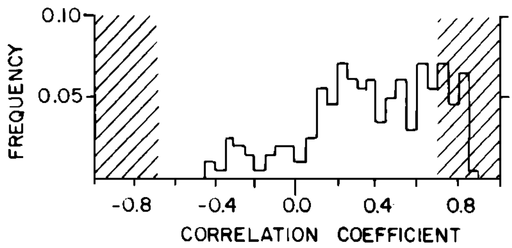

FIGURE 4. The frequency distribution of correlation coefficient values for 200 iterations of a procedure that randomly selects census values for each of eight locations from a larger series of censuses actually conducted at these sites. In this test, the correlations are between total avian biomass censused on the sites and the mean annual precipitation of the sites. The shaded area indicates correlation coefficients for which $P < 0.05$. The exercise simulates the effects of combining single surveys of a series of locations in an attempt to define broad patterns (see text).

very real, no matter how accurate the single censuses are.

CONCLUSIONS

To some extent these scale problems are simply consequences of inadequacies in sampling. The shifting patterns of habitat association as different portions of the grassland-shrubsteppe habitat spectrum are sampled (Fig. 2) may be a result of inappropriate sampling of the actual habitat ranges of the various species, and the density variations recorded on small plots in an unsaturated habitat (e.g., Fig. 3B) may represent sampling error rather than actual biological patterns. It is also possible that the patterns or dynamics seen in a "population" over a large area may simply be statistical artifacts resulting from the summation of a series of local populations whose dynamics vary independently of one another (Poole 1978). *If* processes were uniform in their actions and importance in time and space, such statistical problems could be resolved by adjusting the sampling intensity of scale until it became adequate. But it seems unlikely that such conditions of scale-independent uniformity often exist in nature. Rather, the processes that affect individuals, populations, and communities probably differ qualitatively as well as quantitatively at different scales in space or time. For some species, for example, the limits of geographic range at high latitudes may be set by physiological restrictions, while the low-latitude range boundaries may be determined by biotic interactions such as competition or predation (MacArthur 1972). Attempting to explain variations in local population densities or individual habitat selection by these factors, however, would be simplistic and probably incorrect. Local populations, in turn, may differ in their recruitment rates such that some produce a net excess of individuals while others are incapable of persisting without immigration (Wiens and Rotenberry 1981a). Combining these populations indiscriminately in analyses of patterns at larger geographic scales would obscure the real processes driving their dynamics. This concern with the scale-dependence of processes is by no means confined to censusing or ecological problems; one of the current controversies in evolutionary biology, for example, is over whether large-scale macroevolutionary patterns can be explained by simple extrapolation of small-scale microevolutionary (population) processes, or whether qualitatively different processes are at work (e.g., Bock 1979, Gould 1980, Eldredge and Cracraft 1980).

The problem that confronts us is really *not* that studies are conducted at a variety of different scales in space and time, but that such studies seem generally unaware of the ways in which the processes producing the patterns they seek to define may vary as a function of scale. The problems are most severe and readily observed in "quick and easy" studies, which pay little heed to the spatial scale on which sampling is conducted and usually follow the single-sample survey approach. But even in studies that are designed to produce census estimates of considerable accuracy, the problems posed by spatial and temporal scale are still pervasive. It is not simply a matter of paying attention to the statistical sufficiency of sample size in space or time. Because the processes that influence the population or community features of interest operate in different manners or with different intensities at different scales in space and time, it is quite possible that even well-designed sampling programs that appear to produce statistically sound results may nonetheless lead to erroneous conclusions about patterns and their causes if the scale of sampling does not coincide with the scale of the processes actually influencing the population.

The effects of scale differences in space are not independent of time-scale influences. As Elton and Miller (1954:478) observed, "it is because communities are never stable in time that the determination of their composition by sampling them in space is so perplexing." Something of the nature of these perplexing space-time effects can be seen from the generalized diagrams presented in Fig. 5. First, the sorts of processes that influence population or community patterns differ in space and time (Fig. 5A). Over small areas and short times, direct behavioral adjustments such as shifts in territory po-

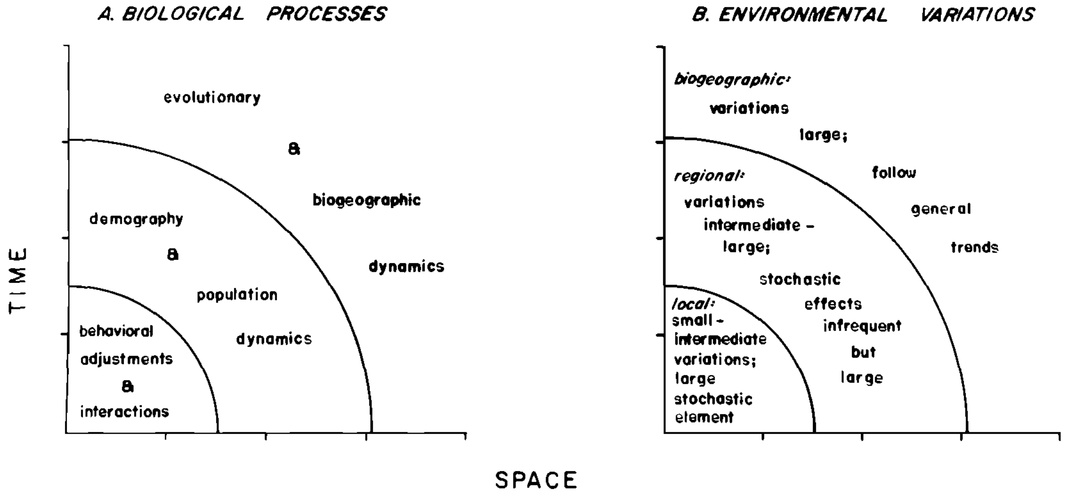

FIGURE 5. Space-time domains of features influencing populations and communities that change with changes in scale. Part A illustrates changes in the dominant biological processes that are operative in populations and communities at different scales in space and time, while Part B depicts the general features of environmental variability that may influence biota at different scales. The patterns shown here are not suggested to be unique or ubiquitous—one can easily think of alternative formulations or exceptions. However, they do indicate the difficulties in uncritically extrapolating processes or patterns from one scale to another. Time and space scales are intentionally dimensionless. The formulation was inspired by a similar treatment of marine plankton systems by Steele (1978).

sitions and sizes or modifications of habitat selection may influence population densities and habitat associations, and direct interactions between individuals of different species, such as competition or predation, may affect community composition. At a somewhat larger spatial scale and over longer time periods, features of the demography of the populations (e.g., reproduction, survivorship, age structure) may become important in dictating patterns, while over even longer periods of time and larger regions, processes of evolutionary change and speciation or the biogeography of range dynamics may be the major determinants of the patterns that emerge. Superimposed on this array of space-time processes, however, are the sorts of environmental variation that characterize natural systems (Fig. 5B). At a local level, the variations in, say, population densities that occur from place to place or over time may generally be small to intermediate (depending upon the sedentariness or reproduction/mortality schedules of the population), and may be quite sensitive to stochastic effects. These are the sorts of variations that may prevent local populations from attaining total habitat saturation or equilibrium. Variation among local populations may also be more tightly linked to localized environmental variation, as through ecotypic adaptation. Regionally, the major variations that influence populations may be somewhat more predictable (e.g., drought cycles) and of larger magnitude in their effects. The effects of stochastic environmental variations may be less important, but when they do occur their influences may often be spectacular and produce long-lasting effects (e.g., 100-year flood levels, record heat waves). Over large areas and long time periods, the environmental variations that affect populations and communities, such as glacial advances and retreats, may be quite large and produce fundamental reorganizations of the biota. Such variations usually follow well-defined trends over time and space, and thus are predictable in a general fashion.

Consideration of these scale relationships is complicated, however, by differences in the space-time scale to which different sorts of species are inherently adjusted. That bacteria and elephants operate in totally different domains in space and time is evident, but within a more coherent group, such as birds, there are still significant differences in the space-time domains of different species. Thus, the dynamics of a small, resident, habitat specialist species, such as an antbird or (in some areas) kinglets, may operate on the scale of small areas over short time periods. The dynamics of a large, migrant, habitat generalist (e.g., many raptors or seabirds), on the other hand, may be attuned to conditions expressed on completely different scales in space and time. Thus, an environmental perturbation that is quite localized in space and time might have profound effects upon a population of a small, resident, specialist (perhaps even leading to local extinction), but be of only minor consequence to the population dynamics of a large and widespread habitat generalist.

Does all of this mean that the situation is hopeless, that we should throw up our hands and become monks or molecular biologists? Hopefully not. The problems posed by the nonuniformity of processes and effects in space and time are formidable, but if we admit their existence and importance, perhaps we can begin to devise procedures of censusing populations, analyzing community patterns, and evaluating habitat relationships that are not so oblivious to the importance of scale. The first step is to attempt to select the size of a study area and the spatial scope and time duration of an investigation on the basis of something other than logistical constraints, or because someone else did it that way, or because some standardized "system" recommends it. These features of a study should be designed to mesh comfortably with the space and time scales of the organisms, the patterns of environmental variations, and the space-time zones of importance of particular biological processes, in the context of the objectives of the study or the questions being asked. Recent attempts to optimize the spatial scale of analyses, given some optimization criterion, such as maximizing diversity per unit area (Phipps 1975, Phipps and Cullen 1976), represent one possible approach, and spatial auto-correlation procedures (Sokal 1979) or time-domain analyses (Mulholland and Gowdy 1978) represent others. The ongoing discussion about optimizing the size of nature reserves (e.g., Diamond 1975b, Diamond and May 1976, Simberloff and Abele 1976, Whitcomb et al. 1976, Gilpin and Diamond 1980, Higgs and Usher 1980), while perhaps too often relying excessively on an incomplete model of island population and community dynamics, nonetheless conveys an encouraging sensitivity to the influences of spatial scale. Although a definitive solution to these scale problems is not in sight, it is apparent that we can no longer continue to ignore the problems produced by the nonuniformities of nature in space and time, or to think that they do not matter. Continued disregard of scale effects can only exacerbate the tendency to discern patterns in nature that may or may not be real, and to interpret them in ways that may or may not be true. Knowledge is likely to advance rather little from such an uncertain foundation.

ACKNOWLEDGMENTS

The research that led to these views has been supported by the National Science Foundation, most recently under Grant No. DEB 78-24364. John Rotenberry shared in the joys and frustrations of this research, and he and Rex Cates, Glenn Ford, Bea Van Horne, Bob Petruszka, Luke George, Dennis Heinemann, and Rich Bradley discussed these ideas and offered comments on the manuscript. Jean Ferner successfully confronted modern technology to prepare the final manuscript draft.