

## The University of Notre Dame

---

Habitat Heterogeneity and Avian Community Structure in North American Grasslands

Author(s): John A. Wiens

Reviewed work(s):

Source: *American Midland Naturalist*, Vol. 91, No. 1 (Jan., 1974), pp. 195-213

Published by: [The University of Notre Dame](#)

Stable URL: <http://www.jstor.org/stable/2424522>

Accessed: 08/03/2012 12:08

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Notre Dame is collaborating with JSTOR to digitize, preserve and extend access to *American Midland Naturalist*.

<http://www.jstor.org>

# Habitat Heterogeneity and Avian Community Structure in North American Grasslands

JOHN A. WIENS

*Department of Zoology, Oregon State University, Corvallis 97330*

**ABSTRACT:** In a variety of environments, patchiness of habitat structure appears related to faunal diversity. I examined the relations between vegetational heterogeneity and several attributes of avian communities over a range of North American grassland and shrub steppe situations. Habitat heterogeneity was measured by assessing the variability in vertical density of vegetation within clustered point samples, and an index to express this horizontal patchiness was derived. Heterogeneity was directly related to the areal coverage of bare ground and woody vegetation and to patchiness in litter distribution of sample plots, and inversely related to grass coverage and litter depth. Heterogeneity generally increased with decreasing annual precipitation and primary production, tall grass-prairie sites being the least and western shrub steppe the most heterogeneous.

Analysis of breeding bird population censuses from these plots revealed no apparent relationships between habitat heterogeneity and the diversity of breeding avifaunas or the extent of spatial (territorial) overlap between species. The density of breeding bird populations decreased slightly with increasing vegetation patchiness; the standing crop biomass of the avian community, however, decreased markedly as heterogeneity increased. This pattern appeared to result from a replacement of large-sized species by medium-sized species in the transition from tall grass to short grass areas and an increasing dominance of small-sized species in the western Palouse and shrub steppe sites.

## INTRODUCTION

Many workers have recently drawn attention to the relation between habitat structure and faunal diversity. In deciduous forests in eastern North America, for example, the diversity of breeding bird species in a community increases with increasing patchiness or vertical layering of the vegetation (MacArthur and MacArthur, 1961; MacArthur, 1965), and a correlation between increasing habitat complexity and diversity in breeding bird faunas seems most general (*e.g.*, Karr and Roth, 1971; Cody, 1970; Orians, 1969). Diversity in lizard faunas also may be related to habitat complexity (Pianka, 1967; Schoener and Schoener, 1971), and the structure of some small mammal communities may be closely tied to structural heterogeneity of the environment (Rosenzweig and Winakur, 1969). These observations and others have led to the development of a rather extensive body of theory of habitat heterogeneity (*e.g.*, Levins, 1968; MacArthur and Levins, 1964, 1967; MacArthur and Pianka, 1966), although a good deal of this theory remains untested.

In forest communities a good share of the increase in bird species diversity with increasing patchiness in the vertical distribution of foliage may be due to an increased vertical layering of the bird species. Spatial overlap between species, as projected on a single horizontal plane, may thus be extensive. In structurally simple habitats such as

grasslands, however, opportunities for vertical layering are absent, and vegetation patchiness should be largely horizontal. Here, one might expect the effects of vegetation structure on avian community organization to be more subtle in one sense, and more evident in another, than in forests. They are more subtle because the number of bird species and the range in habitat complexity are smaller and relationships are thus more easily blurred, and are more evident because the effects of patchiness should be expressed in single horizontal plane and thus be more amenable to direct measurement.

It is my intent here to examine the nature of habitat heterogeneity in North American grasslands and to assess its impact on several aspects of the organization of breeding bird communities. Habitat heterogeneity is emphasized because of its theoretical relationship to community structure, but it should be emphasized that other habitat features may be of equal or greater importance in the habitat selection responses or utilization patterns of individual bird species.

#### STUDY AREAS AND SAMPLING METHODS

The data for this analysis were gathered between 1967 and 1971 in 25 plots at 15 sites which were broadly distributed over the North American grasslands (Fig. 1). Plots were located in tall grass, mixed grass, short grass, Palouse, montane and northern shrub steppe community types (generalized from Küchler, 1964) and were subjected to differing intensities of grazing by domestic or native (bison, antelope) herbivores (Table 1).

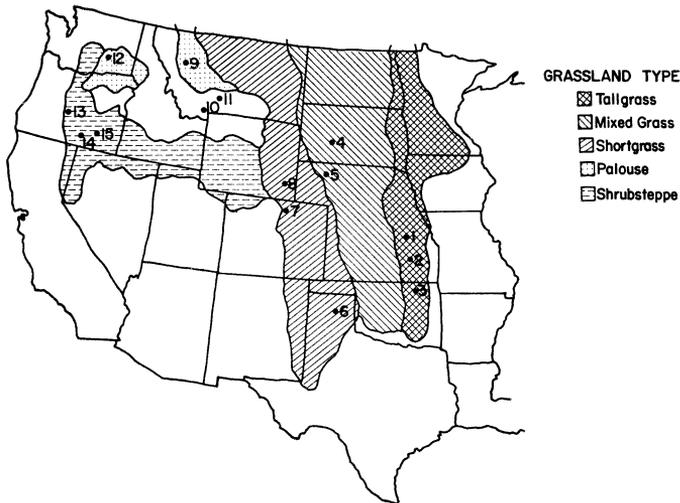


Fig. 1.—Locations of sites included in this analysis. Numerals refer to the study sites listed in Table 1. Sites 10 and 11 are in montane grasslands, which have too disjunct a distribution to be illustrated here. Grassland types generalized from Küchler (1964)

TABLE 1.—Features of the study sites shown in Figure 1

No.	Site Name	Grazing treatment	Elev. (m)	Mean ann. precip. (cm)	Sample	Dates sampled	Heterogeneity index*	Sample unit CV*
1	Donaldson	Moderate	390	80	A	10-11 July 1968	1.19	0.42
2	Elmdale	Moderate	425	82	A	2-3 August 1967	0.90	0.35
					B	7-9 July 1968	1.03	0.40
3	Osage**	Moderate	380	94	A	12-15 June 1970	0.81	0.26
4	Cottonwood**	Heavy	850	38	A	19-20 July 1968	0.88	0.27
					B	25-28 June 1970	0.92	0.29
5	Sandhills	Heavy	1170	50	A	16-17 July 1968	2.25	1.04
		Ungrazed	1158	50	B	17-18 July 1968	1.09	0.42
6	Pantex**	Heavy	1090	53	A	3-5 June 1970	1.18	0.42
		Ungrazed	1090	53	B	5-7 June 1970	1.56	0.36
7	Pawnee**	Heavy winter	1430	30	A	13-15 July 1968	1.39	0.32
					B	3-5 July 1969	1.63	0.38
					C	20-21 June 1970	1.44	0.38
		Heavy summer	1430	30	D	15-16 July 1968	1.56	0.35
					E	5-6 July 1969	1.50	0.38
					F	21-23 June 1970	1.42	0.38
8	Laramie	Light	2130	34	A	1-2 July 1969	1.84	0.41
9	Bison**	Moderate	980	33	A	5-7 July 1970	1.61	0.34
10	Bridger**	Moderate	2320	61	A	1-4 July 1970	1.52	0.51
11	Cliff Lake	Ungrazed	2175	65	A	29-30 June 1969	1.34	0.48
12	Ale**	Ungrazed	372	18	A	7-10 May 1971	2.25	0.54
					B	7-10 May 1971	2.07	0.59
13	Cabin Lake	Light	1365	24	A	15-16 June 1969	2.87	0.71
14	Chevaucan	Light	1311	30	A	7-9 July 1967	2.68	0.95
15	Steens Mountain	Ungrazed	1680	30	A	21-22 June 1967	2.39	0.66

\* See text for explanation

\*\* Sites in the U.S. IBP Grassland Biome Program

At each sample area, a 9.2- to 10.6-ha study plot was delineated by laying out a staked grid with 61-m grid intervals. This grid served as the base for both avian population estimation and vegetation sampling.

*Population estimation.*—Population densities of all species breeding on the study plots were estimated by mapping individual territories using the “territory-flush” procedure (Wiens, 1969). A singing male was flushed from its display site, and its initial position, flight path and landing position were plotted on a scaled field map. This procedure was repeated until a minimum of 20 consecutive flushes were mapped. A line enclosing the periphery of these movements was then drawn to delimit the territory boundary. Breeding individuals generally remained within clearly delimited areas during these flushes, and independent observations indicated a close agreement of these “flush areas” with breeding territories. After all the territories of a species were mapped, the total number of territories and portions of territories lying within the plot boundaries was determined and multiplied by a mating system conversion factor (2.0 for typically monogamous species, 2.5 for typically polygynous species such as meadowlarks [*Sturnella magna* and *S. neglecta*] and dickcissel [*Spiza americana*]) to obtain the plot census. These values were then converted to total individuals/km<sup>2</sup>. Standing crop biomass values for each species population on a plot were obtained by multiplying the population density estimate by the mean live body weight per individual, using weight values from specimens collected nearby. The results of these plot censuses are available upon request.

*Vegetation structure analysis.*—Features of vegetation structure were recorded at sampling positions (hereafter termed “sample units”) located according to a stratified random design, with one unit within each block of the 5 × 5 grid. At each sample unit, four “sample points” were located at the corners of a square with 2-m diagonals (Fig. 2). The standard sampling intensity was thus 2.7 sample units/ha, or 10.8 sample points/ha.

At each sample point a variety of vegetational features were measured (*see* Wiens, 1969), but only the following are of concern here. The vertical distribution or density of the vegetation was measured by recording the number of contacts or “hits” of living or standing dead plant parts in each decimeter height interval of a thin rod passed vertically through the vegetation. Vegetation types were categorized by growth form, and the per cent cover of grass, woody vegetation (*e.g.*, *Artemisia*) or bare unvegetated ground was obtained from the frequency of occurrence of these types at all sample points within a plot. In addition, the depth of the ground litter or mulch was measured at each sample point.

#### THE MEASUREMENT OF HABITAT HETEROGENEITY

While many statistical measures of heterogeneity or patchiness exist (Lloyd, 1967; Greig-Smith, 1964; Clark and Evans, 1955; Morisita, 1954; Pielou, 1969), none of these are really of the same scale or con-

sider the same habitat features that a small ground-dwelling bird might use in assessing patchiness. Since there is considerable evidence that the height-density distribution of vegetation may be important in the habitat responses and utilization patterns of grassland birds (Wiens, 1969; Cody, 1968; Tester and Marshall, 1961), I measured the spatial heterogeneity of this habitat component, although patchiness of litter distribution was also considered. The sampling design used provided two horizontal scales on which the evenness or patchiness of distribution of these features could be considered. First, by examining variation among the four sample points within each sample unit, a measure of heterogeneity over a horizontal distance of 2 m could be obtained. In addition, measures of variation among individual sample units allowed detection of pattern on a horizontal scale of 65 m (the mean distance between sample units) (Fig. 2). While other scales of pattern may also potentially be important to the birds, these two rather arbitrarily selected scales may have some realism, the first perhaps assessing patchiness within localized activity areas of an individual and the second estimating variation more on the level of individual territories.

For a measure of heterogeneity among sample points at a sample unit, perhaps the simplest approach is to use the difference between maximum and minimum values of total vertical vegetation density

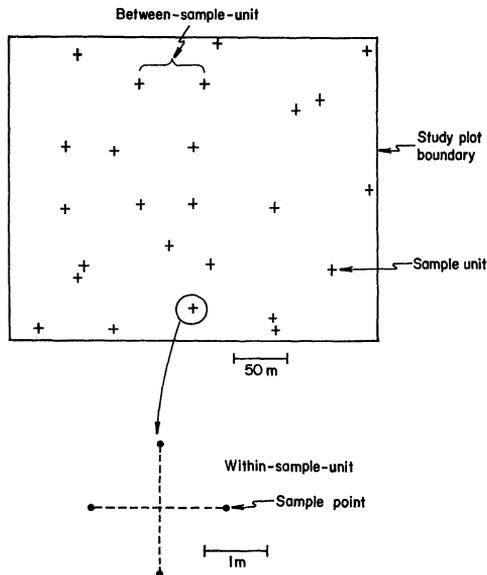


Fig. 2.—Example of two sampling scales at which vegetational heterogeneity was measured. "Between-sample-unit" measures assessed variability in vegetation among the 20-25 sample units located by a stratified random procedure within a study plot. "Within-sample-unit" measures considered variation among the four sample points at each sample unit

(total number of hits on the vertical point sample). For an entire study plot, then, heterogeneity might be measured as

$$\text{Heterogeneity} = \frac{\Sigma(\text{Max-Min})}{N}$$

where Max = maximum total number of contacts recorded among the four sample points; Min = minimum total contacts recorded; and N = total number of sample points. This formulation, however, assumes that the same degree of difference may have equal importance in vastly different habitat situations. Thus, a difference of two contacts among sample points with an overall mean vertical density of 2 (*i.e.*,  $3 - 1 = 2$ ) is equivalent to a variation of two contacts among sample points with a mean vertical density of 12 (*i.e.*,  $13 - 11 = 2$ ), despite one's intuitive feeling that the former difference must be more apparent to a small bird. To correct for this bias, differences may be weighted by the mean vertical vegetation density for each sample unit. Thus, for a study plot

$$\text{Heterogeneity Index} = \frac{\frac{\Sigma(\text{Max-Min})}{N}}{\frac{\Sigma \bar{x}}{N}} = \frac{\Sigma(\text{Max-Min})}{\Sigma \bar{x}} \quad (1)$$

where  $\bar{x}$  = sample unit mean vertical vegetation density.

Patchiness of vegetation at the between-sample-unit scale was measured by the Coefficient of Variation (CV) of the sample-unit mean vertical density values, using

$$\text{CV} = \frac{100s}{\bar{x}}$$

#### RESULTS

*Heterogeneity and other vegetation measures.*—Vegetational heterogeneity, as measured by the patchiness of vegetation vertical density within sample units (Equation 1; Table 1), is related to several other measures of grassland habitat structure. As plot heterogeneity increased, there was a general reduction in grass cover and an increase in cover by woody vegetation and bare ground (Fig. 3). In general, these trends parallel the gradients of decreasing annual precipitation and decreasing annual net primary production recognized in the series tall grass-mixed grass-short grass-shrub steppe (Wiens, in press). This suggests that in grasslands where production and, presumably, absolute food resource abundance are the least, the spatial distribution of these resources is the most uneven or patchy. This is counter to the relationships found in forests, where structural complexity generally increases with increasing productivity (Whittaker and Woodwell, 1972).

The height distribution of vegetation in a field is also related to heterogeneity (Fig. 4A). In tall grass sites, where heterogeneity was

low, the proportion of vegetation occurring within 10 cm of ground level was low. This was also the case in the highly heterogeneous shrub steppe, but here largely because of the high shrub dominance in the vegetation. Short grass sites, with almost all of the vegetation located within 10 cm of the ground, had intermediate heterogeneity index values. The Palouse-prairie plots generally had higher heterogeneity index values than would be predicted on the basis of the height distribution of vegetation; this, of course, is a consequence of the bunchgrass growth form of the dominant grasses (*Festuca*, *Agropyron*).

Litter characteristics were also closely tied to heterogeneity of vertical vegetation density. Litter depth generally decreased with increasing heterogeneity (Fig. 4B) as would be expected from the decrease in aboveground primary production. With the decrease in litter depth, however, the horizontal patchiness of litter (as gauged by Equation 1, using litter depth rather than vertical vegetation density measures) increased, indicating that plots which had patchy standing vegetation also had unevenly distributed litter. Both vertical vegetation density and litter depth have been shown to be important structural features in the habitat responses of grassland birds (Wiens, 1969; Tester and Marshall, 1961), so these variations in the distribution and density of

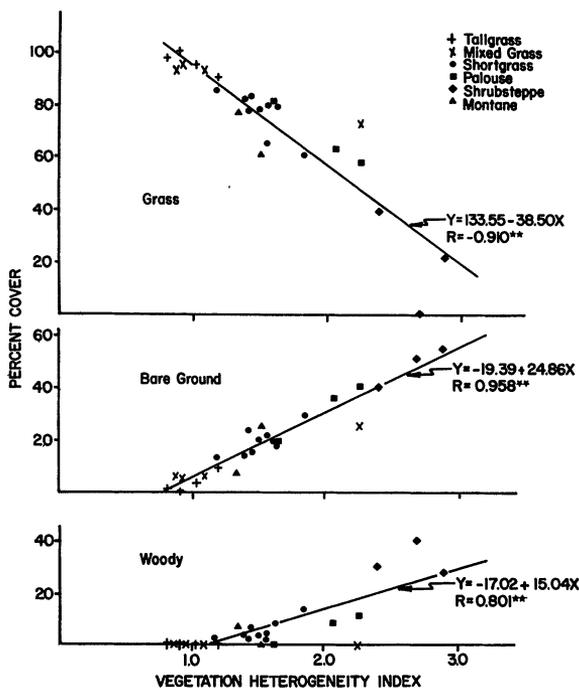


Fig. 3.—Relations between the per cent coverage of grass, bare ground and woody vegetation and vegetational heterogeneity of individual sample plots, as measured by the index described in the text

these features might be expected to have marked effects on breeding populations.

There was, finally, a close association between habitat heterogeneity, measured at the within-sample-unit level, and between-sample-unit variation (Fig. 4D). Plots characterized by high heterogeneity on a small scale were generally patchy on the larger scale as well.

*Avian community organization.*—Given such patterns of variation in habitat patchiness, it is customary to search for related patterns in avian community structure. The diversity of bird populations breeding on the plots, calculated by  $H' = -\sum p_i \log_e p_i$  (where  $p_i$  = the proportion of all individuals belonging to the  $i$ th species:  $i = 1, 2, \dots, S$ ), was relatively uniform and showed no relationship to plot heterogeneity at either the within-sample-unit or between-sample-unit levels (Table 2; Fig. 5A). Cody (1966) and I (Wiens, 1969) have previously noted the uniformly low diversity of breeding bird communities in grasslands. The relatively small number of breeding species (two to six) in grasslands undoubtedly places severe restrictions on the potential range of diversity values, and any trends associated with habitat structure would thus be difficult to detect and quite easily obscured by other variables. It is, nonetheless, interesting to note that extremely patchy habitats such as northern Great Basin shrub steppe

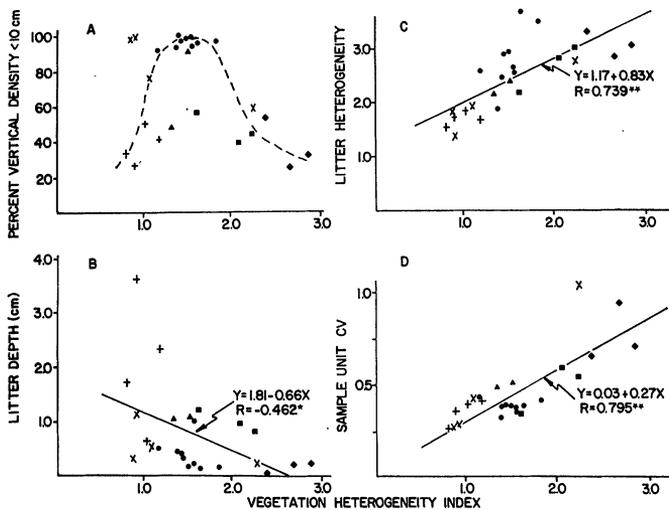


Fig. 4.—Relations between vegetational heterogeneity and census plot values of: (A) the proportion of all vegetation contacts at vertical point samples occurring within 10 cm of the ground (curve approximated by eye); (B) the mean depth of litter in sample plots; (C) the heterogeneity of litter coverage, as measured by Equation 1; and (D) the coefficient of variation (CV) of sample unit mean vertical vegetation density measurements (a measure of "between-sample-unit" heterogeneity)

TABLE 2.—Measures of avian community attributes at the grassland sites listed in Table 1

Site no.	Sample	No. of species	Bird species Diversity	Equi-tability	Diversity	Biomass	Equi-tability	Dominance*	Standing crop biomass (g/ha)	Density (individual/km <sup>2</sup> )	Inter-specific** overlap index
1	A	3	0.95	0.86	0.94	0.31	0.45	116	206	0.33	
2	A	3	1.03	0.94	0.91	0.83	0.51	116	284	0.34	
3	B	4	1.19	0.85	1.06	0.76	0.36	129	275	0.31	
4	A	4	1.22	0.88	1.01	0.73	0.35	133	250	0.33	
5	A	4	1.08	0.78	1.20	0.88	0.57	119	272	0.61	
6	B	3	0.44	0.40	0.61	0.56	0.86	60	152	0.15	
7	A	3	1.06	0.96	0.70	0.64	0.45	101	101	0.22	
8	B	5	1.24	0.77	1.48	0.92	0.52	113	317	0.41	
9	A	4	0.74	0.54	0.83	0.60	0.74	116	266	0.19	
10	B	4	0.95	0.68	0.76	0.55	0.57	112	212	0.31	
11	A	5	1.12	0.69	1.08	0.67	0.64	91	231	0.43	
12	B	4	1.14	0.82	1.11	0.81	0.50	101	333	0.33	
13	C	3	0.94	0.85	0.81	0.74	0.49	89	277	0.30	
14	D	3	0.96	0.87	1.01	0.92	0.55	58	203	0.13	
15	E	3	0.83	0.83	1.07	0.98	0.49	89	261	0.37	
16	F	6	1.26	0.70	1.53	0.86	0.50	97	270	0.24	
17	A	2	0.68	0.99	0.69	1.00	0.57	74	263	0.72	
18	A	3	0.82	0.74	0.56	0.51	0.51	79	144	0.16	
19	A	4	1.24	0.90	1.18	0.85	0.50	40	109	0.25	
20	A	6	1.43	0.80	1.51	0.84	0.46	125	552	0.23	
21	A	3	1.00	0.92	0.96	0.88	0.50	89	213	0.45	
22	B	4	1.11	0.80	1.24	0.89	0.49	119	291	0.51	
23	A	4	1.03	0.74	1.21	0.87	0.55	75	459	0.29	
24	A	5	1.33	0.83	1.04	0.65	0.22	72	139	0.31	
25	A	4	1.21	0.87	1.27	0.92	0.53	54	192	0.29	

\* Relative density of the single most abundant species at the site

\*\* See text and appendix

or Palouse prairie supported no more diverse avifaunas than the structurally simpler Great Plains grassland.

Variations in diversity measures can stem from differences in species richness or in the equitability of distribution of individuals among species, or both (Lloyd and Ghelardi, 1964). The lowest diversity values (0.44 to 0.74) were recorded at Cottonwood, Pantex and Laramie; at the first two sites, single species dominance (or low equitability) had important effects on diversity, while at Laramie the low number of species recorded (two) was responsible for the low diversity index (Table 2). Thus, in the plot censuses, neither diversity component showed any systematic pattern of variation along the heterogeneity gradient.

The density of breeding bird populations was variable among the range of grassland sites (Table 2), but, again, there was no strong association between this aspect of community organization and habitat heterogeneity. There was a weak tendency for density to decrease with increasing within-sample-unit heterogeneity (linear regression;  $R = -0.404$ ;  $F = 4.09$ ;  $0.10 > p > 0.05$ ) (Fig. 5B). This inverse relationship was more strongly expressed in relation to between-sample-unit patchiness, however ( $R = -0.507$ ;  $F = 7.28$ ;  $p < 0.05$ ). Thus, vegetation patchiness at a scale approximating that of individual terri-

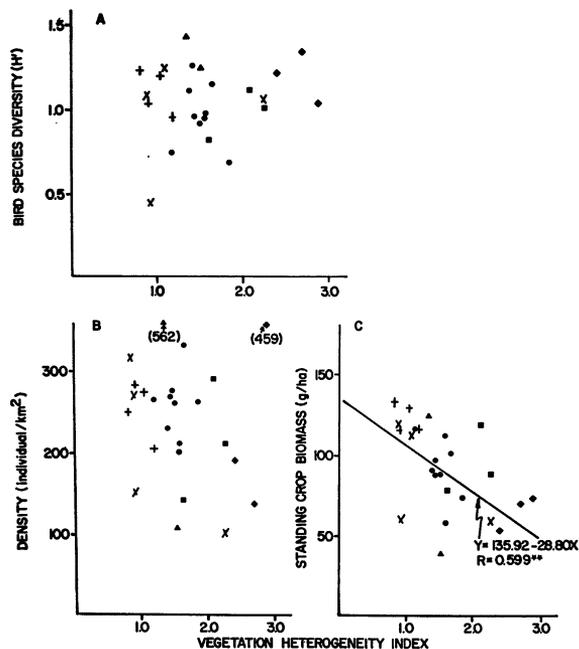


Fig. 5.—Relations between the vegetational heterogeneity of census plots and plot values of: (A) bird species diversity; (B) breeding bird density; and (C) the standing crop biomass of breeding birds

tories may perhaps be more important in relation to total breeding densities than smaller scale, within-territory patchiness. Possibly, general patterns of territorial distribution and the spatial "packing" of territories in a habitat are related to habitat patchiness, while acting to at least partially determine the total breeding density of an area. While it is difficult to assess the role of territoriality in the determination of population densities, the extent of spatial packing of territories of the species breeding on a plot may be estimated by superimposing the territory mappings of the different species made during population censusing. To allow comparisons of plots supporting different numbers of breeding species, and thus having different potentials for interspecific spatial overlap, I used an Index of Interspecific Overlap (IO)

$$IO = \left[ \frac{\sum \left[ i \left( \frac{a_i}{\sum a_i} \right) \right] - M}{N} \right] \left[ \frac{1}{1 - M} \right]$$

where  $i = 2, \dots, N$  species;  $N$  = total number of species present;  $a_i$  = area co-occupied by  $i$  species; and  $M$  = minimum value of  $\frac{a_i}{\sum a_i}$  recorded. This index ranges from  $\frac{1}{N}$  when there is no spatial

overlap among the species present to 1 when territorial overlap among all species is complete (see appendix).

The values of this index for the census plots are given in Table 2. No relationships are apparent, either to variations in breeding densities or to variations in plot heterogeneity. Most values are intermediate, suggesting that at the total density levels characteristic of a wide range of habitat types, the plots were packed to a roughly similar extent. Further, it appears that the plots were not maximally packed with individuals of all species present. This would be expected, of course, only if all areas within a plot were equally suitable to individuals of all species, and the "incomplete" degree of spatial overlap among the species breeding on a plot suggests that the species may react differently to the mosaic of habitat patches characterizing a plot (*see* Wiens, 1969; Wiens, in press).

While relationships between habitat patchiness and the species diversity, dominance, density, and spatial patterns of the avian communities of these grassland plots were thus absent or weak, there was a significant inverse relationship between within-sample-unit vegetational heterogeneity and the total standing-crop biomass of the avian community (Table 2; Fig. 5C). These variations in total community biomass are not paralleled by variations in the density of individuals or the number of breeding species, suggesting that the degree of niche differentiation and the densities of breeding individuals may be limited at generally similar levels over a wide range of grassland and even shrub steppe habitats (Wiens, in press), while avian biomass generally decreases with decreasing primary productivity. There was no significant relationship between standing crop biomass and between-sample-

unit variability (linear regression  $R = -0.364$ ;  $F = 2.61$ ;  $p > 0.10$ ).

Such a pattern might be achieved through an overall increase in the mean body sizes of all species in the less heterogeneous, more productive sites, or through variations in the proportions of different-sized species in the avifaunas. To examine this, I categorized the breeding species by body size (small =  $\geq 25$  g, such as grasshopper sparrows [*Ammodramus savannarum*]; medium = 26 to 80 g, such as horned larks [*Eremophila alpestris*]; and large =  $> 80$  g, for example, meadowlarks). The proportions of these size classes in the breeding bird communities of the different plots are shown in Fig. 6. Clearly, the decreases in standing crop biomass between the tall grass, mixed grass and short grass plots stem largely from a shift in dominance (or replacement) from large-sized species to medium-sized species. Especially noticeable is the contrast between the nearly complete dominance of medium-sized species in most short grass plots and the generally equitable distribution of individuals among the three size classes in the tall grass plots. Montane, Palouse and shrub steppe plots apparently supported lower biomass because of the increased predominance of small-sized species. While the significance or adaptiveness of this pattern of biomass distribution is not entirely clear, I have suggested (Wiens, in press) that food supply may be less limiting in short grass than in tall grass habitats; competition related to food resources may thus be less severe, and selection for divergence in body sizes of coexisting species (related to divergence in food-size specialization) less intense. The apparent convergence in body size in short grass species may reflect common adaptive responses to some noncompetitive niche dimension (e.g., thermal stress). In shrub steppe, most breeding species are essentially carnivorous, in contrast to the largely omnivorous nature of the true prairie species; the predominance of small-sized species there may be associated with the higher metabolic costs of carnivory.

*Responses of individual species.*—The above analysis indicates that,

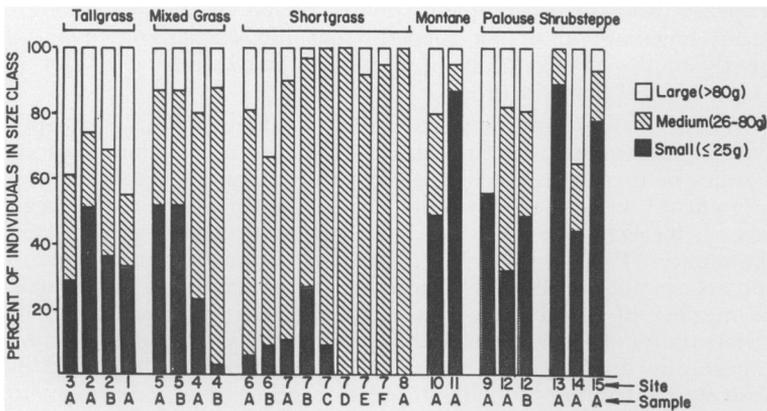


Fig. 6.—The relative density of breeding bird individuals in each of three body size categories at the sample plots

with the exception of biomass changes, there are few well-defined relationships between features of avian community structure in grasslands or shrub steppe and horizontal habitat heterogeneity, as measured here. But while entire breeding avifaunas may show little apparent response to habitat patchiness, individual species should be expected to show relationships, on the strength of the numerous demonstrations that habitat structure has important ecological effects on bird species, not only in grasslands (Wiens, 1969; Cody, 1968) but elsewhere (Hildén, 1965). A more complete analysis of the associations of bird populations with structural properties of grassland habitats will be published elsewhere, but here some examination of species relations to habitat heterogeneity may prove instructive.

Variations in the breeding population densities of several species are related to the gradient of within-sample-unit patchiness in Figure 7. Eastern meadowlark density, for example, was uniformly high in low heterogeneity tall grass plots. Western meadowlarks, normally restricted to more xeric situations than eastern meadowlarks (Lanyon, 1957), occupied plots with greater vegetation patchiness and achieved lower population densities. The considerable variability in western meadowlark density along the heterogeneity scale probably reflects the

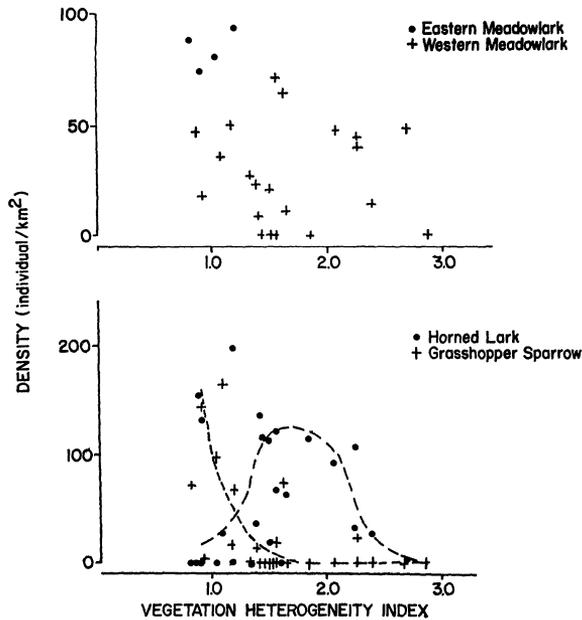


Fig. 7.—Variations in the breeding densities of eastern and western meadowlarks (above) and horned larks and grasshopper sparrows (below) with differences in the vegetational heterogeneity of census plots. Curves approximated by eye

influences of other habitat and/or historical factors unrelated to plot heterogeneity.

While the two meadowlark species were complementary in their distributions among the plots, other species overlapped extensively in their distributions. Grasshopper sparrows and horned larks in particular were widespread through the grasslands. Grasshopper sparrows, however, reached highest density in the low heterogeneity plots, while horned larks were most abundant in moderately patchy plots (Fig. 7B).

While individual species do exhibit distributional patterns paralleling the gradient of plot heterogeneity, the meaning of these relationships is far from clear. The horizontal patchiness of vegetation in a habitat, of course, is only one aspect of its overall structure, and other unrelated structural features may also influence population densities. Also, the response of a species to habitat structure may vary depending upon the numbers and kinds of other bird species present, as potential resource competition becomes more severe or less severe. Still, these single-species responses to horizontal habitat heterogeneity do suggest that this feature, or perhaps structural features correlated with heterogeneity (*see above*), have important effects upon the ecology of the species. The most likely influence is upon patterns of habitat utilization within territories. Individuals of most grassland species distribute their behavioral activities unevenly through their territory, nesting in one area, displaying in others and foraging in still others. Generally, the areas selected for each of these activities have distinctive structural properties (Wiens, 1969), and for some activities, such as foraging, horizontal habitat patchiness especially seems important. The key to understanding these single species relationships to habitat heterogeneity may lie in the patterns of habitat utilization characteristic of a species. Studies of activity budgets and the utilization of habitat structure are currently in progress.

#### CONCLUSIONS

Of the characteristics of avian community organization considered, only the amount and partitioning of standing crop biomass show distinct relationships to variations in habitat patchiness. But if other factors, such as climatic irregularity (Wiens, *in press*), impose limits on species numbers and densities in grasslands, perhaps no well-defined community relationships to habitat structure should be expected. Individual species, on the other hand, apparently do respond to variations in habitat heterogeneity or vegetational features associated with heterogeneity. If these responses are species specific and independent of other species, as seems likely, one would not expect closely co-evolved, coherent groupings of grassland species to exist, but rather diverse, relatively independent patterns of species distributions (Whittaker and Woodwell, 1972). This also would lessen the likelihood of encountering well-defined community patterns.

Obviously, factors others than habitat heterogeneity may influence bird populations and communities in grasslands, and multifactor analyses must be undertaken. Also, any real understanding of the

manner in which habitat patchiness affects breeding birds must rely upon detailed, intensive behavioral studies. Simplistic generalizations, such as those relating structural complexity to avian community attributes (MacArthur, 1965), may be inherently pleasing and may apply in some habitat types, but seem unrealistic in grasslands.

*Acknowledgments.*—This research was initiated under support of the National Science Foundation (Grant GB-6606), and has continued as part of the U.S. IBP Grassland Biome Program which is supported in part by NSF Grants GB-7824, GB-13096, GB-31862X and GB-31862X2, "Analysis of Structure, Function, and Utilization of Grassland Ecosystems." Several individuals allowed me free use of land under their jurisdiction: Mrs. Bert Drake of Elmdale, Kansas (Elmdale); Dr. Clenton Owensby, Kansas State University (Donaldson); Drs. Walter F. Mueggler and James P. Blaisdell, USDA Forest Service, Intermountain Forest and Range Experiment Station (Cliff Lake); Mr. Jens C. Jensen, U.S. Department of the Interior, Bureau of Land Management (Laramie); and Mr. H. F. McCormick, USDA Forest Service, Deschutes National Forest (Cabin Lake). Field work at the Oregon shrub steppe study plots was partially supported by the Oregon State University Graduate Research Council; funds for computer analysis were generously supplied by the Oregon State University Computer Center. The University of Oklahoma Biological Station and the Oklahoma Biological Survey provided the facilities and atmosphere necessary to complete this paper. This is contribution No. 26 of the Behavioral Ecology Laboratory, Oregon State University.

#### APPENDIX: RECONSIDERATION OF THE SPATIAL OVERLAP INDEX

In the text, I suggested measuring interspecific overlap by an index, IO:

$$IO = \left[ \frac{\sum \left[ i \left( \frac{a_i}{\sum a_i} \right) \right]}{N} - M \right] \left[ \frac{1}{1 - M} \right] \quad (1)$$

where  $i = 1, 2, \dots, N$  species

$a_i$  = area (ha) occupied by  $i$  species

$N$  = total number of species present

$M$  = minimum value of  $\frac{a_i}{\sum a_i}$  recorded

The values of  $\frac{a_i}{\sum a_i}$  thus represent percentages of the total occupied area of a plot in which  $i$  species occur together.

While this paper was in press, my attention was drawn to several inadequacies of this index. Most important, the minimal value of the index is  $\frac{1}{N}$  when there is no spatial overlap among the species present. Thus, the range of index values is highly dependent upon the number of species present, substantially reducing the usefulness of the index as a comparative tool. Further, this index is generally unresponsive to situations in which interspecific overlap is low. A more useful (and simpler) overlap index is given by:

$$IO = \frac{\sum \left[ i \left( \frac{a_i}{\sum a_i} \right) \right]}{N} \quad (2)$$

where  $i = 2, 3, \dots, N$  species

$a_i$  = area (ha) co-occupied by  $i$  species (*i.e.*, by 2, 3, . . . ,  $N$  species)

$N$  = total number of species recorded

Areas occupied by only one species are thus ignored, which seems appropriate when one is interested in *interspecific* overlap. This index ranges in value from 0, when there is no spatial overlap among the species present, to 1, when spatial overlap among all species is complete (*i.e.*, when all of the area occupied is co-occupied by  $N$  species).

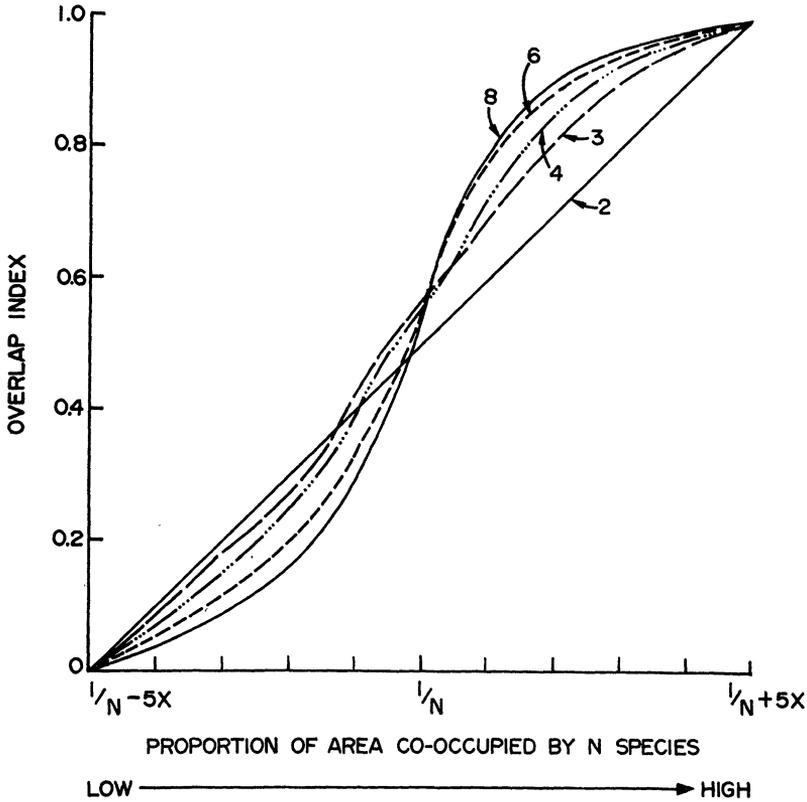


Fig. A-1.—Response of the overlap index (equation 2) to variations in the extent of spatial overlap between species. In these simulations, the distribution of spatial overlap was systematically varied from low overlap (most of the area occupied by one species) to high overlap (most of the area co-occupied by all  $N$  species), with even distribution of overlap areas among all categories intermediate. At the intermediate level, then, the area co-occupied by all  $N$  species =  $\frac{1}{N}$  of the total occupied area. Deviations toward lower or higher overlap were by increments of  $\frac{1}{N} \pm X, 2X, 3X, 4X$  and  $5X$  of the total occupied area, where  $X = 0.2(1 - \frac{1}{N})$

To examine the sensitivity of this index to variations in  $a_1$  and  $N$ , I simulated community situations for a range of species numbers and degrees of spatial packing. Figure A-1 presents the general results of these tests. The index is most sensitive to variations in the degree of spatial overlap at small values of  $N$ . As  $N$  increases, the discrimination of the index between varying degrees of low or of high interspecific overlap decreases. In other words, the sensitivity of the index to small changes in the degree of overlap (*i.e.*, variation in the values of  $\frac{a_i}{\sum a_i}$ ) increases with increasing  $N$  in the zone of intermediate degrees of overlap. As the number of species in a community increases, however, the index shows less ability to discriminate between similar degrees of overlap in communities with different numbers of species. Therefore, at values of  $N$  above eight or ten the effect of  $N$  on index values is negligible, most variation stemming from differences in the degree of overlap (the values of  $\frac{a_i}{\sum a_i}$ ).

In Table 2, I presented overlap index values for the various grassland and shrub-steppe breeding communities. Index values calculated using equation (2) rather than equation (1) are given in Table A-1, along with the values

TABLE A-1.—Values of IO (equation 2) and  $\frac{a_i}{\sum a_i}$  for North American grassland and shrub-steppe breeding avifaunas

Grassland type	Site name	Year censused	N	Values of $\frac{a_i}{\sum a_i}$ for $i =$						IO
				1	2	3	4	5	6	
Tall grass	Donaldson	1968	3	.58	.20	.22	....	....	....	0.35
	Elmdale	1967	3	.43	.46	.11	....	....	....	0.42
	Elmdale	1968	4	.32	.47	.18	.03	....	....	0.40
	Osage	1970	4	.31	.41	.25	.04	....	....	0.43
	$\bar{X}$ for Tall grass									
Mixed grass	Sandhills B	1968	5	.28	.34	.37	.02	....	....	0.37
	Sandhills A	1968	3	.65	.27	.08	....	....	....	0.26
	Cottonwood, grazed	1968	4	.14	.55	.29	.02	....	....	0.51
	Cottonwood, grazed	1970	3	.70	.30	....	....	....	....	0.20
	Cottonwood, lightly grazed	1970	6	.12	.33	.29	.14	.12	....	0.45
	$\bar{X}$ for Mixed grass									
Short grass	Laramie	1969	2	.28	.72	....	....	....	....	0.72
	Pawnee, heavy summer	1968	3	.75	.24	.01	....	....	....	0.16
		1969	3	.36	.56	.08	....	....	....	0.45
		1970	6	.19	.51	.18	.12	....	....	0.34
	Pawnee, heavy winter	1968	3	.52	.33	.15	....	....	....	0.37
		1969	4	.32	.41	.20	.07	....	....	0.43
		1970	3	.41	.57	.01	....	....	....	0.39
	Pantex, grazed	1970	4	.53	.38	.09	....	....	....	0.26
Pantex, ungrazed	1970	4	.19	.74	.07	....	....	....	0.42	

TABLE A-1 — CONTINUED

$\bar{X}$ for Short grass										0.39
Montane	Cliff Lake	1969	6	.27	.41	.24	.05	.02	.01	0.30
	Bridger	1970	4	.51	.40	.09	....	....	....	0.27
$\bar{X}$ for Montane										0.28
Palouse	Bison	1970	3	.66	.31	.03	....	....	....	0.24
	ALE 1	1971	4	.09	.35	.54	.03	....	....	0.61
	ALE 2	1971	3	.32	.47	.21	....	....	....	0.52
$\bar{X}$ for Palouse										0.46
Shrub steppe	Cabin Lake	1969	4	.31	.51	.18	....	....	....	0.39
	Steens Mountain	1967	4	.62	.34	.04	....	....	....	0.20
	Chewaucan	1967	5	.65	.33	.02	....	....	....	0.14
$\bar{X}$ for Shrub steppe										0.24

of  $\frac{a_i}{\sum a_i}$  for  $i = 1$  to six species (*i.e.*, the proportions of the total occupied area containing one, two, . . . , six species). This table corrects the values given earlier, but does not alter the basic conclusions: the extent of interspecific spatial overlap, while variable, shows no apparent relationship to species numbers, species diversity, total breeding densities, standing crop biomass, habitat heterogeneity, species dominance or annual precipitation. Regression tests also indicate the lack of any significant linear relationship between these variables and spatial overlap.

Frank Pitelka focused my attention on the errors in my initial attempts to define spatial overlap and inspired this reconsideration, and Kirk Steinhorst offered comments on the index.

## REFERENCES

- CLARK, P. J. AND F. C. EVANS. 1955. On some aspects of spatial pattern in biological populations. *Science*, **121**:397-398.
- CODY, M. L. 1966. The consistency of intra- and inter-continental grassland bird species counts. *Amer. Natur.*, **100**:371-376.
- . 1968. On the methods of resource division in grassland bird communities. *Ibid.*, **102**:107-147.
- . 1970. Chilean bird distribution. *Ecology*, **51**:455-464.
- GREIG-SMITH, P. 1964. Quantitative plant ecology, 2nd ed. Butterworths, London. 256 p.
- HILDÉN, O. 1965. Habitat selection in birds. *Ann. Zool. Fennici*, **2**:53-75.
- KARR, J. R. AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several new world areas. *Amer. Natur.*, **105**:423-435.
- KÜCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. *Amer. Geograph. Soc. Spec. Publ. No. 36*. Map + 154 p.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. *Publ. Nuttall Ornithol. Club No. 1*. 67 p.
- LEVINS, R. 1968. Evolution in changing environments. Some theoretical explorations. *Monogr. Pop. Biol. No. 2*. Princeton Univ. Press. 120 p.
- LLOYD, M. 1967. "Mean crowding." *J. Anim. Ecol.*, **36**:1-30.
- AND R. J. GHELARDI. 1964. A table for calculating the "equitability" component of species diversity. *Ibid.*, **33**:217-225.

- MACARTHUR, R. H. 1965. Patterns of species diversity. *Biol. Rev.*, **40**:510-533.
- AND R. LEVINS. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proc. Nat. Acad. Sci. U.S.A.*, **51**:1207-1210.
- AND ———. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Natur.*, **101**:377-385.
- AND J. MACARTHUR. 1961. On bird species diversity. *Ecology*, **42**:594-598.
- AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Amer. Natur.*, **100**:603-609.
- MORISITA, M. 1954. Estimation of population density by spacing method. *Mem. Fac. Sci. Kyushu Univ. Ser. E Biol.*, **1**:187-197.
- ORIANI, G. H. 1969. The number of bird species in some tropical forests. *Ecology*, **50**:783-801.
- PIANKA, E. R. 1967. On lizard species diversity: North American flatland deserts. *Ibid.*, **48**:333-351.
- PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York. 286 p.
- ROSENZWEIG, M. L. AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology*, **50**:558-572.
- SCHOENER, T. W. AND A. SCHOENER. 1971. Structural habitats of West Indian Anolis lizards. I. Lowland Jamaica. *Brevoria No. 368*. 53 p.
- TESTER, J. R. AND W. H. MARSHALL. 1961. A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota. *Occas. Pap. Minn. Mus. Natur. Hist.*, **8**:1-51.
- WHITTAKER, R. H. AND G. M. WOODWELL. 1972. Evolution of natural communities, p. 137-159. In: J. A. Wiens (ed.). *Ecosystem structure and function*. Oregon State Univ. Press, Corvallis.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.*, **8**:1-93.
- . 1973. Interterritorial habitat variation in Grasshopper and Savannah Sparrows. *Ecology*, **54**:877-884.
- . In press. Climatic instability and the "ecological saturation" of bird communities in grasslands. *Condor*.

SUBMITTED 3 JANUARY 1973

ACCEPTED 26 FEBRUARY 1973