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The role of habitat in avian community composition: physiognomy or floristics?

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Summary. It has been proposed that within rather broad habitat types the distribution and abundance of bird species may be more closely associated with plant taxonomic composition than with the structure and configuration of the vegetation. Birds from a sample of eight representative grassland habitats in middle and western North America are consistent with this hypothesis. Over half (55%) of the variation in bird community composition was associated with floristic variation, but only a third (35%) was associated with physiognomy. Separating the interacting effects of floristics and physiognomy from each other served to accentuate the difference between them with respect to the avifauna. It is postulated that bird species/plant taxa associations, especially within similar habitat types, are mediated by the specific food resources that different plant taxa provide. Summary indices such as diversity measures obscure the taxonomic information content of plant or animal assemblages, and the use of such indices has likely impeded detection of the relationships described here.

In an assessment of the effects of habitat structure on avian communities in semi-arid steppe vegetation, which was undertaken over a broad area of the North American continent, Rotenberry and Wiens (1980a) demonstrated strong patterns of association between bird community structure (i.e., species diversity and its components) and the physical configuration of the environment. These results were consistent with the widely held view that vegetation structure and habitat configuration ("physiognomy"; Whittaker 1975) are more important to the determination of habitat occupancy patterns of birds than the particular plant taxonomic composition ("floristics") of the vegetation (e.g., Hildén 1965; Wiens 1969; James 1971; Anderson and Shugart 1974). Indeed, a variety of studies have shown strong associations between physiognomy and patterns of species distributions and community structure (e.g., MacArthur and MacArthur 1961; MacArthur et al. 1966; Willson 1974; James and Wamer 1982).

Subsequent, more intensive, investigations of a regional, physiognomically distinct subset of steppe habitat, however, revealed substantially different patterns. Instead of detecting significant relationships between bird assemblages and habitat physiognomy in northern Great Basin shrubsteppe ecosystems, Wiens and Rotenberry (1981) discovered strong correlations between avian community composition and

plant (shrub) species composition. Additional analyses revealed that these relationships were persistent through time (Rotenberry and Wiens 1980b). Floristics clearly appears more important than structure in determining habitat associations of shrubsteppe bird communities.

These differences in the apparent nature of bird/habitat associations were attributed to differences in the relative geographic scale over which they were measured; the same species that appear to respond to the physical configuration of the environment at the "continental" level show little correlation with physiognomy at the "regional" level. Such observations led us to propose that while birds may be differentiating between gross habitat types on the basis of physiognomy (i.e., occupying a general habitat type that is "proper" in its structural configuration), further refinements of their distributions within the proper habitat type may occur with reference to plant taxonomic composition. Such a proposition reconciles the observations of large scale or between-habitat type surveys that associate bird community composition and physiognomic factors (e.g., Willson 1974; Cody 1975; Rotenberry and Wiens 1980a) with those of regional or within-habitat type surveys where the composition of bird communities appears more closely associated with floristics (e.g., Tomoff 1974; Power 1975; Wiens and Rotenberry 1981).

The purpose of this paper is to evaluate the preceding proposition with respect to that portion of the steppe biome avifauna not previously considered: grassland bird assemblages. Is grassland bird community composition, which is clearly related to aspects of physiognomy if sampled over a large habitat scale (Rotenberry and Wiens 1980a), more strongly associated with floristics when examined within a more limited habitat type? If such relationships exist, what processes may be responsible for producing them? The answers to these questions may provide clues to mechanisms underlying habitat selection in birds.

Methods

All data analyzed in this paper, along with details of the sampling methodology involved in their collection, have previously been published. What follows is only a brief summary of the field techniques employed; see Wiens (1973), Sims et al. (1978), and other references for a complete description of study areas, field methods and data. Statistical methods, however, merit more thorough exposition. Their application to these data is new and they yield interpreta-

tions that differ substantially from those that emerged previously.

Study areas

During the spring and summer of 1970, data were collected on 8 plots spanning the range of normal variation in grassland habitats characteristic of middle and western United States (Table 1). These plots are a subset of a number of US International Biological Program (IBP) Grassland Biome sites, and represent all those for which a complete set of simultaneous avian, floristic, and physiognomic data has been reported. Additionally, these plots were included as part of a previous "continental" scale analysis (Rotenberry and Wiens 1980a).

Bird populations

Bird population studies were undertaken on marked grids of 8.4–10.6 ha. Population densities of all bird species breeding on each plot were estimated by mapping individual territories using the "consecutive flush" technique (Wiens 1969). Wide-ranging raptorial species were not included, although nonpasserines such as plovers were. All species censused forage on the ground and are primarily insectivorous during the breeding season. In general, plots supported an average of 4 species and a total density of slightly more than 200 individuals/km². Densities and standing crop biomass of all censused species are given by Wiens (1973: Appendix II).

Vegetation structure

Physiognomic data were collected at the same time on the same plots as the avian censuses. These data consisted of 9 structural measurements designed to describe the horizontal and vertical density and spatial dispersion of stems,

leaves, and various physiognomic classes of vegetation. The vegetation was sampled by passing a slender (5-mm) metal rod vertically through the herbage and recording the type and number of vegetational contacts in each 10-cm height interval. The distance to and height of the forb nearest the rod was recorded in each of 4 quarters surrounding a sample point. These measurements, averaged over 80–100 points per plot, yielded estimates of 1) vertical density (average total vegetation contacts per point); 2) percent of vertical density < 10 cm from ground level; 3) an index of overall horizontal spatial heterogeneity (Wiens 1974); 4) mean distance to nearest forb; and 5) average height of nearest forb. Additionally, percent coverage of litter was visually estimated around the sample point, and its depth measured at that point. Finally, average height at which a narrow (3-cm) board was obscured by vegetation was estimated, and degree of light penetration to the ground (percentage of open sky light intensity) was measured with a light meter. Raw data from these measurements are given by Wiens (1973: Table 4), and interrelationships among these and other structural measures are more fully explored by Rotenberry and Wiens (1980a).

Plant taxonomic composition

At each site the above-ground plant biomass was sampled by the harvest plot method at biweekly intervals throughout the 1970 growing season (French 1970). Each species was sorted out, oven-dried, and weighed to estimate its production on a g/m² basis. Species were then combined into major taxonomic groups (7 tribes of grasses, 25 families of forbs, sedges, and 4 species of shrubs) for numerical analyses (Grant 1971). One sample date from each plot was selected to be used in between-plot comparisons. Each date was chosen so as to represent the period during the growing

Table 1. Characteristics of IBP grassland plots for which simultaneous avifaunal, floristic, and physiognomic data were available. Pawnee and Pantex sites each contain two plots that differ in grazing treatment

Plot	Grazing treatment	Location	Structural type	Dominant ^a vegetation	Dominant ^b bird species
Osage	moderate	NE Oklahoma	tall-grass prairie	<i>Andropogon scoparius</i> <i>Sorghastrum nutans</i>	<i>Sturnella magna</i> <i>Spiza americana</i> <i>Ammodramus savannarum</i>
Cottonwood	heavy	SW South Dakota	mixed-grass prairie	<i>Agropyron smithii</i> <i>Buchlœe dactyloides</i> <i>Artemisia frigida</i>	<i>Eremophila alpestris</i>
Pawnee – HS and Pawnee – U	heavy summer heavy winter	N Colorado	short-grass prairie	<i>Bouteloua gracilis</i> <i>Artemisia frigida</i> <i>Atriplex</i> spp. <i>Opuntia</i> spp.	<i>Eremophila alpestris</i> <i>Calamospiza melanocorys</i> <i>Calcarius mccowni</i>
Pantex – H and Pantex – U	heavy ungrazed	N Texas	short-grass prairie	<i>Bouteloua gracilis</i> <i>Buchlœe dactyloides</i> <i>Opuntia</i> spp.	<i>Eremophila alpestris</i> <i>Sturnella neglecta</i>
Bison	moderate	NW Montana	bunchgrass prairie	<i>Festuca scabrella</i> <i>Festuca idahoensis</i> <i>Agropyron spicatum</i> <i>Lupinus sericus</i>	<i>Sturnella neglecta</i> <i>Ammodramus savannarum</i>
Bridger	light	S Montana	mountain grassland	<i>Festuca idahoensis</i> <i>Agropyron subsecundum</i> <i>Lupinus argenteus</i>	<i>Eremophila alpestris</i> <i>Turdus migratorius</i> <i>Poocetes gramineus</i>

^a From Sims et al. (1978) and references therein

^b From Wiens (1973). Taxa listed account for > 85% of total individuals censused at a site

season when plant composition first attained a relatively stable condition (little change in dry weight species composition between successive collection dates; Grant 1971). Overall site vegetation characteristics and relationships are described more completely by Sims et al. (1978), who provide references for the raw floristic data for each site.

Statistical analysis

The relationships between each plot and every other plot with respect to bird community composition, floristic composition, and physiognomy can be estimated using similarity or distance indices. These values are arranged in similarity matrices that describe the position of each plot relative to all others in a multidimensional "hyperspace" whose axes are the relative abundances of all bird species or plant taxa censused, or all structural attributes measured. The similarity index used for the grassland flora and avifauna is R_o , Horn's (1966) index of overlap, which ranges from 0 (no shared species) to 1 (identical relative abundances). Because the structural variables cannot be represented by relative abundances, R_o is inappropriate to express plot relationships in this "space." Therefore, the relationship between each pair of plots with respect to their structural composition was defined as the Euclidean distance between each pair based on the 9 standardized physiognomic variables. Because Euclidean distance is closely but inversely related to similarity, similarity values were subtracted from 1 to yield a "dissimilarity" index that varied directly as distance between samples in hyperspace. The original similarity values employed for bird species and plant taxa may be found in Wiens (1971: Appendices II and V; see also Grant 1971); the original structural distances are available from me on request.

Determination of whether or not bird species community composition in grasslands is more closely related to floristics than to physiognomy requires a rephrasing of the question: are the relative locations of plots in the multidimensional space defined by avian composition more closely associated with their locations in plant taxonomic space or in habitat structure space? This question may be addressed by considering the degree of congruence of the plot similarity matrices in the various hyperspaces, as measured by the correlation coefficient between them (Power 1975; Rotenberry and Wiens 1980b). This measure is analogous to the cophenetic correlation coefficient of numerical taxonomy (Sokal and Sneath 1963) and, when squared, is an index of the amount of information in one similarity matrix that is reliably reproduced in another.

Unfortunately, standard tests of the statistical significance of such correlations are invalidated by the lack of independence among cells of distance or similarity matrices; the distance between any two samples is in part constrained by their distances to a third. Thus simple correlations or r^2 can be interpreted only as a qualitative description of matrix congruence. However, the Mantel test (see below) provides a simple, nonparametric multivariate evaluation of the likelihood that the degree of association between two matrices is random. The Mantel procedure is based on a comparison of the observed relationship of rows and columns of two matrices to relations based on all possible permutations of rows and columns under a null hypothesis of no association. It is described in detail by Douglas and Endler (1982), who also provide a computational example to facilitate understanding of the technique.

Results

Thirty-five percent of the relationships among samples represented in the bird abundance similarity matrix was reproduced in the habitat structure distance matrix, a result that differed significantly from chance ($P < 0.05$, Fig. 1A). A nonrandom relationship between bird community composition and physiognomy is not unexpected, given that densities of individual species in this same sample were observed to covary strongly with habitat structure (Rotenberry and Wiens 1980a). Perhaps more surprising, however, is the finding that over half ($r^2 = 55\%$, Fig. 1A) of the information about plot relationships expressed by avian community compositions is reproduced by their floristic composition ($P < 0.01$).

The association between floristics and physiognomy is also marginally significant ($r^2 = 22\%$, $P = 0.07$, Fig. 1A). This is to be expected, as different taxa of plants have different growth forms and thus should contribute differentially to the development of vegetation structure. It suggests, however, a possible confounding effect of one on the other's association with bird communities. Such an effect may be removed by the use of partial correlation (Thorndike 1978), which allows examination of the correlation between two variables while statistically controlling for their covariation with a third. Controlling for floristics, the correlation between habitat structure and avian composition drops substantially, and physiognomy accounts for only an insignificant 17% of the variation in bird communities ($P > 0.05$, Fig. 1B). When the effects of structure are partialled out, the association between floristics and avian composition is also diminished ($r^2 = 43\%$, Fig. 1B) but still retains a very high level of significance ($P < 0.01$). Thus, it seems apparent from these analyses that knowledge of the floristic composition of representative grassland habitats provides a better resolution of the bird communities they support than does information about the details of their structural configuration. Although these same bird species evidenced significant correlations with physiognomic features when examined on a broad scale, at a less heterogeneous sampling level these correlations are replaced by those with overall plant taxa.

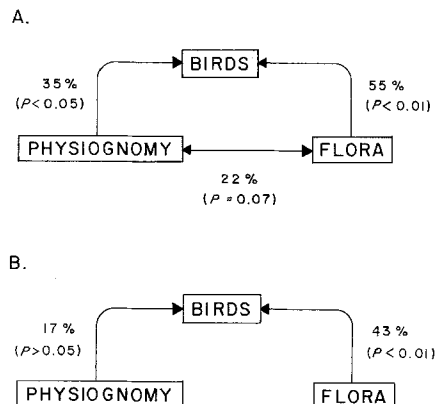


Fig. 1. A Coefficients of determination ($r^2 \times 100$) between similarity and distance matrices based on avian, floristic, and physiognomic composition of 8 grassland study sites (Table 1). Significance levels of association given in parentheses. B Partial coefficients of determination, as above. Correlation between physiognomy and flora has been partialled out

Discussion

The primacy that some avian ecologists have given physiognomic measurements no doubt depends to some extent on studies that failed to find significant correlations between bird communities and plant taxa, while simultaneously demonstrating associations between these communities and habitat physiognomy (e.g., MacArthur and MacArthur 1961; Abbott 1976). These observations have been reinforced by persuasive explanations based on habitat selection behavior and niche theory (Hildén 1965; Wiens 1969; James 1971). Indeed, measures of habitat structure that are largely independent of plant taxonomic composition now form the focus of many approaches to assessing the quality of avian habitats (e.g., Asherin et al. 1979).

However, the observation here that bird community composition is closely correlated with floristics is not unique nor limited to structurally simple steppe environments (e.g., Tomoff 1974, Sonoran desert scrub; Lovejoy 1974, neotropical forest; Power 1975, Galapagos archipelago). More important, perhaps, is the increasing number of studies that demonstrate at a local population level a strong association between individual bird species and one or more individual plant species (e.g., Snow and Snow 1971; Smith 1977; Holmes et al. 1979; Holmes and Robinson 1981; Maurer and Whitmore 1981; Wiens and Rotenberry 1981; Rice et al. 1983; Robinson and Holmes 1984). Indeed, most avian ecologists are familiar with similar specific associations from their own field experiences. Why, then, do such relationships only occasionally emerge at the community or assemblage level?

I suggest that such associations likely exist in most systems but are obscured by the loss of information that results from summarizing community composition and structure, which are complex and intrinsically multivariate, with only one or a few simple indices. Such indices (usually species diversity or its components; see Peet 1974 for examples) ignore the taxonomic composition of a sample of species (plants or animals); indeed, two samples that share no species in common can still yield identical diversity indices. Thus even if individual bird species respond strongly to individual plant species, as seems evident from the references above, to the extent that these responses differ among species any comparison between simple, single measures of plant community (physiognomic or floristic) and similar measures of bird community will not detect such relationships. The methodology employed here preserves taxonomic differences and circumvents this problem.

It seems likely that the most significant source of variation among plants (especially species of generally similar gross morphology) to which birds are likely to respond is the provision of food. In cases where factors determining the linkages between birds and plants were evident, the mechanism responsible appears to be related to food and foraging behavior (Snow and Snow 1971; Lovejoy 1974; Holmes and Robinson 1981; Maurer and Whitmore 1981; Robinson and Holmes 1984). For birds that are rather specialized frugivores or nectarivores, associations with particular plant species seem obvious. For more generalized frugivores, nectarivores, granivores, or insectivores, one-to-one relationships are less likely, and such species may instead respond to a suite of particular plant species. Plant species-rich tropical forests, for example, support significantly more species of birds than temperate forests of comparable habi-

tat structure but of lesser plant species richness (Karr 1971). As much as 50% of this increase in number of tropical breeding birds compared to similar temperate habitats has been attributed to the addition of a new food source, namely fruit (Karr 1971). In any event, this suggested mechanism is readily amenable to verification or falsification by direct observation and experimentation, and other plausible alternatives exist (e.g., Schoener 1971).

The observation that birds may respond more directly to plant taxa than habitat structure has important implications for practical aspects of species management and conservation as well. While the replacement of one key plant species by another may preserve the structural configuration of a particular ecosystem, substantial changes in bird community composition could nonetheless result. Thus, habitat evaluation schemes that rely solely on physiognomic measurements may be inadequate or even misleading. Likewise, management strategies that emphasize the maintenance or even increase of species diversity by physiognomic manipulation (e.g., increasing "edge" habitat; Bureau of Land Management 1973) ignore the particular composition of a community, and as a result may hasten the local extinction of many desirable species (Balda 1975).

In conclusion, it is apparent that patterns in the structure and composition of communities exist, and that many of these patterns are a result of ecological processes. These processes likely reflect mechanisms that operate at the level of the population or at the interface between populations, and thus small scale within-habitat type investigations are best suited to detecting these mechanisms. Furthermore, this detection will more likely be obscured than illuminated by simplification of community composition to single indices. I suggest this not only for the bird taxa/plant taxa linkage observed here, but even for more general bird diversity/habitat structure relationships (see also James and Rathbun 1981; James and Wamer 1982). It may well be that the simple community statistics will reveal only those patterns that are expressed over a relatively broad biogeographical scale. However, it seems increasingly clear that only by considering communities as gatherings of distinct but potentially interacting populations will we ultimately be able to identify unambiguously those mechanisms responsible for producing those patterns.

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