Studies in Avian Biology No. 6:522–532, 1981.

CENSUSING AND THE EVALUATION OF AVIAN HABITAT OCCUPANCY

JOHN A. WIENS AND JOHN T. ROTENBERRY[1]

ABSTRACT.—Determination of the habitat occupancy of bird populations is central to considerations of community structuring and niche relationships, as well as to intelligent management of those populations or habitats. The design of any population censusing program should thus include habitat measurement or evaluation whenever possible. We consider several methods of gathering habitat information along with censuses. Habitat measures may be obtained during station counts (e.g., roadside counts) by categorizing the habitat features within a defined area about each station, for example. Methods employing strip transect or plot procedures offer the potential for more detailed sampling and measurement of habitat features, which in turn permit more comprehensive analyses of bird-habitat associations. Applications of these approaches to breeding bird communities in grassland and shrubsteppe environments indicate that variations in features of habitat structure exhibit clear correlations with the distribution and abundance of several bird species, but that variation in habitat floristics (e.g., shrub species coverages) is also strongly associated with the density patterns of some species. These findings suggest that habitat evaluation schemes based upon only a few variables, or upon definition of a generally applicable "system" of habitat categorization, are not likely to produce sufficient detail to enable us to understand why the associations are important. Instead, consideration must be given to many habitat variables. Even if this is done, however, differences in the demographic structure of populations of a species in different habitats may complicate the interpretation of any bird-habitat relationships that seem apparent.

A major emphasis in avian ecology, as in ecology as a whole, is upon determining the distribution and abundance of species (Andrewartha and Birch 1954, Krebs 1978). It is this goal that drives us to be so concerned about properly estimating numerical abundance of populations and leads us to consider censusing methodology and analysis in such detail. But knowing the number of individuals of a species present in an area, or how abundance changes in time or space, is in a sense incomplete knowledge. In order to begin to understand *why* distribution and abundance vary in the ways they do, and in order to develop any means of making accurate predictions of future changes in population features, we must know how populations relate to the underlying habitat.

Habitat is thus the templet for ecological and evolutionary processes (Southwood 1977). In a basic or theoretical context, information about habitat is essential to any full understanding of the patterns of life history, adaptation, or behavior of a species (Rotenberry, In press), features that are expressed in modern ecology under the rubric "niche relationships." Similarly, habitat information is essential to interpreting community patterns. Alternative views, for example, suggest that bird species may be distributed along habitat gradients more or less independently of one another (Rotenberry and Wiens 1980a; Wiens and Rotenberry 1981b), or that interpopulational interactions such as competition produce distinctly nonrandom distributions of species assemblages along habitat gradients (Terborgh 1971, Cody 1974). In either case, habitat variation has a profound influence on the patterns that are observed, and to begin to distinguish such alternatives requires detailed knowledge of the habitat distributions of species and species assemblages.

In a more applied context, information about habitat relationships of populations is essential to their intelligent management, as it is almost invariably habitat conditions that are most directly and drastically influenced by human activities and resource demands. Habitat evaluation is therefore increasingly emphasized as an essential initial step (and at times the only step) in wildlife or environmental management. Several agencies are currently attempting to develop a unified habitat evaluation system that will permit a rapid and accurate determination of the relative value of land as wildlife habitat prior to development decisions (Flood et al. 1977, Whelan et al. 1979, Asherin et al. 1979, Ellis et al. 1979). Unfortunately, such habitat evaluation schemes are usually founded on the assumptions that habitat quality is a direct function of habitat diversity and that faunal diversity (especially bird species diversity, BSD) is a reliable index of the quality or "health" of the biota or is a good indicator of the relationship of wildlife to habitat conditions (Asherin et al. 1979, Thomas et al. 1979). This may lead those charged with resource management responsibilities to believe that areas with limited habitat diversity and low bird species diversity may be potentially suitable for resource development. Asherin et al. (1979), for example, found that BSD was closely related to both the complexity of vertical structuring of

---

[1] Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131; present address of JTR: Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403.

vegetation and the mixture of vegetation types: from this, they suggested that "resource development within a region will impact wildlife and wildlife habitat the least when that development is confined to large homogeneous areas with little vegetative stratification and relatively low cover type diversity" (1979:413). Such conclusions—indeed any management recommendations founded upon the premise that maintaining high bird species diversity will ensure proper wildlife management—are premature and ignore the many limitations of measures such as BSD (Balda 1975a, Wiens 1975, Thomas et al. 1979). These shortcomings, however, only point to the need for more thorough and careful consideration of the relationships of single species and species assemblages to the detailed features of their habitats in resource management (Willson 1974, Murton and Westwood 1974).

Knowledge of the habitat relationships of populations is thus important to both theoretical and applied pursuits. In view of this, it seems that the benefits to be gained from gathering information on habitat features along with censuses of bird populations are so great that they more than justify the additional effort required. The design stage for a project involving censusing of birds should thus include consideration of ways of obtaining appropriate quantitative habitat information. Our objectives here are to describe several ways in which habitat information may be gathered during census surveys, and to offer some brief comments on what sorts of habitat variables may be important to measure and how the resulting data may be analyzed. Our treatment is by no means intended as a review; instead, we draw heavily upon our own work on breeding bird communities in grassland and shrubsteppe systems.

COUPLING HABITAT MEASUREMENT WITH BIRD SURVEYS

There are a great many ways in which one may determine bird populations, as the contributions to this symposium demonstrate. Here we consider how habitat measurement may be combined with three different sorts of censusing procedures. These survey methods differ in the accuracy with which they enumerate bird populations, and the degree of resolution of habitat features generally varies concordantly.

STATION COUNTS

One of the more widely employed count procedures is the station count or roadside count procedure employed in the North American Breeding Bird Survey (Robbins and Van Velzen 1967, 1974, 1979). The details of the counting method vary, but in general an observer follows a predetermined route on roads through an area, stopping at points 0.5 mi (0.8 km) apart and recording all individuals seen or heard within a 0.25-mi (0.4-km) radius circle during a 3-min observation period. The NABBS surveys have used 50 stations on each route; in our roadside surveys in relatively homogeneous grassland and shrubsteppe habitats (Wiens et al. 1972, Rotenberry and Wiens 1976) we used 25 stations. The roadside count method produces values that represent the frequency of occurrence of species among the stations and the overall number of individuals of each species recorded per count route; it does not permit an accurate determination of the density (individuals per unit area) of the species. Its primary value, therefore, is in charting broad continental or regional patterns of distribution or in assessing the relative change in the abundance or range of species over successive years.

Usually no information on habitat features is obtained during such breeding bird surveys. Peterson (1975) conducted a post facto analysis in which he assigned breeding bird census routes among 56 ecological regions covering North America, and then evaluated how species diversity varied among regions or with latitude. Such an analysis can reveal only the most general patterns of variation, however, and accordingly contributes rather little to our overall understanding of the habitat relationships of communities or individual bird species. There is considerable potential, however, for charting the general habitat affinities of bird species within a region and assessing temporal changes in habitat occupancy by recording even simple categorizations of habitats at the stations along a survey route. In a study in southern Wisconsin, for example, visual estimates of the relative coverage of various general habitat types were made within a 200 yd (183 m) radius of each station for 30–60 roadside surveys (Emlen and Wiens 1965, Wiens and Emlen 1966). These surveys were conducted primarily to assess the dynamics of Dickcissel (*Spiza americana*) distribution and abundance at the northern edge of the species' range during an "invasion" year (1964) and a "decline" year (1965), but the availability of even general habitat categorizations for the stations permitted a consideration of the patterns of habitat occupancy of the species and their changes as the distribution of the species in the state changed (Fig. 1).

In this study, observers simply estimated the occurrence of several major and easily categorized habitat types at each station as they conducted the bird census. More detailed habitat measurements could be obtained by sampling features at each station before or after the cen-

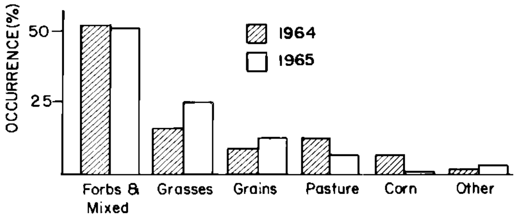

FIGURE 1. Distribution of Dickcissels in major habitat types in southern Wisconsin during 1964 and 1965, as measured by the percentage of all sightings occurring in the habitat types. "Forbs" includes alfalfa and other legumes. From Wiens and Emlen (1966).

sus is conducted, or by combining ground surveys with analyses of aerial imagery. Limitations on the quantitative accuracy of the census estimates derived using roadside survey techniques make it impractical to devote much time to obtaining very detailed and precise habitat measurements. Just as a series of roadside surveys can reveal trends in the distribution and abundance of species, however, they can also portray patterns of general habitat affinities if appropriate information on habitat features is gathered along with the census data.

STRIP TRANSECT SURVEYS

Strip transect surveys of various types provide more accurate and detailed census estimates of population densities in a more localized area than roadside counts, and therefore they can potentially provide the framework for more detailed habitat measurements and analyses. The sort of habitat sampling design that one follows will depend upon the overall goals of the investigation and the design of the strip transect survey; here we develop an example of one approach, drawn from our studies of bird assemblages in northwestern shrubsteppe habitats (Wiens and Rotenberry 1981b, Rotenberry and Wiens 1980b). We surveyed 14 plots at 9 locations, visiting each during the breeding seasons of 1977–1979. Bird densities were estimated on a linear transect placed in more or less uniform habitat at each plot, following the procedures of J. T. Emlen (1971, 1977a). Features of vegetation composition and structure were also recorded along each transect at the time the bird populations were censused. At 61-m intervals along the transect, 50-m tapes were laid out perpendicular to the transect on each side. Random numbers were then used to locate a sampling point in each 10-m interval of the tapes. Ten intervals along the transect were sampled in this manner, yielding 100 point samples of vegetation for each transect. Measures of coverage of different plant species and of physiognomic vegetation types, of several features of vertical and horizontal habitat structure, and of several indices of vertical and horizontal habitat patchiness or heterogeneity were then derived from the point samples taken at each plot. Two experienced observers could generally gather the vegetation information along a transect in 1–2 h.

The combination of bird censusing with habitat measurement permits us to evaluate not only the variations in abundances of species over the region sampled, but to begin to associate these variations with variations in habitat composition and structure, through various bivariate and multivariate correlational procedures. Table 1, for example, indicates the significant correlations between variations in the abundances of the two numerically dominant species in this system, Sage Sparrows (*Amphispiza belli*) and Brewer's Sparrows (*Spizella breweri*), and variations in single habitat features. These species exhibited relatively few significant correlations with the 20 measures of habitat structure or physiognomy, but apparently did vary in concert with variations in the coverages of several of the desert shrub species. Such observations hint at

TABLE 1

CORRELATIONS BETWEEN BIRD DENSITIES AND PHYSIOGNOMIC VARIABLES AND SHRUB SPECIES COVERAGES OVER 14 PLOTS SAMPLED FOR THREE YEARS IN THE NORTHERN GREAT BASIN[a]

Coverage	Sage sparrow	Brewer's sparrow
Rock	—	−0.47*
Shrub species diversity	−0.33*	−0.59***
Sagebrush (*Artemisia tridentata*)	0.61***	—
Hopsage (*Atriplex spinosa*)	—	−0.44**
Budsage (*Artemisia spinescens*)	—	−0.38*
Cottonthorn (*Tetradymia spinosa*)	−0.37*	—
Greasewood (*Sarcobatus vermiculatus*)	−0.53***	—

[a] Only significant correlations are shown: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. From Wiens and Rotenberry (1981b).

possible causal relationships, and provide the starting point for more thorough investigations of the linkages between these birds and habitat features (Wiens, Cates, and Rotenberry, research in progress).

PLOT CENSUSES

Some of the more reliable (and most time-consuming) avian census methods are based upon counting the number of individuals occupying a measured plot of ground by spot-mapping, mapping territorial locations, or some other procedure. Some of the most widely applied plot survey programs in North America have been the Breeding-Bird Census and the Winter Bird-Population Study, sponsored by the National Audubon Society. Each of these programs uses established plots from which estimates of species densities are obtained. In 1970, James and Shugart proposed a method of coupling quantitative habitat descriptions with these plot censuses that has been employed in a large number of subsequent censuses (James 1978). The method involves locating 5–10 0.1-acre (0.04-ha) circular plots at random within the study area. Within each sample plot, measures are then taken that enable one to calculate the density, basal area, and frequency of tree species, canopy height, shrub density, and percentage canopy cover for the study plot as a whole.

Although a fair number of breeding bird censuses have been taken incorporating James/Shugart habitat measurements, relatively few studies have attempted to analyze the accumulated data. Wamer and James (MS) conducted multivariate analyses of habitat associations using adjusted census results and habitat measures from such surveys, and Robbins (1978b) conducted both univariate and stepwise analyses of values from 80 deciduous and mixed woodland surveys to assess the habitat relations of selected bird species. Robbins added information on the latitude, precipitation, and extent of contiguous habitat for each stand to the James/Shugart measures in his analysis. He found that one of the strongest relationships that emerged was between habitat size and the overall abundance of breeding birds, leading him to recommend that the James/Shugart system be amended to include additional information on habitat size and precipitation.

The James/Shugart habitat description system works only in wooded habitats. In our work in more open grassland or steppe environments (Rotenberry and Wiens 1980a), we have followed a somewhat different approach to combining plot censuses of bird densities with habitat measurements. There we censused the populations of birds occupying 9.2–10.6-ha plots by mapping the territories of individuals using the "consecutive flush" procedure (Wiens 1969). Within these same plots, we sampled vegetation physiognomy at sample units that were located randomly within each 61 × 61-m block of the plot grid. At each sampling location, we recorded information on the coverage of various physiognomic categories of vegetation, the vertical and horizontal structuring of the habitat, and vertical and horizontal heterogeneity, using a combination of point samples and point-centered quarter samples (Cottam and Curtis 1956).

The resulting measures of habitat configuration can be analyzed at two levels of resolution. The most direct is simply to use bivariate and multivariate correlation procedures to examine the relations between variations in the densities of bird species or bird community attributes and variations in single habitat features, using both bird density values and habitat measurements for each entire plot. One of the analyses that we conducted was a Principal Components Analysis (PCA) of the habitat measures taken on the steppe plots. This analysis indicated that variation in habitat structure over the range of locations we considered (from tallgrass prairies in the eastern Great Plains to sagebrush shrubsteppe in the northern Great Basin) could be arrayed along three independent dimensions, representing variation in horizontal heterogeneity, variation in vertical heterogeneity, and variation in the abundance of forbs (chiefly wildflowers). The distributions of several bird species were significantly associated with these PCA vegetational axes, and these birds in fact were arrayed in "clusters" in the PCA-space (Fig. 2). Species that are normally considered "tallgrass prairie" birds, such as Dickcissels, Eastern Meadowlarks (*Sturnella magna*), Grasshopper Sparrows (*Ammodramus savannarum*), and Upland Sandpipers (*Bartramia longicauda*), reached their highest abundances on plots that exhibited the lowest horizontal heterogeneity and were high in vertical heterogeneity. Sage Sparrows and Sage Thrashers (*Oreoscoptes montanus*), birds more typical of arid shrubsteppe habitats, showed a similar response to increasing vertical patchiness but differed from the tallgrass species in their response to horizontal heterogeneity, joining with the remaining shrubsteppe species at the high-heterogeneity end of this gradient. "Shortgrass prairie" species such as Horned Larks (*Eremophila alpestris*), Lark Buntings (*Calamospiza melanocorys*), and McCown's Longspurs (*Calcarius mccowni*) did not differ in abundance with respect to changes in horizontal patchiness, but were negatively correlated with increasing vertical heterogeneity. The groupings of these species are not altogether unexpected,

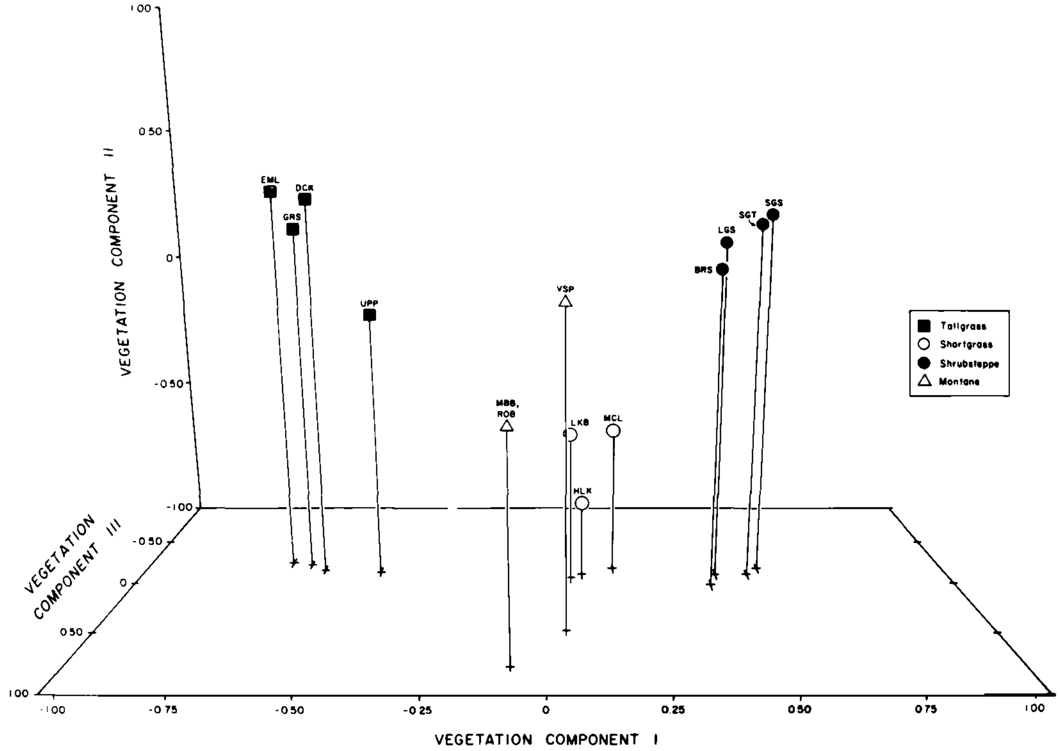

FIGURE 2. Correlations between bird species abundances and site factor scores on vegetational principal components for a series of locations in the North American Great Plains and western shrubsteppe. The axes represent the three major components derived from a Principal Components Analysis of features of habitat structure for the sites, scaled by the relative contribution of each component in accounting for variation in the total vegetation data set. Bird species codes are as follows: EML = Eastern Meadowlark, GRS = Grasshopper Sparrow, DCK = Dickcissel, UPP = Upland Sandpiper, MBB = Mountain Bluebird, ROB = American Robin, VSP = Vesper Sparrow, LKB = Lark Bunting, HLK = Horned Lark, MCL = McCown's Longspur, BRS = Brewer's Sparrow, LGS = Loggerhead Shrike, SGT = Sage Thrasher, SGS = Sage Sparrow. From Rotenberry and Wiens (1980a).

but the importance of variations in vertical and horizontal patchiness as components of habitat variation would not have been intuitively obvious without incorporation of the proper sorts of habitat measurements.

Such habitat analyses may be presented in other ways, some of which make the potential management applications (and the need for consideration of single-species responses in management) more apparent. As an example, one may use PCA to determine habitat gradients and then position the plots in the PCA-space according to their factor scores on the PCA axes. By then labelling each plot location with the density of a species, one may group together plots having similar densities to define isopleths or contours of abundance of a species in the PCA-space (Rotenberry and Wiens, In press). Because each plot is located in the PCA space according to its habitat features, it should be possible to predict how the position of a site might change were the habitat to be altered in some defined fashion. By relating this to the density contours of a species, one might then predict the patterns of response of the species to the habitat alteration. In the hypothetical case given in Figure 3, for example, an alteration that caused the plot to move in habitat space as indicated in Part A would likely result in an increase in the abundance of this species, while a different sort of change (part B) might be more likely to result in a decrease. Some other changes might foster the invasion of the species into a previously unoccupied area (part C), or lead to local extinction (part D).

Because our censusing procedure involves mapping the locations of individual territories within each plot, we can distinguish between vegetation sampling points falling within occupied portions of the plot and those occurring in

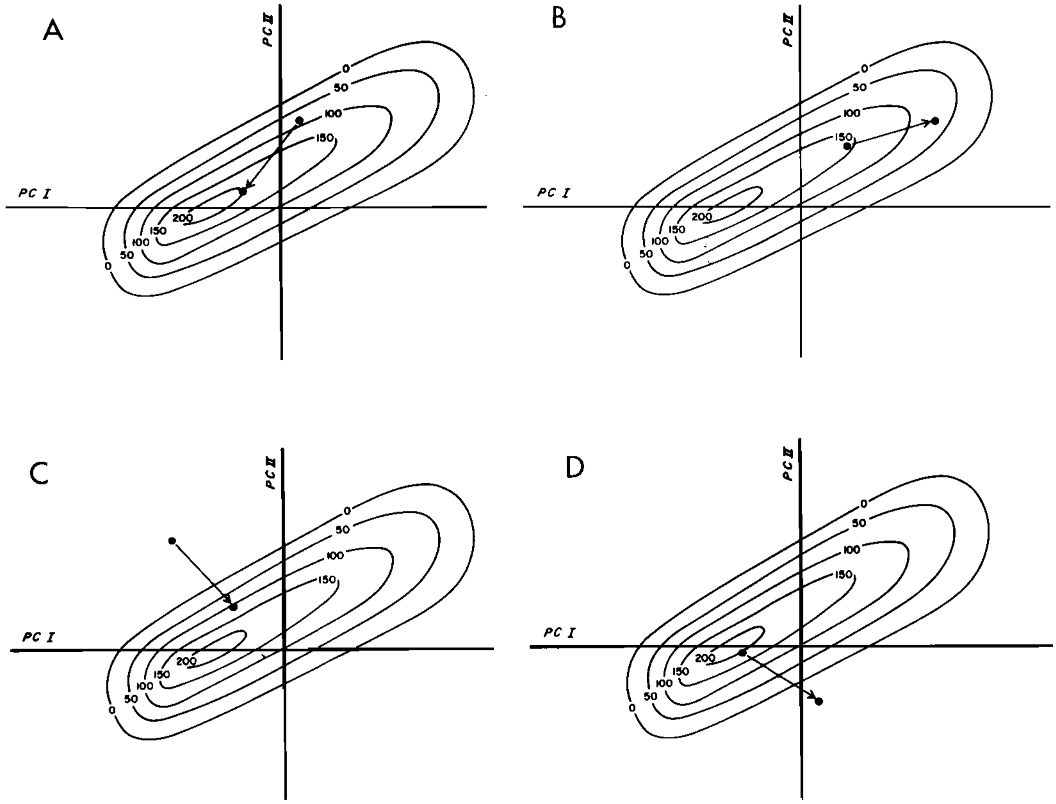

FIGURE 3. Hypothetical contours of species abundance patterns plotted in the environmental space defined by the first two principal components (PC I and PC II) of site-based environmental measures. The contours represent isopleths of density. The arrow denotes change in site characteristics as a result of habitat alterations. These changes may effect the following changes in the abundance of the species at the site: A = increase, B = decrease, C = local invasion, D = local extinction. From Rotenberry and Wiens (In press).

unoccupied portions. This permits a finer resolution of habitat associations of species, for if not all of a study plot is occupied by territories of a species, the average values for habitat features characterizing the territories of the species may deviate from those for the plot as a whole (Fig. 4). This level of resolution has been employed in analyses based upon the determination of mean habitat vectors of species in PCA (Anderson and Shugart 1974, Whitmore 1975, Rotenberry and Wiens 1980a), and Wiens (1973) used it to determine habitat differences associated with differences in the location of territories or the time of territorial establishment in two grassland bird species.

WHAT HABITAT FEATURES TO MEASURE

Given that one has decided that measuring or evaluating habitat is important and has defined a method of combining census surveys with habitat measurement, one still must determine which of the many measurable elements of the environment should be measured to characterize the habitat of a species or community. Those factors that are potentially important in influencing the distribution and abundance of species, or that might be coupled as direct or indirect selective forces to the adaptations of the species, are obvious candidates for inclusion in any measurement program, but it is far easier to speak of such general categories of habitat features than to define them precisely and determine how and at what scale they are to be measured. Since the suggestion of Lack (1933) and others nearly 50 yr ago that birds may select the habitats they occupy on the basis of the structural configuration or physiognomy of the habitat, most studies of bird-habitat relationships have emphasized such structural features (see Hildén 1965, Wiens 1969). Thus, for example, "each species requires a 'patch' of vegetation

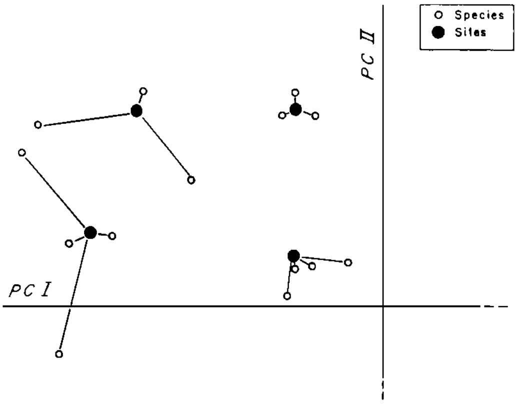

FIGURE 4. Hypothetical species and sites plotted in the environmental space defined by the first two principal components (PC I and PC II) of site-based environmental variables. The solid dot depicts a site's location, while each species is positioned in the PCA-space according to the environmental characteristics of only the areas actually occupied by the species at the site. Lines connect species to the sites on which they occur. From Rotenberry and Wiens (In press).

TABLE 2
PERCENTAGES OF TESTS CORRELATING THE DENSITIES OF BIRDS IN THREE MAJOR GROUPINGS WITH PHYSIOGNOMIC VARIABLES AND WITH SHRUB SPECIES COVERAGES THAT WERE SIGNIFICANT AT $P < 0.05$[a]

Species group	Significant correlations with: Physiognomic features	Shrub species
Widespread shrubsteppe species	10	26
"Local" shrubsteppe species	13	20
"Grassland" species	24	16

[a] From Wiens and Rotenberry (1981b).

with a particular profile for its selected habitat, and . . . the variety of 'patches' within a habitat determines the variety of bird species breeding there" (MacArthur et al. 1962:167), or "habitat structure appears to be the major factor responsible for the complexity of associated bird communities" (Anderson 1979b:432). Such an emphasis has spawned a wide variety of habitat description schemes based upon physiognomy (e.g., Emlen 1956, 1977b; Dansereau et al. 1966; Wiens 1969). In general, however, most such systems do not consider the possible importance of plant species, independent of their physiognomy. Bevanger, for example, noted that "the structural complexity of the vegetation is a factor of prime importance for a bird community. There is therefore no point in devising a classification system of the same complexity as that used by phytosociologists for their plant communities" (1977:68), and DesGranges stated that "the influence of species composition of the vegetation on avifauna within a given habitat is only indirect. The species composition affects the physiognomy of the vegetation which, in turn, influences the composition of the avian community" (1980:5). Despite such assertions, several investigations have found that consideration of habitat structure alone provides only a partial explanation of the variations in distribution and abundance of species or the structuring of communities (Tomoff 1974, Ulfstrand 1975, Balda 1975a), and some of these studies have explicitly documented significant relationships with certain plant species. In the arid northwestern shrubsteppe systems that we studied (Wiens and Rotenberry 1981b), several of the bird species that are widespread in and characteristic of the shrubsteppe exhibited more significant relationships with the coverages of shrub species than with features of habitat physiognomy (Table 2), while bird species with localized distributions in the shrubsteppe also were correlated with a higher proportion of the floristic variables than of the physiognomic features. Species whose distributional patterns and habitat affinities lie more in the grassland regions to the east of the shrubsteppe, on the other hand, seemed more strongly associated with variations in habitat physiognomy than shrub species coverages. Despite their apparent association with several shrub species within the shrubsteppe region, the characteristic shrubsteppe species evidenced strong patterns of correlation with variations in several physiognomic habitat features when we considered them on a broader, "continental" level of analysis (Fig. 2; Rotenberry and Wiens 1980a). This suggests to us that at a large-scale, between-habitat level these birds may respond to elements of general habitat configuration, but within a habitat type their responses may be more strongly associated with the details of habitat floristics. To the extent that these findings apply to species in other systems, they complicate approaches to habitat analysis, for they suggest that in order really to understand the factors determining avian habitat occupancy patterns, we must evaluate both habitat structure and vegetational floristics. This has rarely been done.

The habitat measurement scheme that one follows also depends upon the overall objectives and scope of the study. We can distinguish three major approaches that seem to have dominated recent attempts to assess avian habitat patterns. One approach, exemplified by MacArthur and his followers (MacArthur and MacArthur 1961; MacArthur et al. 1962; Cody 1968, 1974) has alleged that avian habitat relationships can be understood from consideration of only a few easily measured habitat features. Indeed, MacArthur's early attempts to predict bird species diversity from variations in only the diversity of the vertical foliage profile met with sufficient success to lead to the adoption of this relationship as a tenet of at least some management schemes (e.g., Asherin et al. 1979), and Cody (1968) suggested that he could predict the niche patternings of species in grassland bird communities by examining just four measures of grassland habitat structure. Levins (1966) and Rosenzweig (1975) have clearly stated this view that by considering only a few key or "sufficient" parameters that incorporate the effects of a variety of lower-level parameters, one may gain a clear understanding of relationships and dispense with the need to measure a large number of parameters. This "few variables" approach has been somewhat reinforced by recent multiple regression analyses that have shown that a relatively small proportion of a larger set of habitat measures can provide good inductive models of variations in breeding bird populations (e.g., Robbins 1978b, Capen, In press).

A second approach features measurement of a large number of habitat variables. The initial attempts to quantify the association of bird species with many habitat features were those of Bond (1957) and Beals (1960), which provided at least some of the impetus for the subsequent analyses of Wiens (1969) and Emlen (1977b) (this approach should thus perhaps be termed the "Wisconsin approach"). The more recent development and application of multivariate techniques has facilitated the analysis of data on many habitat variables, and such investigations have generally been successful in distinguishing habitat features or more often suites of habitat features that are correlated with variations in the abundances of bird species or avian community attributes (e.g., James 1971; Anderson and Shugart 1974; Smith 1977; Rotenberry and Wiens 1980a; Wiens and Rotenberry 1981b; papers in Capen, In press).

The third basic approach is more strongly guided by management objectives. As pressures on natural resources have increased, the need for some form of evaluation of the suitability of habitats for wildlife has become increasingly apparent and urgent. In response, several habitat evaluation plans have been suggested (e.g., Whitaker et al. 1976, Thomas et al. 1976, Boyce 1978, Flood et al. 1978, Berry 1978, Whelan et al. 1979, Ellis et al. 1979, Asherin et al. 1979). While these systems vary in their details, they are similar in that: (1) each attempts to devise a habitat evaluation plan that will be broadly applicable to a wide variety of habitats and management objectives (i.e., a "unified" scheme); (2) each considers a moderate number of habitat measures, including features other than vegetation structure alone; (3) each aims to define an index or a small number of measures that will provide a good prediction of habitat suitability to wildlife as a whole; and (4) each relies heavily (some exclusively) on measures or rankings of features that are derived from literature sources, expert opinion, or aerial imagery—none places initial emphasis on direct field measurements, although some do intend that the habitat evaluations they produce serve as guides to designing the most efficient field studies in a follow-up phase.

Each of these approaches has a different frame of applicability and different limitations. The general habitat evaluation systems tend to be very general and to rely heavily upon indirect measures. They therefore lack sensitivity to conditions in local areas, and as population censuses are generally not taken at all, they are incapable of indexing the relations between variations in the distribution and abundance of species and habitat conditions with any real accuracy. Their emphasis upon development of a unitary approach to habitat evaluation is perhaps misdirected, as any single system is unlikely to be useful if the study objectives or the underlying organization of the biotic systems vary from study to study or place to place. The "few variables" approach is simple and easy, but provides little detailed information on the habitat relationships of species or local species associations (Anderson 1979b). Generally this approach is not combined with carefully conducted population censuses, so its chief applicability would seem to be in broad intercommunity comparisons involving variations in species lists rather than population densities. Historically, this approach has been followed especially by those who believe ecological communities to be saturated and species assemblages to be in equilibrium (Cody 1966, MacArthur 1972); if this is so, one might expect a small set of habitat features to determine the community patterns. The "many variables" approach, on the other hand, developed in the context of the philosophy that communities are composed of species that respond to ecological variations largely independently of one another (Curtis 1959), and more recent multivariate analyses of data gathered in this fashion provide support for this view (Rotenberry and Wiens 1980a; Wiens and Rotenberry 1981b; see also Wiens 1977). If in fact bird species do respond to habitat variations independently of one another, there is no reason to expect a few key variables to be equally important to all of the species present in an area, and consideration of a large number of habitat features, coupled with accurate censusing of the bird populations, becomes critical. This approach, however, is considerably more complex and time-consuming than either of the others. If one ultimately wishes to assess the significance of the patterns of habitat occupancy or of the distributional correlations with habitat features of a species, however, none of these approaches is sufficient; this requires more critical studies of habitat utilization, which may begin to reveal what the various habitat features actually mean to the birds (Verner 1975, Balda 1975).

THE ANALYSIS OF BIRD-HABITAT RELATIONSHIPS

The sorts of analyses that one performs in order to discern habitat relationships to bird species abundances are to a considerable extent conditioned by the approach to habitat measurement that has been followed. Obviously, if one has followed the "few variables" approach, data often may be analyzed using relatively uncomplicated methods. If many variables have been quantified, however, multivariate analytical techniques are likely to provide greater insights than less sophisticated procedures. Indeed, multivariate analyses may be of considerable value even if only a few variables have been quantified. Many of those techniques have been treated in detail in a recent symposium (Capen, In press); here we shall offer only a few brief comments on some of the more popular multivariate procedures.

Multiple regression or correlation analysis provides a relatively straightforward technique for coupling bird species abundance estimates with any number of measured habitat variables. Multiple regression models yield precise quantitative predictions of a species' density for given values of environmental measures, and as such can be a useful tool in a species management-oriented project (e.g., Robbins 1978b). Unfortunately, such precision is invariably gained at the cost of generality, as a model constructed for one species is seldom useful for another. Even for one species a model is useful only over the numerical range of habitat variables used in constructing the model; extrapolation beyond these ranges yields estimates of dubious reliability.

Although more often employed in the analysis of habitats in which a species is merely present or absent (e.g., James 1971, Whitmore 1975), discriminant function analysis (DFA) can be associated with estimates of relative abundance (i.e., species absent, rare, or common) to evaluate habitat variables with respect to their ability to distinguish such density classes (Anderson and Shugart 1974). DFA combines all measured variables into a linear function that is best able to separate the three abundance groups, taking into account all covariance relationships among the habitat variables. However, such an approach focuses only upon differences in habitat occupancy, and as a result may often overlook any other biologically important factors that do not otherwise contribute to these differences.

A variety of ordination technqiues may be used to extract patterns of covariance in habitat variables, and the resulting patterns may be interpreted as representing multidimensional environmental gradients. Species abundances may then be plotted along the gradients and significant correlations interpreted as representing species' responses to these derived habitat clines. The most commonly employed ordination is Principal Component Analysis (PCA) (e.g., Cody 1975, Rotenberry and Wiens 1980a); although many are available (e.g., Gauch and Whittaker 1972). In addition to ordination, PCA is also useful for reducing the number of habitat variables with which one need be concerned (by extracting covariance patterns) and summarizing the important points of species similarity or correlation matrices (i.e., identifying ecological groups; Nichols 1977). Unfortunately, PCA is not without hazards quite apart from its rather rigid statistical requirements and assumptions (Johnson, In press). Because by definition components are independent of one another there is a strong tendency to attribute each component to independent phenomena ("one component-one cause"), ignoring the fact that each original variable contributes at least in part to the construction of each component. In addition, there is no a priori expectation that the linear combinations of variables that PCA extracts (the components) are precisely the same combination that the birds deem important; hence, the absence of correlation does not necessarily imply an absence of habitat response.

Canonical correlation analysis extracts not only patterns of covariation in habitat variables but also patterns of covariation in species' abundances, with the purpose of maximizing the joint correlation between the two data sets. It is analogous to multiple regression or correlation analysis, only now more than one "dependent" variables are being considered simultaneously. While the notion of emphasizing correlations between habitat "components" and species "components" is intuitively appealing, the technique is beset with analytical difficulties. This, combined with apparently very stringent requirements for linearity of input values, limits its current usefulness in species-environment investigations (Gauch and Wentworth 1976).

We must emphasize that by the very nature of the kinds of data collected (field measurements of species' abundances and habitat variables), which are both subject to statistical sampling error, we are restricted to correlational analyses of one sort or another. While this is not to say that such interrelationships cannot be investigated experimentally, we must constantly bear in mind that we are defining habitat *correlations,* not habitat *selection,* and should hedge our biological inferences accordingly.

CONCLUDING COMMENTS

We hope that it is obvious from the above discussions that proper measurement and evaluation of avian habitat occupancy patterns is a tricky business, but that, despite this, conducting avian censuses without recording information on the associated habitat features leaves one with information that is of limited value. Even if one takes care to record both bird density and habitat characteristics following careful quantitative procedures, however, problems may still remain. First, proper analysis of such data may reveal intriguing and interpretable patterns of correlations, but such correlation does not necessarily imply that the relationships are directly causal and meaningful to the birds. It is a statistical triviality to point out that correlation does not imply causation, yet the ecological literature is replete with studies that, having demonstrated correlations, proceed to develop grandiose explanations of the adaptive significance of the patterns as if they were unquestionably true. Statistical correlation only shows that a particular pattern holds in the particular data set with a given degree of probability, and while these patterns may suggest many interesting and important potential linkages between birds and their habitats, to believe them proven, and to proceed to frame management policies upon them, would be premature.

A second problem is related to this. When we record density variations between habitats or fluctuations through time, we assume that these differences are directly related to underlying environmental (habitat) factors. This is implicit in correlational analyses of bird-habitat relationships. Without some knowledge of the demography of local populations, however, this assumption is not secure. Different habitat types may differ in their suitability or degree of optimality to a species. If the distribution of individuals among habitat types is some direct function of habitat suitability, as visualized in the Ideal Free Distribution model of Fretwell and Lucas (1969), then we may conclude that density variations between habitats do indeed index habitat suitability. But there are many reasons (e.g., territorial behavior, philopatry, time lags, and perhaps most important, the inability of individuals to exercise precisely optimal habitat choice, complicated by stochastic variations in environmental factors) not to expect an Ideal Free Distribution to be realized. This clouds interpretations of the observed density variations. Further, it is a mistake to believe that the size of any local population is at an equilibrium determined by local resource conditions. Instead, species' distributions may be broken into a mosaic of "source" and "sink" populations (Fig. 5). "Source" populations occupy habitat suitable for reproduction, and their output of offspring in fact exceeds the capacity of the local habitat, promoting dispersal. Here densities may be fairly stable through time, but the true suitability or productivity of the habitat is underestimated by considering only breeding density. "Sink" populations, on the other hand, may occupy habitat types that are generally unsuitable for reproduction or in which reproductive output is inadequate to maintain local population levels. These populations may be replenished by emigrants from the source populations, and individuals in sink population habitats may rapidly move into nearby source population habitats should vacancies arise. The densities and dynamics that characterize populations in these sink habitats thus vary not in response to local habitat conditions, but as consequences of

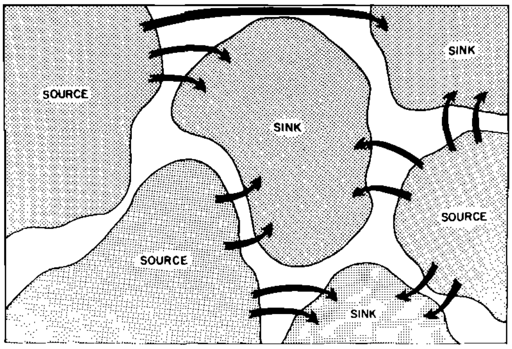

FIGURE 5. Hypothetical example of the "source-sink" structuring of populations. In "source" segments of the population, reproduction may exceed local carrying capacity, leading to net dispersal of individuals into other "sink" segments, in which reproduction alone cannot maintain population levels. The observed densities in either "source" or "sink" segments thus may not bear a close relationship to local habitat conditions.

events in the nearby source populations. Interpretation of population density-habitat correlations in populations structured in this manner would be difficult. Such a pattern seems evident in the Great Tit (*Parus major*) populations occupying woodlands and adjacent hedgerows in England (Krebs 1971; but see also Krebs and Perrins 1978, who suggest that these results may be equivocal), and may in fact be commonplace, especially where the interspersion of habitat types is close-knit. Unfortunately, detailed study of the demography of local populations is necessary to reveal the nature of such "source-sink" habitat occupancy patterns.

These problems call attention to the need for considerable care in the design and interpretation of ecological survey work. This symposium attests to the importance of developing and following rigorous methodology when censusing bird populations, and similar attention is demanded in the measurement and analysis of associated habitat features. As Elton and Miller (1954:474) observed some time ago, "because surveys must take up a great deal of time and labour and technical ingenuity, their aims should be clear, progressive and knit into ideas of dynamic ecology. They have to show a convincing reason for their existence, and not just accumulate a vague mass of field records."

ACKNOWLEDGMENTS

This synthesis and our research were supported by grants from the National Science Foundation, most recently Grant No. DEB-78-24364. Jean Ferner prepared the manuscript. John Emlen sparked the interests in avian habitat associations that have guided our research.