Technical Report No. 63

AVIAN POPULATIONS AND PATTERNS OF HABITAT OCCUPANCY AT THE PAWNEE SITE, 1968-1969

John A. Wiens

Department of Zoology

Oregon State University

Corvallis, Oregon

GRASSLAND BIOME

U. S. International Biological Program

November 1970

ABSTRACT

This report analyzes the ecological relations of breeding birds on two 10.6 ha plots subjected to different grazing regimes at the Pawnee Site. Emphasis is given the relation of various population parameters (species diversity, density, interspecific spatial overlap, biomass) to vegetational heterogeneity, and the position of the Pawnee results in relation to a spectrum of grassland-shrubsteppe samples from other areas. In addition, characteristics of vegetation structure in areas occupied and not occupied by each of the breeding species are analyzed and are discussed in the context of interspecific differences, year-to-year changes, and responses to grazing treatment.

INTRODUCTION

This report presents the results of studies of breeding bird populations conducted in 1968 and 1969 on two plots in the Pawnee Study Area of the US IBP Grassland Biome investigation.

This work was part of a larger study of which the primary objective was to determine the patterns or "strategies" of avian community organization in simple, essentially one-layered habitat types (grassland and shrubsteppe). In addition, I sought to determine the relations of habitat features to inter-specific relations (primarily spatial) and the distribution, abundance, and behavior of individual species. These objectives can be framed as a series of questions; for example:

(i) What habitat features relate to variations in bird species diversity, or avian density, or trophic or spatial organization?

(ii) Is there any consistent structure or organization in grassland and shrubsteppe bird communities?

(iii) Can various features of grassland avifaunal organization be predicted from a knowledge of habitat features?

(iv) Do species associations exist in these habitat types, and, if so, do these result from ecological or behavioral interactions?

(v) What habitat features correlate with variations in the distribution and abundance of a species?

(vi) How variable are the patterns of habitat occupancy of grassland species, and what factors contribute to this?

(vii) How do patterns of habitat utilization, habitat occupancy, and spatial organization relate to habitat heterogeneity?

(viii) How stable are the ecological relations of grassland species and the structure of the avian communities, particularly in relation to the stability of habitat structure?

Other questions are, of course, possible, and little insight into those posed above can be obtained from investigations at Pawnee alone. The last question has received particular attention in the Pawnee studies and will continue to do so. The approach used in attempting to answer these questions is physiognomically based. The rationale for this approach has been discussed fully elsewhere (Wiens 1969).

METHODS

In this section I will briefly outline the methods employed in data collection; analytical methods will be covered, where appropriate, with the results.

Plot Design

Sampling sites were selected after an initial reconnaissance of each area. The prime requirements considered in plot location were: (i) the plot had to be relatively uniform in vegetational features, and representative of the area as a whole; (ii) it had to be a true grassland or shrubsteppe --areas including isolated trees or large shrubs, or thicketed gulleys, or streambeds, were thus excluded; and (iii) it had to be bordered by extensive areas of similar habitat. Where possible, topographic, edaphic, and logistic factors were also considered in determining plot location. It is important to note that plot selection was based solely on habitat features, not on the basis of the bird species present. In each 10.6 ha study plot, a sampling grid was laid out with grid points, marked with 1 m stakes, located at 200 ft (61 m) intervals. This grid served as the framework for the location of sampling sites for vegetation analysis and provided reference points for mapping the movements of individuals during territory estimation. While the grid stakes provided conspicuous elevated perches for the birds, there were no indications that the short-term presence of the stakes altered the species inventory or densities.

Milner and Hughes (1968) have pointed out the need to "buffer" intensive study plots with zones of similar habitat or vegetation. At all sites I studied, the sample plots were placed well within larger areas (at least 30 ha) of apparently homogenous or structurally similar habitat; in no case was there any evidence that "edge" bird species, or species responding to habitat transitions rather than to the grassland habitat itself, were present on the sample plots. Obviously, if one is to examine the nature of the ecological responses of birds to any habitat type such as grasslands, "alien" bird species, or species that "have no business being there," cannot be properly included; their presence in a plot is strongly suggestive that the plot is transitional, or that it is a mosaic of distinctly different habitat types or is immediately adjacent to different types. Thus, while useful in testing other ideas (e.g., "edge effect"), it has no utility in testing the responses to "pure" habitat conditions. Thus, the presence of a buffer zone in studies of this sort is exceedingly important.

Vegetation

I sampled vegetation in the plots following procedures developed in earlier work and described in detail elsewhere (Wiens 1969). Sampling sites (hereafter termed *sample units*) were located following a stratified random design, one unit within each of the 25 grid blocks derived from the 5 × 5 grid design. At each sample unit, four *sample points* were located at the four corners of a square with 2 m diagonals. The standard sampling intensity was thus 2.4 sample units/ha, or 9.6 sample points/ha.

At each sample point, measurements were recorded on the habitat features listed in Table 1, following the methods of Wiens (1969, p. 14-19). In addition, the diagonals of the square served to delimit four quarters, within each of which the type of the non-gramoid plant closest to the central point, its distance from the point, and its height were recorded (Cottam and Curtis 1956). The criticisms of this method raised by Risser and Zedler (1968) were not considered applicable to this study, where the derived values were used only as comparative or relative, rather than absolute values.

Habitat measures derived from this sampling regime can be used, not only to carefully document the characteristics of each study plot, but to evaluate habitat responses of the bird species as well. By superimposing a map of the area occupied by a species in a plot on a map of the sample unit locations, this area can be characterized by analyzing the included sample units. Areas not occupied by the species, or occupied by other species, can be characterized in a like manner. This study of habitat responses and ecological relationships is thus conducted through detailed "within plot" as well as "between plot" comparisons and analyses. This level of approach has been criticized by Sturman (1968), who champions regression analyses of entire plot values with species abundance variations. There is a rather considerable information loss in this latter approach, however, for the differences between areas occupied and those rejected by a species within a plot are ignored. Such differences may be crucial indicators of the exact nature of the ecological responses of the species, whether they be tempered solely by habitat features or modified by behavioral interactions with other species.

Population Estimation, Territory Mapping, and Spatial Overlap Analysis

At each study plot, the breeding territories of all individual males of each species occurring in the plot were mapped, with an accuracy of ±10 ft, following the "territory flush" technique developed in earlier work (Wiens 1969, p. 20-21). Only singing individuals (presumably males) were flushed. Territories of which only a portion occupied the study plot were mapped completely. Territory sites were determined using Bryan's (1943) modified acreage grid.

The territory mappings of a species, in addition to determining its pattern of plot occupancy, were used to determine the abundance and density of the species in the plot and to assess its spatial relationships with other species also occupying the plot. Population estimates were made simply by calculating the total number of territories and proportions of territories included within the plot boundaries. This value was then multiplied by a mating system conversion factor (2.0 for monogamous species, 2.5 for polygamous species) to obtain the number of individuals of the species occupying the 10.6 ha plot. While the estimation thus assumes that all territorial males are mated, general observations indicate that this is not an unrealistic assumption.

The territory mappings also yielded information on the nature and extent of spatial (horizontal) overlap between species; coupled with the habitat analyses; this can provide detailed insight into the nature of habitat occupancy in grasslands. The amount (ha) of overlap among all species pairs at site was determined from the overlaid maps using the acreage grip. This approach thus yielded area values for the portion of the study plot co-occupied by species A and B, occupied only by A, occupied only by B, or occupied by neither (totally 10.6 ha). Such data are amenable to 2^2 contingency table association tests (Cole 1949), which were made on all species pairings.

STUDY AREAS

Location and General Features

Two sites were selected for study at Pawnee. One (Pawnee HW) was located in the east 1/2 of section 22 (T 10N, R66W) and was subjected to heavy winter grazing; work on this plot was conducted 13-15 July 1968 and 3-5 July 1969. The second plot (Pawnee HS) was located on a pasture subjected to heavy summer grazing in the east 1/2 of section 23; this plot was sampled 15-16 July 1968 and 5-6 July 1969.

One major limitation of this study was that, in order to work in a broad range of grassland and shrubsteppe situations, little time could be spent at any single site. Thus, avian populations and habitat structure had to be sampled at one point along a phenological continuum. While the bird populations may undergo relatively little flux once breeding is underway, vegetation structure continues to change through the growing season. I have previously documented the extent of these changes on a single grassland site (Wiens 1969), and there is no doubt that the conditions birds encounter upon their arrival at a breeding area are vastly changed when they are feeding and fledging young. The habitat features instrumental in the process of habitat selection must be among those available at a time of the birds' arrival, but the adaptive significance of this selection may be predicated upon conditions which exist at the crucial phases of offspring production. For this reason, field work at the various sites was phenologically coordinated to examine each situation at the local peak of breeding activity. While intensive searches for nests were not made, many were discovered in the course of other observations; these nesting records (Appendix I) provide some indication of the breeding phase at the time of sampling.

Vegetation Features

In order to understand the ecology of the bird species breeding at Pawnee, it is necessary to consider both the avifauna and the plots themselves in the context of a broader range of grassland and shrubsteppe conditions.

Vegetationally, the Pawnee plots were intermediate with respect to heterogeneity and ground coverage of grass, woody, and unvegetated areas (Fig. 1). The overall height of the vegetation was comparatively low, and the proportion of plant biomass lying close to ground level was high (Fig. 2). Vertical vegetation density profiles (similar to the "foliage height profiles" of MacArthur and MacArthur 1961) also indicate different patterns of plant biomass distribution in the different situations (Fig. 3). This gradient of sites generally parallels a gradient of decreasing mean annual precipitation and decreasing annual primary production. Detailed vegetational characterizations of the Pawnee plots are given in Table 5.

The measure of heterogeneity used in this analysis was developed after much careful thought and many false starts. While there are many conventional statistical measures of heterogeneity or patchiness (e.g., Lloyd 1967, Greig-

Smith 1964, Clark and Evans 1955, Morisita 1954, Pielou 1969), it is difficult to obtain some measure that is roughly on the same scale and considers the same features that a small bird might use in assessing patchiness. Of the habitat features I measured, vegetation height-density distribution, litter depth, and the density of emergent vegetation (forbs, woody plants) seem likely possibilities, but scale is still a problem. The sampling design used here provided two horizontal scales on which the patchiness of these features could be considered: (i) Within Sample Unit analyses examined heterogeneity of measures from the four points within a sample unit; thus, patchiness could be detected on a horizontal scale of 2 m; and (ii) Between Sample Unit analyses used variation between values characterizing individual sample units as a measure of patchiness; here, the level of resolution is on the order of 65 m (the mean distance between sample units). Thus, habitat heterogeneity could be partitioned into potentially meaningful scales, rather than simply considering the degree of variation among all sample points as is usually done.

For a within sample unit measure of heterogeneity, some value related to the extent of variation among the four points of a unit is needed. The simplest approach, perhaps, is to use the mean of maximum-minimum differences within the unit as a heterogeneity index:

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

This index, however, assumes that the same degree of difference may have equal importance in vastly different habitat situations, e.g., for measures of vertical vegetation density, situations (a) and (b) below are considered equivalent, despite one's intuitive feeling that a

(a) 3-1 = 2 (b) 13-11 = 2

2 cm variation in vegetation height must be considerably less important and less apparent to a small bird in a 12 cm matrix than where the vegetation is only 2 cm deep. To correct this, differences may be adjusted by considering the mean value for each sample unit:

$$HI = \frac{\frac{\Sigma(\text{max-min})}{N}}{\frac{\Sigma\bar{x}}{N}} \qquad (1)$$

While this reduces the importance of equal differences at higher mean values (compare (c) and (d) below), some further adjustments may still be necessary, since the same index value may be obtained in different situations (c vs. e).

(c) $\frac{3-1}{2} = 1$ (d) $\frac{13-11}{12} = 0.17$ (e) $\frac{9-3}{6} = 1$

Again, intuitively, one must expect that a 6 cm variation in a 6 cm matrix is potentially more important than a 2 cm variation in a 2 cm matrix. Equation (1) may be further modified to account for this:

$$HI' = \frac{\frac{\Sigma(\text{max-min})}{N}}{\left(\frac{\Sigma\bar{x}}{N}\right)^{\frac{1}{2}}} \qquad (2)$$

Various values calculated according to equations (1) and (2) were calculated and from these, variation in vertical vegetation density calculated by equation (1) was selected as the most appropriate index of heterogeneity.

For a measure of heterogeneity at the between sample unit scale, the coefficient of variation (CV) of the sample unit means seems most realistic to me at this time. CV values are listed in Table 5, but these will not be further considered in this report.

RESULTS: AVIFAUNAL ORGANIZATION

Results of the avian censuses on the Pawnee plots are presented in Tables 2 and 3. From these data it is apparent that grazing seasonality has pronounced effects on the breeding avifauna of an area. Further, there are year-to-year differences on both plots, and these are more evident for some species than for others. McCowan's Longspurs and Lark Buntings, for example, appeared to maintain fairly stable breeding densities during the two years, while Horned Larks and Brewer's Sparrows increased in 1969. These results agree with those reported by Giezentanner and Ryder (1969) for these pastures at Pawnee.

It is difficult to discern patterns of avian community organization (if any exist) from results from only two sites. Therefore, I have compared the avifaunas of the Pawnee sites with those of a variety of other grassland areas in the analyses which follow.

Species Diversity

Cody (1966) has suggested that there is a certain consistency in the number of species and species diversity of breeding bird populations in grasslands. Given that species diversity shows some relationship to habitat complexity (MacArthur 1965), this is not surprising; and the relatively low diversity of grassland avifaunas, as compared with forests, agrees with theoretical expectations. Within the grassland-shrubsteppe habitat type, however, there may be considerable variation in the degree of vegetational complexity. The number of breeding bird species and the bird species' diversity for the 15 plots I studied are given in Fig. 4.

Diversity calculations were made according to the following (see Pielou 1966, 1969, Lloyd et al. 1968):

$$H = -\Sigma p_i \log_e p_i$$

where, p_i = specified variable for i^{th} species/specified variable for all species combined.

$$HMAX = \log_e S$$

where, S = the number of species

These data show that there was no direct relationship between variations in grassland structure and species diversity. Again, the range of possible values of H which can be obtained with only two to six species is small, and thus any distinct trends associated with habitat structure would be difficult to detect and quite easily obscured by other variables if they did exist. Note, however, that the values of H are close to the maximum attainable for the given number of species; thus, in general, there are not great disparities in species abundances.

Avian Density

Another aspect of avifaunal structure is the combined population density of breeding birds (individuals/unit area). Although Salt (1957, p. 376) has suggested that numbers of individuals is not a meaningful feature of avifaunal composition, this is somewhat akin to proposing that population size is an insignificant ecological parameter; that only the population biomass really matters. Individuals, if nothing else, are units of behavior, and their interactions may potentially be very significant in determining spatial relationships and, indirectly, standing crop.

The avian densities on the plots I visited (Fig. 5) were generally low, in comparison with more complex habitat types, and decreased slightly with increasing horizontal heterogeneity (and the associated trends in vegetation structure). The trend was far from distinct, however, and the rather large degree of site-to-site variation does not permit generalization.

Biomass

A third structural or organizational aspect of grassland bird communities, and one perhaps more directly related to productivity and energy flux in grassland ecosystems, is avian biomass. In these analyses, *Standing Crop Biomass* has been calculated for each plot according to the formula:

$$SCB = \Sigma (N_i W_i)$$

where, N_i = plot density of i^{th} species (indiv/100 ha)

W_i = mean net weight of i^{th} species (g)

Mean weights are listed in Appendix II. Standing Crop Biomass data are summarized in Fig. 6.

These measures show that, as the horizontal patchiness of habitats increases, the Standing Crop Biomass shows an overall decrease. Since the gradient of sites from tallgrass through mixed and shortgrass prairies into shrubsteppe is roughly one of decreasing annual primary production, secondary consumer biomass appears related to primary production in the expected manner.

In terms of competition and coexistence, these results are intriguing. If in fact the heterogeneity gradient parallels decreasing annual primary production, resources should be more restricted and, at the same time, less evenly distributed in the patchier shortgrass and shrubsteppe situations. Still, the degree of niche differentiation and species densities appears to be limited to a similar extent over a wide range of grassland and even shrubsteppe conditions; biomass, however, appears to change as productivity changes. This might be achieved either through an overall increase in the size of all species in the more productive sites or through variations in densities and proportions of small vs. large species. To examine these possibilities, species were classed according to their mean weight (Fig. 7). This analysis suggests that, in general, with the shift from shrubsteppe to shortgrass, the increase in Standing Crop Biomass is accompanied by a decrease in the proportion of small individuals and an increase in medium-sized (25-50 g) individuals and, generally, slightly higher densities. The increase in Standing Crop Biomass between shortgrass and tallgrass and mixed sites, on the other hand, appears to result primarily from a *replacement* of medium-sized species by large species (80-130 g; predominately meadowlarks).

Thus, while the restriction in alternative modes of resource partitioning may limit the number of species occupying grasslands, and the densities may be kept at a relatively low level by this combined with territory size limitations, size class replacements may constitute an effective response to productivity changes.

Salt (1957) has suggested that, in theory, *Consuming Biomass* may be a more appropriate measure of community structure than Standing Crop Biomass, since it is more directly related to the caloric intake of individuals under standard conditions (i.e., it adjusts for the lower metabolism per gram of large birds relative to small ones). Consuming Biomass values were calculated according to the equation of King and Farner (1961):

$$CB = \Sigma (n_i W_i^{0.744})$$

The effect of this analysis, other than to place the calculations on a supposedly more realistic metabolic footing, is to accentuate the relative importance of small individuals. Thus, plots with large components of small individuals have higher biomasses, relative to the other plots, than in the Standing Crop Biomass analysis--this effect is also indicated in the CB/SCB ratio. Other than this, the basic relationships (Fig. 6) remain unchanged.

Interspecific Spatial Overlap

If spatial overlap between species is any indication of ecological differentiation, it should be related to habitat patchiness: in relatively homogeneous cover, patch specialization must be restricted, and, while the greater productivity of these tallgrass sites might permit greater spatial overlap, one might alternatively expect a relatively high incidence of interspecific territorial exclusion or non-overlap (Orians and Willson 1964). While the territory mappings obtained in this study permit precise assessment of the degree of interspecific overlap, they do little to elucidate the underlying causes of these spatial patterns. A small amount of spatial overlap between two species occupying a site ("small" in relation to the overlap expected by chance, given the proportion of the site occupied by each species) may result either from active behavioral interaction (territorial exclusion) or from differential habitat responses to plot heterogeneity.

Similarly, a large degree of spatial association may be behaviorally (e.g., social attraction) or environmentally dictated. Distinguishing between these two sources of association or disassociation is difficult (see Pielou 1969 for a full discussion of theory and analytical methods), but some entry to the problem may be gained through analysis of habitat responses of the sites.

Several measures of the degree of interspecific overlap for the plots were derived from the territory mappings (Table 2). The *Overlap Index* was calculated in an attempt to adjust overlap values according to the extent of total plot occupancy and the number of species present. It was calculated by:

$$OI = \frac{\sum \left| i \left(\frac{a_i}{\Sigma a_i} \right) \right|}{N}$$

Where, i = 1, 2, . . ., N species

a_i = area (ha) co-occupied by i species

N = total number of species present

For example, in plot 12 (Pawnee HS 69), 86% of the plot was occupied; of this area, 36% was occupied by one species, 56% by two species, and 8% by all three species. Thus,

$$OI = \frac{1(36) + 2(56) + 3(8)}{3} = 0.575$$

The data on overlap in plot occupancy show no relationship to plot heterogeneity (Fig. 8), and with few exceptions, suggest that a remarkably uniform degree of interspecific overlap characterizes grassland and shrub-steppe systems. The implications of this must await further analysis.

Since overlap is determined by the patterns of territory occupancy, however, it should be expected that, as territory size has multiple determinants, so should overlap.

As indicated above, the extent of interspecific overlap on a plot is a manifestation of the territorial relations of species occupying the plot, and thus results from species associations or disassociations. One further analysis using the territory mappings directly evaluated the nature of the spatial associations between all species pairs on each plot. In this analysis 2×2 contingency tables were constructed, using the data on spatial overlaps between pairs of species (Table 4) and association indices calculated (Cole 1949, Pielou 1969, in press, Hurlbert 1969). As noted above, these associations or disassociations may be behaviorally or environmentally determined; it is apparent from this preliminary analysis that, whatever the causation, it is inconsistent and complex.

RESULTS: AVIAN HABITAT OCCUPANCY PATTERNS

Given the sorts of data obtained in this study, there are three basic levels at which one can analyze patterns of habitat occupancy by the species. The simplest involves noting trends in the presence or absence, or the population density, of a species through a range of sites in association with variations in habitat components. A variety of statistical aids may be employed in such an approach; Sturman (1968) used stepwise multiple regression in his analysis of chickadee (*Parus*) habitat relations in Washington. This level is perhaps the least discriminating, but is nonetheless useful, particularly where the range in habitat conditions is large. But in many areas, habitat occupancy by a species is not continuous over entire sample plots; this suggests that the species (i) is exercising some preference for certain portions of the range of habitat variation within the plot; or (ii) may be behaviorally and/or ecologically excluded from some areas by the presence of another species; or (iii) may occupy only a portion of the plot as a result of small population size, site tenacity, and/or historical "accidents"; or (iv) any or all of these operating together. It is exceedingly difficult to sort out these causes of habitat occupancy patterns (thus references to habitat "preferences" or habitat "selection" should be made with great care), but it is nonetheless obvious that the distinction between characteristics of occupied and unoccupied areas is worth making. Thus, at a somewhat more intense second level of analysis, species habitat occupancy patterns can be considered, using measures only from areas actually occupied by the species, data from all areas sampled combined. Finally, such occupied-unoccupied discrimination may be carried to a site-by-site level of analysis. Here, only results of the latter level of analysis on the Pawnee plots will be considered.

This analysis (Table 5, Fig. 9, 10) reveals differences (not yet subjected to statistical analysis) in the features of habitats occupied by different species at each site (for some reason, presently obscure to me, greatest in site 9, the 1968 sampling of the heavy-winter site), but the relationships of these differences are not consistent from site-to-site or from year-to-year. Some, but not all, of the yearly variation is undoubtedly due to changes in the vegetation substrate; some appear to be manifestations of habitat preferences (e.g., in Pawnee HS (Fig. 9B) where yearly differences in study plot means were slight, the species responded in quite different manners to at least these two aspects of grassland structure). These yearly shifts in occupancy pattern, only partially related to yearly shifts in the habitat as a whole, raise some intriguing points regarding environmental and avifaunal stability, niche stability, and competitive relationships. Superficial comparisons with the interspecific association test results (Table 4) disclose nothing that is not already apparent from the habitat occupancy results.

These data also give some indication of the "selectivity" of the bird species when confronted with a spectrum of habitat features. Some features seem to be particularly important in habitat responses at Pawnee (e.g., vertical density, effect height, heterogeneity), while others (e.g., litter depth and coverage, forb height) generally seem unimportant (in that occupied-unoccupied differences are slight). Particularly perplexing are situations in which a species occupies habitat conditions one year which the year before were apparently rejected (e.g., Fig. 9A, Horned Lark).

Some aspects of the population densities and habitat response patterns of individuals may be considered in greater detail. Horned Larks attained fairly high population densities on both plots, although population levels on both plots were roughly 1.5 times greater in 1969 (Table 3). While the increase in population density was accompanied by an increase in the extent of plot occupancy, there are no indications that this increase was related to changes in populations or associations with other species breeding on the plots (Table 4). There were no indications that Horned Larks "selected" or "rejected" any portions of the range of habitat conditions available on these plots, aside from the yearly shift in vertical density features already noted. There was less litter on the heavy-winter plot in 1969 than in 1968, but on the heavy-summer plot litter remained unchanged (but very sparse).

Brewer's Sparrows were roughly eight times more abundant on the heavy-winter plot in 1969 than in 1968. Again, there are no apparent relations with other bird species which might account for this change; examination of the vegetation data (Table 5) shows that vertical vegetation density was greater in this plot in 1969 and litter depth and forb density were less. Whether these shifts in vegetation structure were causally associated with the changes in population density is unclear from this analysis of these data.

Lark Buntings and Brewer's Sparrows occurred at relatively high densities only in the heavy-winter plot, while McCowan's Longspurs were restricted to the heavy-summer pasture. There were marked and consistent differences in the vegetation structure of these two habitats which may give some general indication of parameters important in the habitat responses of these species. In both years, vertical vegetation density, effective height, forb density, and emergent vegetation height were less in the sparser summer-grazed plot, while litter depth and forb coverage were less, and heterogeneity and bare ground coverage were greater in this plot in 1968 only. Lark Buntings showed a "preference" for areas with taller emergent vegetation in the winter-grazed plot and tended to occupy areas with generally lower vegetation stature than that characterizing this plot as a whole. In the range of conditions available in the summer-grazed plot, McCowan's Longspurs generally occupied areas with low vertical vegetation density.

ACKNOWLEDGMENTS

Drs. Don Jameson, George Van Dyne, Ronald Ryder, and Paul Baldwin, Colorado State University, provided assistance in the field studies at Pawnee. Field studies reported here represent a portion of a broader investigation of avian ecology in grassland ecosystems. Financial support for these studies was provided by the National Science Foundation (GB-6606); funds for computer programming and analysis were generously supplied by the Oregon State University Computer Center.

LITERATURE CITED

Amadon, D. 1943. Bird weights and egg weights. Auk, 60:221-234.

Bryan, M. M. 1943. Area determinations with the modified acreage grid. J. Forestry, 41:764-765.

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.

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30:411-424.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phyto-sociological sampling. Ecology 37:451-460.

Giezentanner, J. B. and R. A. Ryder. 1969. Avian distribution and population fluctuations at the Pawnee site. Grassland Biome, U.S. International Biological Program, Tech. Rep. No. 28. 29 p.

Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Butterworths, London. 256 p.

Hartmann, F. A. 1955. Heart weight in birds. Condor 57:221-238.

Hurlbert, S. H. 1969. A coefficient of interspecific association. Ecology 50:1-9.

Johnston, D. W. 1963. Heart weights of some Alaskan Birds. Wilson Bull. 75:435-446.

King, J. R. and D. S. Farner. 1961. Energy metabolism, thermoregulation and body temperature. *In* A. J. Marshall [ed.] Biology and comparative physiology of birds. Vol. 2. Academic Press, New York. p. 215-288.

Lloyd, M. 1967. "Mean crowding." J. Anim. Ecol. 36:1-30.

Lloyd, M., J. H. Zar, and J. R. Karr. 1968. On the calculation of information-theoretical measures of diversity. Amer. Midland Natur. 79:257-272.

MacArthur, R. H. 1965. Patterns of species diversity. Biol. Rev. 40:510-533.

MacArthur, R. H. and J. MacArthur. 1961. On bird species diversity. Ecology, 42:594-598.

Milner, C. and R. E. Hughes. 1968. Methods for the measurement of the primary production of grassland. IBP Handbook No. 6. Blackwell Sci. Publ., London.

Morisita, M. 1954. Estimation of population density by spacing method. Mem. Fac. Sci. Kyushu Univ. Series E. (Biol.). 1:187-197.

Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Pielou, E. C. 1966. Shannon's formula as a measurement of specific diversity and its use and misuse. Amer. Natur. 100:463-465.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley, New York. 286 p.

Pielou, E. C. 1970. The measurement of structure in animal communities. *In* J. A. Wiens [ed.] Ecosystem structure and function. Oregon State Univ. Press, Corvallis. (In press).

Risser, P. G. and P. H. Zedler. 1968. An evaluation of the grassland quarter method. Ecology 49:1006-1009.

Salt, G. W. 1957. An anlysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373-393.

Sturman, W. A. 1968. Description and analysis of breeding habitats of the chickadees *Parus atricapillus* and *P. rufescens*. Ecology 49:418-431.

Tordoff, H. B. and R. M. Mengel. 1956. Studies of birds killed in nocturnal migration. Univ. Kansas Publ. Mus. Natur. Hist. 10:1-44.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. No. 8. 93 p.

Table 1. Features measured in the characterization of grassland habitats.

Feature	Measurement
Vertical vegetation density	Number of vegetation contacts with a thin rod passed vertically through the vegetation, in decimeter height intervals
Light intensity	Percent of open sky intensity, recorded at 10 cm intervals from ground level upward
Litter depth	In cm
Litter coverage	Visual estimation of percent of ground covered in 3 cm radius about point
Litter composition	Estimated, using 9 categories
"Effective Height"	Height at which a narrow board is 90 percent obscured by vegetation within 3 cm of board; recorded by 5 cm height intervals
Percent coverage of physiognomic types	Calculated directly as frequency of occurrence, from presence/absence records at point samples
Horizontal density	Calculated for each non-gramoid physiognomic type, from distance measures in quarter sampling
Physiognomic type descriptions	See Wiens (1969, p. 14-19).

Table 2. Avian population parameters for the 15 study sites.

	Species Diversity				Density	Spatial Overlap			
	# Species	H'	H'MAX	H'/H' MAX	Birds/100ha	Species/point	% Plot Occupied	%Plot in Overlap	% Overlap % Occupied
9 Pawnee HW 68	5	1.118	1.609	0.69	231.3	1.40	78	37	0.47
10 Pawnee HS 68	3	0.960	1.099	0.87	203.3	1.36	77	19	0.25
11 Pawnee HW 69	4	1.135	1.386	0.82	332.5	1.96	89	60	0.67
12 Pawnee HS 69	3	0.915	1.099	0.83	260.7	1.72	86	55	0.64

	Spatial Overlap		Biomass			Biomass Diversity		
	Overlap Index	% Overlap/ Species	Study Crop (g/ha)	Consuming g/ha	CB/SCB	H'	H'MAX	H'/H' MAX
9 Pawnee HW 68	0.541	9.5	90.5	34.6	0.38	1.080	1.609	0.67
10 Pawnee HS 68	0.418	8.3	58.2	24.7	0.42	1.009	1.099	0.92
11 Pawnee HW 69	0.503	16.9	100.8	40.9	0.41	1.111	1.368	0.81
12 Pawnee HS 69	0.575	21.3	89.0	35.3	0.40	1.075	1.099	0.98

Table 3. Avian population census results for the four sites considered in this report.[a/]

Site	Species	Plot Census	Birds/ 100 ha	Area Occupied (ha)[b/]	Territory Size (ha)[c/]	Standing Crop Biomass (g/ha)	Consuming Biomass (g/ha)
Pawnee HW 68	Horned Lark	3.76	35.6	3.2 (30)	1.7 (2)	11.3	4.7
	Western Meadowlark	2.40	22.7	2.9 (27)	3.2 (1)	22.8	7.0
	Lark Bunting	15.63	148.0	6.5 (61)	1.1 (7)	52.7	21.1
	Grasshopper Sparrow	1.50	14.1	0.9 (8)	1.6 (1)	2.5	1.2
	Brewer's Sparrow	1.14	10.9	0.8 (7)	1.5 (1)	1.2	0.6
Pawnee HS 68	Horned Lark	7.08	66.9	3.3 (31)	1.3 (3)	21.3	8.8
	Lark Bunting	2.74	25.9	1.4 (13)	1.0 (2)	9.2	3.7
	McCowan's Longspur	11.68	110.5	6.3 (59)	1.1 (6)	27.7	12.2
Pawnee HW 69	Horned Lark	6.87	64.9	4.2 (40)	1.5 (2)	20.7	8.5
	Western Meadowlark	1.20	11.4	1.2 (11)	3.2 (1)	11.4	3.5
	Lark Bunting	17.48	165.3	10.6 (100)	1.0 (10)	58.9	23.6
	Brewer's Sparrow	9.62	90.9	5.3 (50)	1.1 (6)	9.8	5.3
Pawnee HS 69	Horned Lark	11.80	111.7	7.5 (71)	1.5 (6)	35.6	14.7
	Western Meadowlark	2.25	21.3	1.9 (18)	-	21.3	6.6
	McCowans' Longspur	13.50	127.7	6.4 (60)	1.0 (5)	32.1	14.0

a/ Scientific names of all species are given in Appendix 2.

b/ Percent of total plot in parentheses.

c/ N in parentheses.

Table 4. Matrices of spatial overlap among species. For each species, the area occupied and the area held in overlap with each of the other species occurring on the plot are given (in ha) to the right and above the diagonal. Below the diagonal are given association indices (Cole's "C", 1949) for all species pairings. * = p<.05; ** = p<.01.

9 Pawnee HW 68

	Lark Bunting	Horned Lark	Brewer's Sparrow	Western Meadowlark	Grasshopper Sparrow
Area Occupied:	6.5	3.2	0.8	2.9	0.9
Lark Bunting		2.3	0.2	1.7	0.6
Horned Lark	+0.27		0.1	0.6	0.8
Brewer's Sparrow	-0.59*	-0.59		0.0	0.0
Western Meadowlark	-0.04	-0.31	-1.00**		0.0
Grasshopper Sparrow	+0.14	+0.84*	-1.00**	-1,00**	

10 Pawnee HS 68

	McCowan's Longspur	Horned Lark	Lark Bunting
Area Occupied:	6.3	3.3	1.4
McCowans's Longspur		1.7	0.1
Horned Lark	-0.13		0.6
Lark Bunting	-0.88**	+0.17	

11 Pawnee HW 69

	Horned Lark	Brewer's Sparrow	Lark Bunting	Western Meadowlark
Area Occupied	4.2	5.3	8.5	1.2
Horned Lark		2.2	3.7	1.0
Brewer's Sparrow	+0.05		4.8	0.8
Lark Bunting	+0.35*	+0.56**		1.1
Western Meadowlark	+0.77**	+0.31*	+0.64*	

Table 4. (Continued).

12 Pawnee HS 69			
	Western Meadowlark	Horned Lark	McCowan's Longspur
Area Occupied:	1.9	7.5	6.3
Western Meadowlark		0.8	1.9
Horned Lark	-0.09		4.7
McCowan's Longspur	+0.98**	+0.12	

Table 5. Habitat features of areas occupied (O) and not occupied (U) by species breeding on the two Pawnee sites in 1968 and 1969. Values given are means, with standard deviations in parentheses.

PAWNEE HEAVY-WINTER 1968

Species		N (points)	Total Vertical Density	Vertical Density 0-10 cm	Maximum Interval[a/]	Effective Height (cm)	Litter Depth (cm)	Litter Coverage	Litter Composition
Total		100	2.30(1.53)	2.14(1.31)	0.96(0.51)	1.12(1.58)	0.47(0.50)	42.0(37.9)	1.7(1.6)
Horned Lark	O	32	2.22(1.36)	2.19(1.31)	0.91(0.39)	0.94(1.41)	0.52(0.55)	42.2(39.9)	1.6(1.6)
	U	68	2.34(1.61)	2.19(1.32)	0.99(0.56)	1.21(1.66)	0.44(0.48)	41.9(37.3)	1.8(1.6)
Western Meadowlark	O	20	2.15(1.69)	1.90(1.45)	0.95(0.61)	1.45(1.79)	0.41(0.34)	43.8(36.2)	1.9(1.7)
	U	80	2.34(1.49)	2.20(1.28)	0.96(0.49)	1.04(1.53)	0.48(0.54)	41.6(38.6)	1.7(1.5)
Lark Bunting	O	64	2.06(1.26)	2.03(1.26)	0.89(0.40)	0.92(1.48)	0.42(0.48)	38.3(38.0)	1.6(1.5)
	U	36	2.72(1.86)	2.33(1.39)	1.08(0.65)	1.47(1.72)	0.56(0.53)	48.6(37.3)	2.0(1.6)
Grasshopper Sparrow	O	8	2.00(1.51)	2.00(1.51)	0.88(0.35)	0.50(0.93)	0.43(0.50)	34.4(42.1)	1.5(1.9)
	U	92	2.33(1.53)	2.15(1.30)	0.97(0.52)	1.17(1.62)	0.47(0.51)	42.7(37.7)	1.7(1.5)
Brewer's Sparrow	O	12	1.92(2.02)	1.58(1.31)	0.83(0.84)	0.50(0.90)	0.37(0.57)	25.0(33.7)	1.1(1.2)
	U	88	2.35(1.46)	2.22(1.30)	0.98(0.45)	1.20(1.64)	0.48(0.49)	44.3(38.0)	1.8(1.6)

a/ Maximum decimeter interval of vertical point recording vegetation contacts.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1968

		No. Points where Litter Depth (cm) =					Light Reduction[b/]		Density[c/]			Total Non-gramoid Height (cm)[c/]
		0	0.5	1	2	3	0-10	10-20	Forb	Cactus	Woody	
Total		35	47	14	3	1	2	-	196	52	-	12.5 (8.8)
Horned Lark	O	12	11	7	2	-	2	-	268	105	-	12.8 (10.6)
	U	23	36	7	1	1	2	1	174	37	-	12.2 (7.9)
Western Meadowlark	O	7	10	3	-	-	2	-	275	92	-	12.5 (8.4)
	U	28	37	11	3	1	2	-	183	46	-	12.4 (9.0)
Lark Bunting	O	26	27	10	0	1	-	-	262	49	-	12.7 (9.6)
	U	9	20	4	3	-	6	1	122	54	-	11.9 (7.3)
Grasshopper Sparrow	O	4	1	3	-	-	-	-	628	90	-	8.7 (5.2)
	U	31	46	11	3	1	2	1	181	50	-	12.8 (9.0)
Brewer's Sparrow	O	6	5	0	1	-	-	-	149	30	-	12.1 (7.8)
	U	29	42	14	2	1	2	1	205	57	-	12.5 (9.0)

b/ Percent reduction of open sky intensity at decimeter height intervals, from point samples.

c/ From quarter method measurements.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1968

		Within-Sample Unit Differences (Max-Min)					CV Sample Unit Mean Vertical Density[d/]
		Vertical Density	Litter Depth	Effective Height	Forb Distance	Heterogeneity Index	
Total		3.20(1.38)	0.9(0.7)	3.0(1.8)	14.4(9.7)	1.39	0.32
Horned Lark	O	2.88(0.99)	1.1(0.4)	2.3(1.9)	15.0(11.9)	1.30	0.32
	U	3.35(1.54)	0.8(0.7)	3.3(1.7)	14.1(8.9)	1.43	0.33
Western Meadowlark	O	3.60(1.82)	0.7(0.4)	3.8(1.6)	14.0(10.8)	1.67	0.31
	U	3.10(1.29)	0.9(0.7)	2.8(1.8)	14.5(9.7)	1.32	0.33
Lark Bunting	O	2.63(0.81)	0.9(0.6)	2.6(1.9)	14.7(10.9)	1.28	0.33
	U	4.22(1.64)	0.9(0.7)	3.7(1.6)	13.9(7.9)	1.55	0.26
Grasshopper Sparrow	O	3.50(0.71)	1.0(0.0)	2.0(0.0)	10.0(7.1)	1.75	0.18
	U	3.17(1.44)	0.9(0.7)	3.0(1.9)	14.8(9.9)	1.36	0.33
Brewer's Sparrow	O	4.33(2.31)	1.0(0.9)	1.3(1.2)	16.7(7.6)	2.25	0.49
	U	3.05(1.21)	0.9(0.7)	3.2(1.8)	14.1(10.1)	1.30	0.31

d/ Coefficient of variation of the sample unit means for total vertical vegetation density.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1968

		Percent Cover[e/]									
		Grass	Forb	Woody	Cactus	Bare	Rock	VN Grass	N Grass	cl Grass	e Grass
Total		82	10	0	4	14	0	71	21	23	69
Horned Lark	O	84	3	0	9	12	0	71	25	25	71
	U	80	13	0	1	14	0	69	19	21	67
Western Meadowlark	O	75	15	0	5	20	0	70	20	20	70
	U	83	8	0	3	12	0	70	21	23	68
Lark Bunting	O	81	6	0	3	14	0	69	14	15	68
	U	83	16	0	5	13	0	71	33	35	69
Grasshopper Sparrow	O	87	0	0	0	12	0	50	50	50	50
	U	81	10	0	4	14	0	72	18	20	70
Brewer's Sparrow	O	66	8	0	0	33	0	58	16	16	58
	U	84	10	0	4	11	0	72	21	23	70

e/ From point samples: VN = very narrow leaves; N = narrow leaves; cl = distributed in small clumps; e = distributed in an even matrix.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1968

Species		N (points)	Total Vertical Density	Vertical Density 0-10 cm	Maximum Interval[a/]	Effective Height (cm)	Litter Depth (cm)	Litter Coverage	Litter Composition
Total		100	1.80(1.34)	1.78(1.32)	0.81(0.44)	0.51(1.11)	0.19(0.32)	17.0(27.7)	0.7(1.1)
Horned Lark	O	40	1.70(1.28)	1.68(1.29)	0.83(0.45)	0.33(0.97)	0.16(0.24)	14.4(23.9)	0.6(0.9)
	U	60	1.87(1.38)	1.85(1.34)	0.80(0.44)	0.63(1.18)	0.21(0.36)	18.8(30.1)	0.8(1.2)
Lark Bunting	O	20	1.70(1.53)	1.70(1.53)	0.70(0.47)	0.55(1.28)	0.15(0.24)	16.3(28.4)	0.6(0.9)
	U	80	1.83(1.30)	1.80(0.43)	0.84(0.43)	0.50(1.07)	0.20(0.33)	17.2(27.7)	0.8(1.2)
McCowan's Longspur	O	76	1.75(1.35)	1.72(1.31)	0.80(0.46)	0.54(1.18)	0.20(0.34)	17.1(27.8)	0.8(1.2)
	U	24	1.96(1.33)	1.96(1.33)	0.83(0.38)	0.42(0.83)	0.15(0.23)	16.7(28.2)	0.6(0.9)

a/ Maximum decimeter interval of vertical point recording vegetation contacts.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1968

		No. Points where Litter Depth (cm) =					Light Reduction[b/]		Density[c/]			Total Non-gramoid Height (cm)[c/]
		0	0.5	1	2	3	0-10	10-20	Forb	Cactus	Woody	
Total		67	30	2	1	-	-	-	52	43	-	9.9(4.5)
Horned Lark	O	27	13	-	-	-	-	-	47	38	-	10.6(4.7)
	U	40	17	2	1	-	-	-	57	46	-	9.5(4.4)
Lark Bunting	O	14	6	-	-	-	-	-	95	51	-	11.0(5.0)
	U	53	24	2	1	-	-	-	46	41	-	9.7(4.4)
McCowan's Longspur	O	50	23	2	1	-	-	-	45	47	-	10.5(4.6)
	U	17	7	-	-	-	-	-	79	26	-	8.1(3.8)

b/ Percent reduction of open sky intensity at decimeter height intervals, from point samples.

c/ From quarter method measurements.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1968

		Within-Sample Differences (Max-Min)				Heterogeneity Index	CV Sample Unit Mean Vertical Density[d/]
		Vertical Density	Litter Depth	Effective Height	Forb Distance		
Total		2.80(1.26)	0.5(0.4)	1.6(1.6)	7.3(4.2)	1.56	0.35
Horned Lark	O	2.70(1.34)	0.4(0.2)	1.1(1.7)	7.5(4.3)	1.59	0.37
	U	2.87(1.25)	0.6(0.5)	1.9(1.6)	7.1(4.4)	1.53	0.34
Lark Bunting	O	2.60(1.52)	0.3(0.3)	1.8(2.1)	8.0(4.5)	1.53	0.66
	U	2.85(1.23)	0.6(0.4)	1.5(1.5)	7.1(4.3)	1.56	0.26
McCowan's Longspur	O	2.89(1.24)	0.6(0.4)	1.6(1.8)	7.5(4.4)	1.65	0.31
	U	2.50(1.38)	0.3(0.3)	1.3(1.0)	6.7(4.1)	1.28	0.45

d/ Coefficient of variation of the sample unit means for total vertical vegetation density.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1968

		Percent Cover[e/]									
		Grass	Forb	Woody	Cactus	Bare	Rock	VN Grass	N Grass	cl Grass	e Grass
Total		79	1	0	4	20	1	78	5	4	79
Horned Lark	O	80	0	0	2	20	0	80	5	5	80
	U	78	1	0	5	20	1	76	3	3	76
Lark Bunting	O	70	0	0	0	30	0	70	5	5	70
	U	81	1	0	5	17	1	81	3	4	80
McCowan's Longspur	O	77	0	0	3	21	1	77	5	6	76
	U	83	4	0	4	16	0	83	0	0	83

e/ From point samples: VN = very narrow leaves; N = narrow leaves; cl = distributed in small clumps; e = distributed in an even matrix.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1969

Species		N (points)	Total Vertical Density	Vertical Density 0-10 cm	Maximum Interval[a/]	Effective Height (cm)	Litter Depth (cm)	Litter Coverage	Litter Composition
Total		100	2.40(1.98)	2.28(1.69)	0.88(0.50)	1.01(2.71)	0.13(0.31)	12.0(29.0)	0.6(1.4)
Horned Lark	O	56	2.36(2.19)	2.18(1.78)	0.86(0.59)	1.23(3.21)	0.13(0.32)	12.1(30.9)	0.5(1.4)
	U	44	2.46(1.70)	2.41(1.58)	0.91(0.36)	0.73(1.87)	0.14(0.31)	11.9)26.7)	0.6(1.3)
Western Meadowlark	O	4	1.00(2.00)	1.00(2.00)	0.50(1.00)	1.25(2.50)	0.19)0.39)	12.5(25.0)	0.5(1.0)
	U	96	2.44(1.94)	2.33(1.67)	0.90(0.47)	1.00(2.73)	0.13(0.32)	12.0(29.2)	0.6(1.4)
Lark Bunting	O	88	2.42(2.01)	2.28(1.68)	0.89(0.51)	0.90(2.63)	0.14(0.33)	13.1(30.3)	0.6(1.4)
	U	12	2.25(1.82)	2.25(1.82)	0.83(0.39)	1.83(3.22)	0.04(0.14)	4.2(14.4)	0.2(0.9)
Brewer's Sparrow	O	48	2.56(2.00)	2.42(1.58)	0.94(0.48)	0.96(3.05)	0.15(0.33)	14.1(31.3)	0.7(1.6)
	U	52	2.25(1.97)	2.15(1.79)	0.83(0.51)	1.06(2.37)	0.12(0.31)	10.1(26.8)	0.4(1.1)

a/ Maximum decimeter interval of vertical point recording vegetation contacts.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1969

		No. Points where Litter Depth (cm) =					Light Reduction b/		Density c/			Total Non-gramoid Height (cm) c/
		0	0.5	1	2	3	0-10	10-20	Forb	Cactus	Woody	
Total		84	6	10	-	-	3	-	160	69	73	10.2(6.2)
Horned Lark	O	48	2	6	-	-	3	-	145	69	85	11.2(7.1)
	U	36	4	4	-	-	3	-	181	70	55	9.1(4.6)
Western Meadowlark	O	3	1	-	-	-	-	-	361	-	1082	17.5(6.5)
	U	81	5	10	-	-	3	-	157	69	63	9.9(6.0)
Lark Bunting	O	73	5	10	-	-	3	-	154	69	79	10.5(6.2)
	U	11	1	-	-	-	5	-	202	76	25	8.3(5.8)
Brewer's Sparrow	O	39	4	5	-	-	3	-	110	74	68	10.5(5.9)
	U	45	2	5	-	-	3	-	223	63	77	10.0(6.5)

b/ Percent reduction of open sky intensity at decimeter height intervals, from point samples.

c/ From point samples: VN = very narrow leaves; N = narrow leaves; cl = distributed in small clumps; e = distributed in an even matrix.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1969

		Within-Sample Unit Differences (Max-Min)					
		Vertical Density	Litter Depth	Effective Height	Forb Distance	Heterogeneity Index	CV Sample Unit Mean Vertical Density[d/]
Total		3.92(2.16)	0.5(0.4)	3.3(4.5)	8.4(6.2)	1.63	0.38
Horned Lark	O	4.36(2.50)	0.5(0.5)	3.9(5.4)	8.9(6.6)	1.85	0.40
	U	3.36(1.57)	0.5(0.4)	2.6(3.1)	7.7(6.1)	1.37	0.36
Western Meadowlark	O	6.00(-)	0.5(-)	5.0(-)	15.0(-)	6.00	-
	U	3.83(2.16)	0.5(0.5)	3.3(4.6)	8.1(6.2)	1.57	0.37
Lark Bunting	O	4.05(2.26)	0.5(0.5)	3.2(4.5)	8.6(5.6)	1.67	0.35
	U	3.00(1.00)	0.2(0.3)	4.0(5.3)	6.7(11.6)	1.33	0.68
Brewer's Sparrow	O	4.17(2.59)	0.6(0.4)	3.7(5.4)	6.3(5.3)	1.63	0.29
	U	3.69(1.75)	0.4(0.5)	3.0(3.7)	10.4(6.6)	1.64	0.46

d/ Coefficient of variation of the sample unit means for total vertical vegetation density.

Table 5. (Continued).

PAWNEE HEAVY-WINTER 1969

		Percent Cover[e/]									
		Grass	Forb	Woody	Cactus	Bare	Rock	VN Grass	N Grass	cl Grass	e Grass
Total		79	4	5	3	16	1	76	15	15	76
Horned Lark	O	75	1	5	5	23	0	71	16	16	71
	U	84	6	4	0	6	2	81	13	13	81
Western Meadowlark	O	25	0	0	0	75	0	25	0	0	25
	U	81	4	5	3	13	1	78	15	15	78
Lark Bunting	O	78	3	5	2	15	1	76	13	13	76
	U	83	8	0	8	16	0	75	25	25	75
Brewer's Sparrow	O	81	2	8	4	12	0	79	16	16	79
	U	76	5	1	1	19	1	73	13	13	73

e/ From point samples: VN = very narrow leaves; N = narrow leaves; cl = distributed in small clumps; e = distributed in an even matrix.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1969

Species		N (points)	Total Vertical Density	Vertical Density 0-10 cm	Maximum Interval[a/]	Effective Height (cm)	Litter Depth (cm)	Litter Coverage	Litter Composition
Total		100	2.05(1.55)	2.01(1.47)	0.79(0.43)	0.38(0.93)	0.18(0.30)	20.7(35.0)	0.7(1.2)
Horned Lark	O	76	2.07(1.38)	2.09(1.38)	0.83(0.38)	0.33(0.87)	0.19(0.31)	23.7(36.9)	0.8(1.3)
	U	24	1.92(2.02)	1.75(1.73)	0.67(0.57)	0.54(1.21)	0.13(0.30)	11.5(26.6)	0.4(0.9)
Western Meadowlark	O	28	1.82(1.42)	1.82(1.42)	0.75(0.44)	0.21(0.63)	0.13(0.26)	12.5(25.0)	0.5(0.9)
	U	72	2.14(1.60)	2.08(1.49)	0.81(0.43)	0.44(1.06)	0.19(0.32)	24.0(37.9)	0.8(1.3)
McCowan's Longspur	O	68	1.96(1.37)	1.96(1.37)	0.81(0.40)	0.26(0.68)	0.15(0.29)	16.5(30.4)	0.6(1.1)
	U	32	2.25(1.88)	2.13(1.68)	0.75(0.51)	0.63(1.36)	0.22(0.33)	29.7(42.3)	0.9(1.4)

a/ Maximum decimeter interval of vertical point recording vegetation contacts.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1969

		No. Points where Litter Depth (cm) =					Light Reduction[b/]		Density[c/]			Total Non-gramoid Height (cm)[c/]
		0	0.5	1	2	3	0-10	10-20	Forb	Cactus	Woody	
Total		72	21	7	-	-	-	-	42	23	-	7.2(2.8)
Horned Lark	O	52	19	5	-	-	-	-	36	15	-	6.9(2.8)
	U	20	2	2	-	-	-	-	83	98	-	8.1(2.3)
Western Meadowlark	O	22	5	1	-	-	-	-	41	23	-	8.4(2.7)
	U	50	16	6	-	-	-	-	43	23	-	6.7(2.7)
McCowan's Longspur	O	51	13	4	-	-	-	-	42	24	-	7.3(2.8)
	U	21	8	3	-	-	-	-	43	20	-	7.0(2.8)

b/ Percent reduction of open sky intensity at decimeter height intervals, from point samples.

c/ From quarter method measurements.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1969

		Within-Sample Unit Differences (Max-Min)					
		Vertical Density	Litter Depth	Effective Height	Forb Distance	Heterogeneity Index	CV Sample Unit Mean Vertical Density[d/]
Total		3.08(1.44)	0.5(0.4)	1.4(1.5)	4.6(2.5)	1.50	0.38
Horned Lark	O	2.63(1.07)	0.5(0.3)	1.1(1.4)	5.0(2.4)	1.26	0.39
	U	4.50(1.64)	0.4(0.5)	2.2(1.6)	3.3(2.6)	2.34	0.37
Western Meadowlark	O	2.86(1.21)	0.4(0.3)	0.9(1.1)	2.9)2.7)	1.57	0.45
	U	3.17(1.54)	0.5(0.4)	1.6(1.6)	5.3(2.1)	1.48	0.36
McCowan's Longspur	O	2.71(1.05)	0.5(0.4)	0.9(1.0)	4.1(2.6)	1.38	0.41
	U	3.88(1.89)	0.5(0.5)	2.3(1.9)	5.6(1.8)	1.72	0.34

d/ Coefficient of variation of the sample unit means for total vertical vegetation density.

Table 5. (Continued).

PAWNEE HEAVY-SUMMER 1969

		Percent Cover[e/]									
		Grass	Forb	Woody	Cactus	Bare	Rock	VN Grass	N Grass	cl Grass	e Grass
Total		78	1	0	3	19	1	78	0	0	78
Horned Lark	O	82	0	0	1	17	0	82	0	-	82
	U	62	4	0	8	25	4	62	0	-	62
Western Meadowlark	O	75	0	0	3	21	3	75	0	0	75
	U	79	1	0	2	18	0	79	0	0	79
McCowan's Longspur	O	80	0	0	2	17	1	80	0	0	80
	U	71	3	0	3	21	0	71	0	0	71

e/ From point samples: VN = very narrow leaves; N = narrow leaves; cl = distributed in small clumps; e = distributed in an even matrix.

APPENDIX I

Breeding Records of Grassland Bird Species, 1968-1969

9 Pawnee HW 68

Lark Bunting	1	13 July 68	4 pin-feathered young
		15 July 68	young fledged
	2	13 July 68	4 eggs
		15 July 68	4 eggs
	3	14 July 68	3 eggs
		15 July 68	4 eggs
Horned Lark		14 July 68	3 downy young
		15 July 68	3 downy young

10 Pawnee HS 68

McCowan's Longspur		15 July 68	4 4-5 day-old young
		16 July 68	4 4-5 day-old young
Mourning Dove		15 July 68	2 eggs
		16 July 68	2 eggs; deserted
Nighthawk		16 July 68	2 well-feathered young

11 Pawnee HW 69

Lark Bunting	1	4 July 69	4 eggs
		5 July 69	4 eggs
	2	4 July 69	1 egg; deserted
	3	4 July 69	1 egg
		5 July 69	1 egg; female incubating
	4	4 July 69	5 eggs
Brewer's Sparrow	1	4 July 69	2 eggs
		5 July 69	3 eggs
	2	4 July 69	empty
		5 July 69	1 egg
Nighthawk		4 July 69	2 eggs
		5 July 69	2 eggs

12 Pawnee HS 69

no nests discovered

APPENDIX II

Mean Wet Weight (g) of Grassland Species Considered in this Study

Species	Mean Weight, W	$W^{0.744}$	Number of Specimens	Area	Source
Horned Lark (*Eremophila alpestris*)	31.9	13.15	49	Texas, S.D.	Wiens (IBP)
Western Meadowlark (*Sturnella neglecta*)	100.4	30.86	23	Texas, S.D.	Wiens (IBP)
Lark Bunting (*Calamospiza melanocorys*)	35.6	14.26		Colorado	P. Baldwin (personal communication)
Grasshopper Sparrow (*Ammodramus savannarum*)	17.6	8.44	16	Eastern U.S.	Hartman 1955, Norris & Johnston 1958, Tordoff & Mengel 1956
Brewer's Sparrow (*Spizella breweri*)	10.8	5.87	12	Oregon	R. Moldenhauer (personal communication)
McCowan's Longspur (*Rhynchophanes mccowani*)	25.1	11.00		Colorado	R. Ryder (personal communication)

FIGURE TITLES

Fig. 1. Percent ground coverage of grass, woody vegetation, and bare (unvegetated) ground, as recorded from point samples in relation to plot heterogeneity. Sites 9 and 11 are Pawnee heavy-winter, 1968-1969; sites 10 and 12 are Pawnee heavy summer, 1968-1969. For the other plots, diamond = tallgrass; square = mixed grass; circle = shortgrass; star = montane; and triangle = shrubsteppe.

Fig. 2. Vegetation height with respect to plot heterogeneity. "Mean maximum interval" is the mean highest decimeter interval recording vegetation contacts at point samples; "Percent in 0-10 cm Interval" refers to the proportion of all vegetation contacts occurring within the first decimeter height interval. The Pawnee sites are indicated.

Fig. 3. Vegetation height-density profiles for 15 grassland and shrub-steppe sites in North America. For each site, the mean number of vegetation contacts in each decimeter height interval of a rod passed vertically through the vegetation is recorded. The Pawnee sites are numbered as in Fig. 1.

Fig. 4. Bird species diversity as related to plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

Fig. 5. Avian density as related to plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

Fig. 6. Avian standing crop biomass vs. plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

Fig. 7. Partitioning of biomass by size classes in 15 grassland and shrub-steppe study plots. For each stand, the first vertical bar is calculated according to individuals, the second according to biomass. For each, the proportion of the total contributed by small (<25g) species (black), medium (25-50g) species (cross-hatched), and large (>80g) species (white) is presented. The Pawnee sites are numbered as in Fig. 1.

Fig. 8. The extent of interspecific spatial overlap (in a horizontal plane), as measured by an overlap index (see text), as related to plot heterogeneity. The Pawnee sites are indicated.

Fig. 9. Mean effective vegetation height vs. mean total vertical vegetation density at the Pawnee study plots. Capital letters denote mean values for areas occupied by each species; lower case letters denote mean values for unoccupied areas; dots mean values for the entire study plots. Values for each sampling are enclosed by lines. Key to study plots:

9 = Pawnee HW68	10 = Pawnee HS68
11 = Pawnee HW69	12 = Pawnee HS69

Fig. 9. (Continued).

Key to species:

H = Horned Lark	G = Grasshopper Sparrow
W = Western Meadowlark	B = Brewer's Sparrow
L = Lark Bunting	M = McCowan's Longspur

Fig. 10. Mean grass coverage vs. vegetational heterogeneity at the Pawnee study plots. Symbols as in Fig. 9.

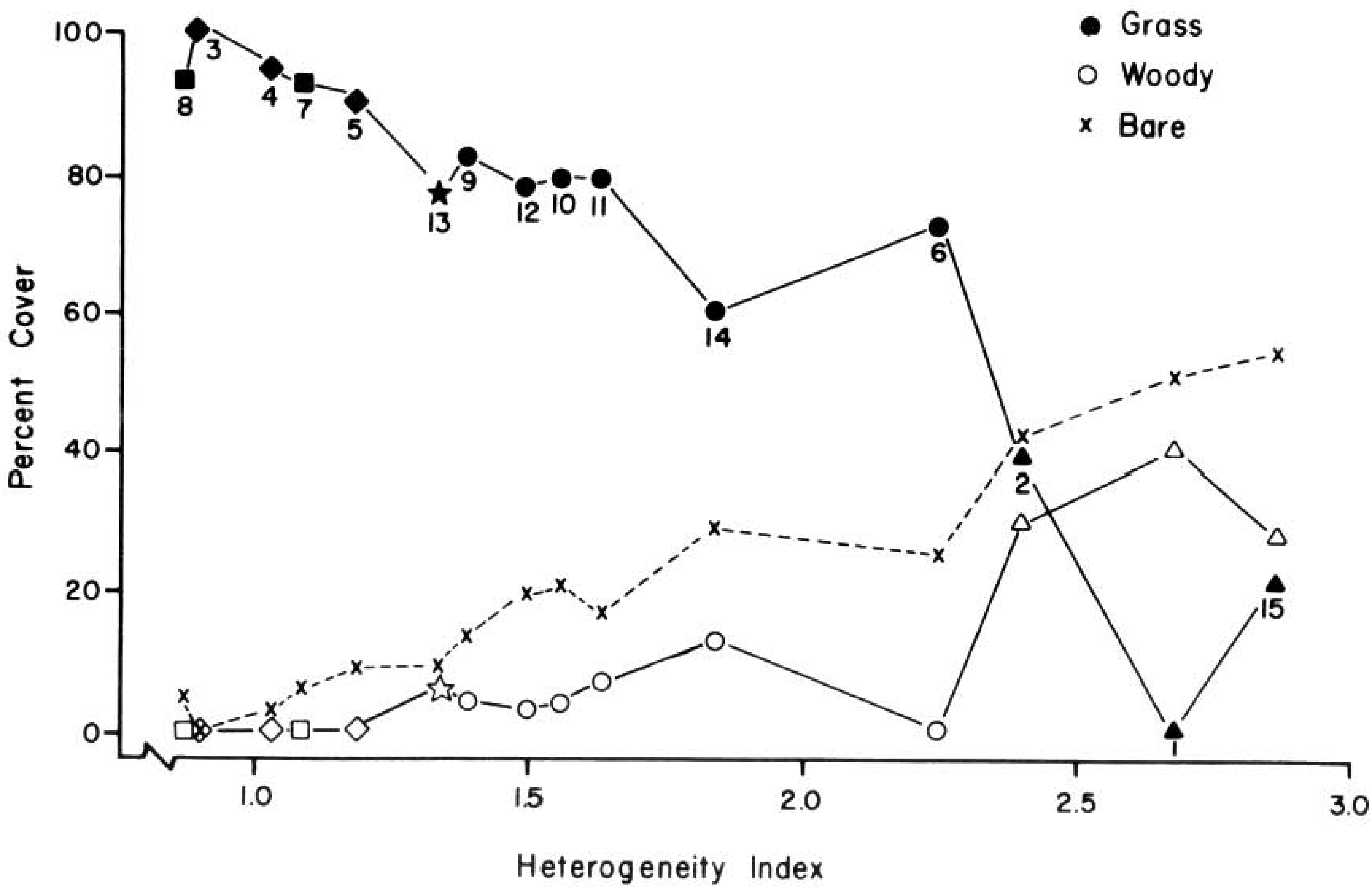

Fig. 1. Percent ground coverage of grass, woody vegetation, and bare (unvegetated) ground, as recorded from point samples in relation to plot heterogeneity. Sites 9 and 11 are Pawnee heavy-winter, 1968-1969; sites 10 and 12 are Pawnee heavy summer, 1968-1969. For the other plots, diamond = tallgrass; square = mixed grass; circle = shortgrass; star = montane; and triangle = shrubsteppe.

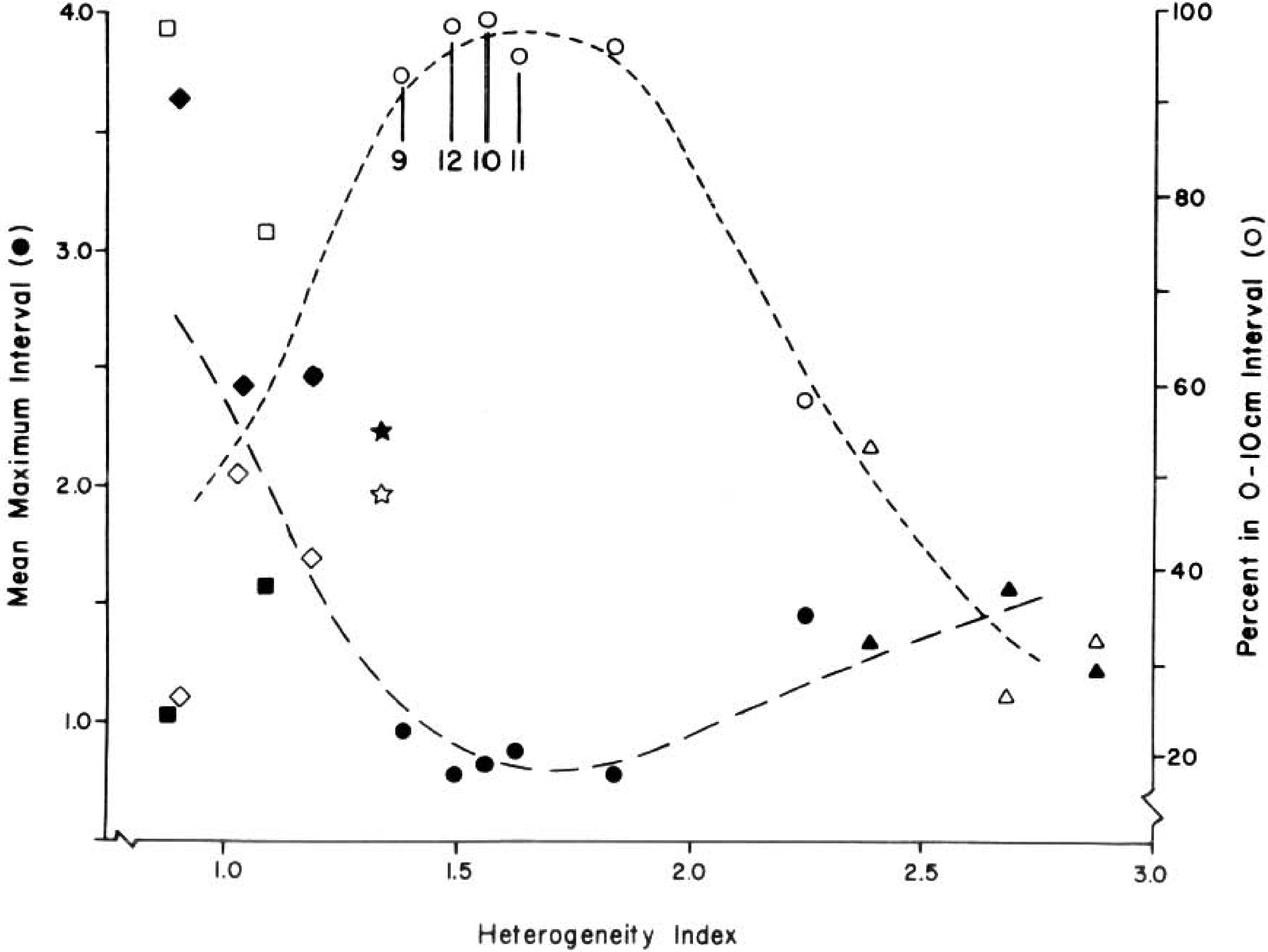

Fig. 2. Vegetation height with respect to plot heterogeneity. "Mean maximum interval" is the mean highest decimeter interval recording vegetation contacts at point samples; "Percent in 0-10 cm Interval" refers to the proportion of all vegetation contacts occurring within the first decimeter height interval. The Pawnee sites are indicated.

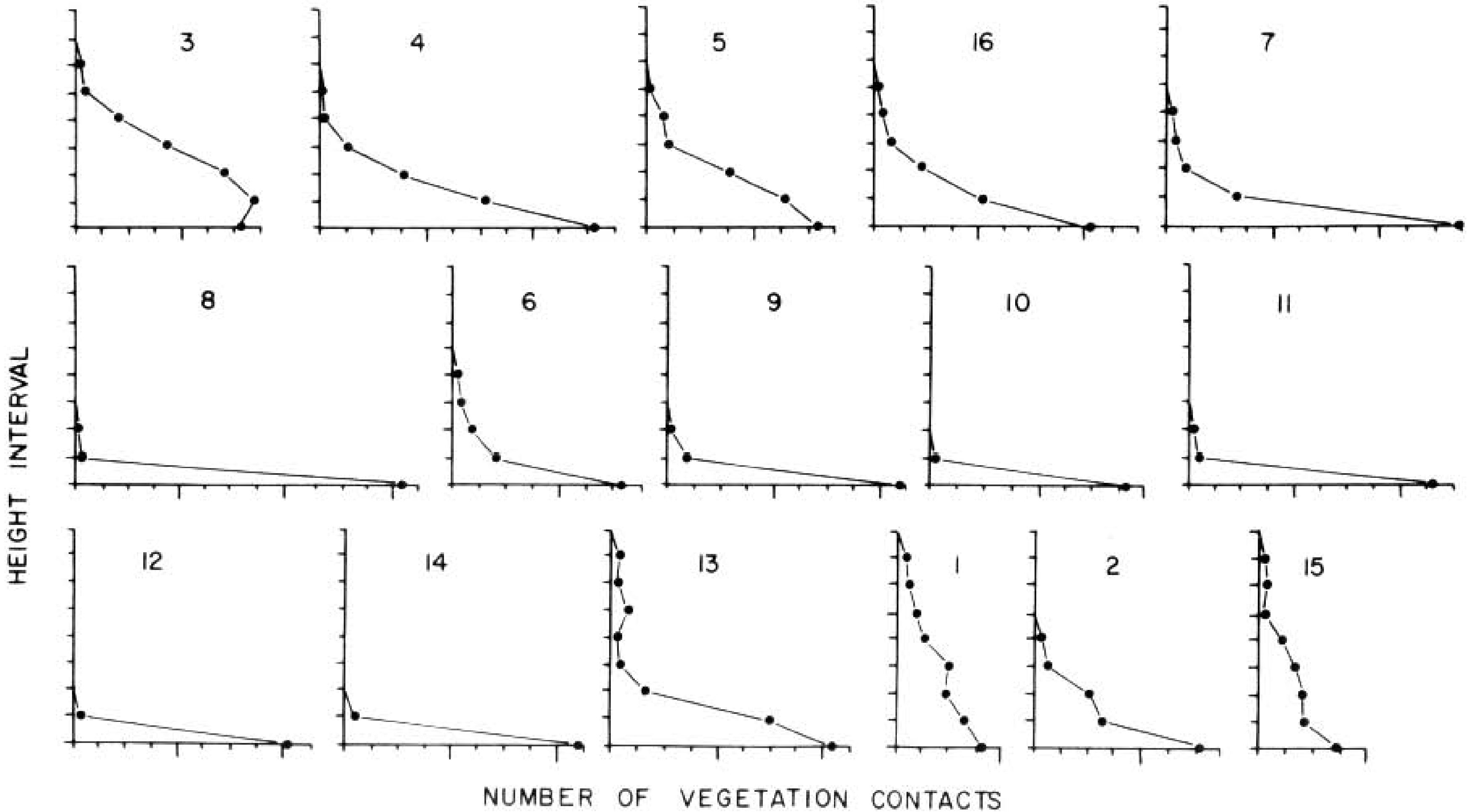

Fig. 3. Vegetation height-density profiles for 15 grassland and shrub-steppe sites in North America. For each site, the mean number of vegetation contacts in each decimeter height interval of a rod passed vertically through the vegetation is recorded. The Pawnee sites are numbered as in Fig. 1.

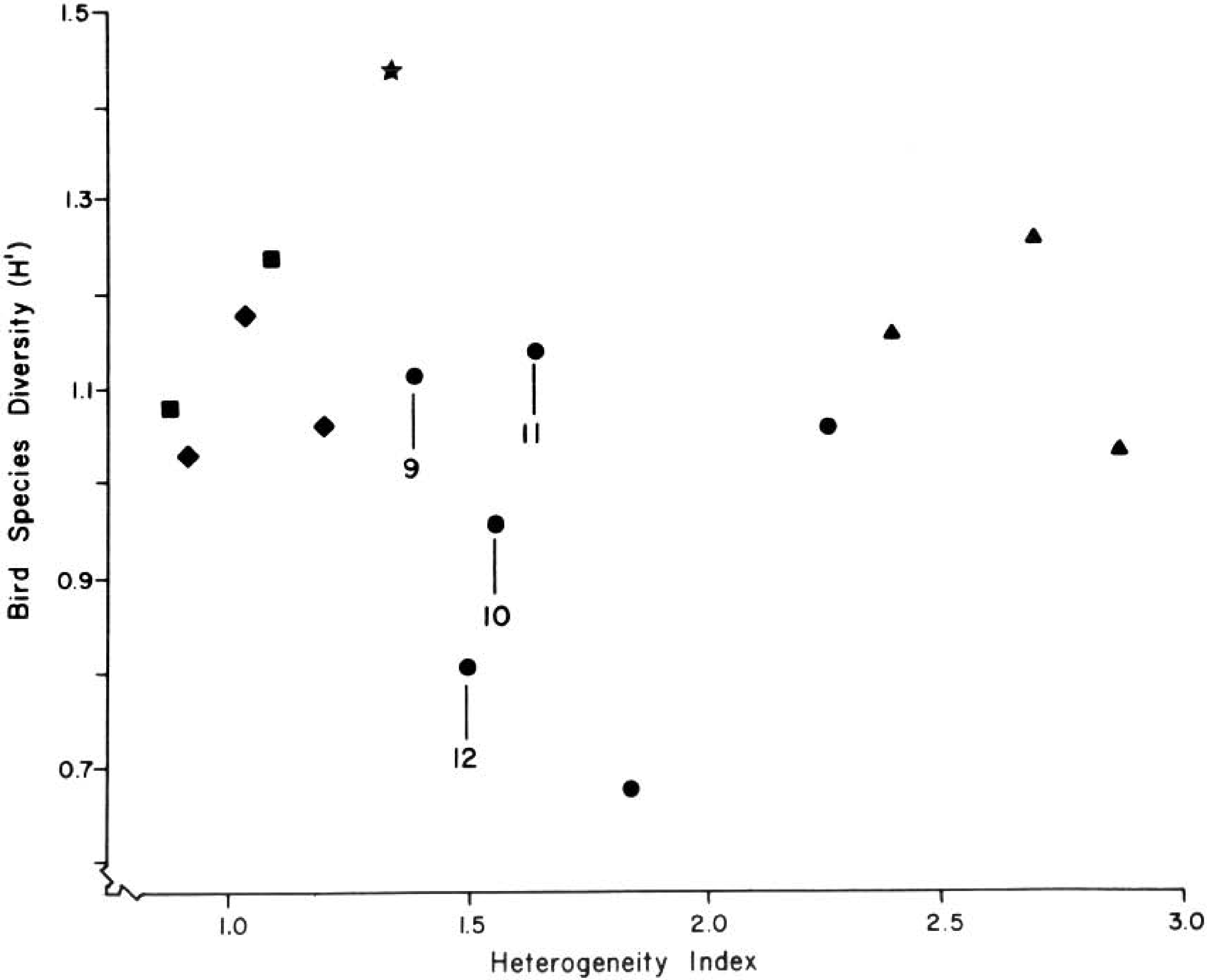

Fig. 4. Bird species diversity as related to plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

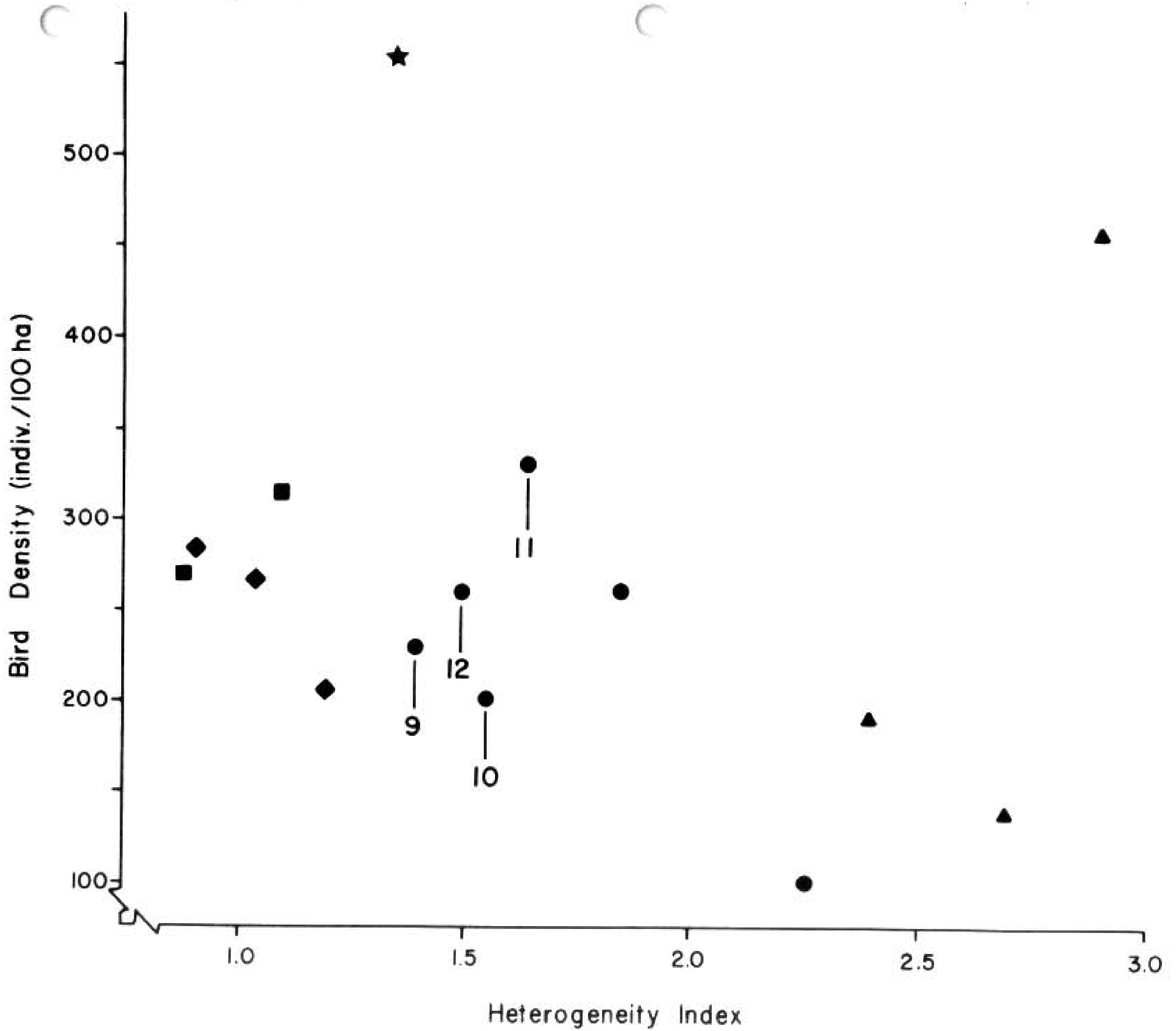

Fig. 5. Avian density as related to plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

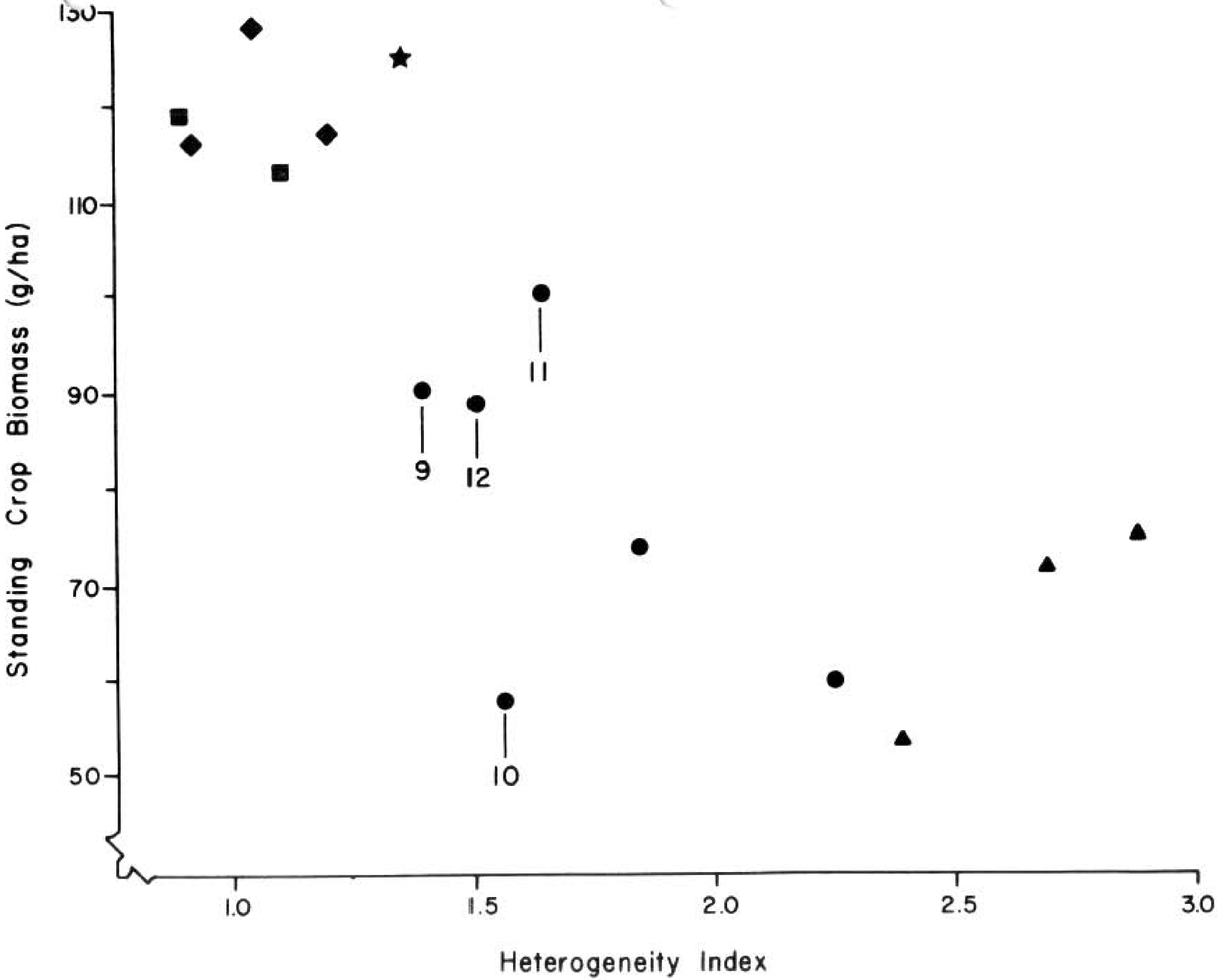

Fig. 6. Avian standing crop biomass vs. plot heterogeneity. Plot symbols as in Fig. 1. The Pawnee sites are indicated.

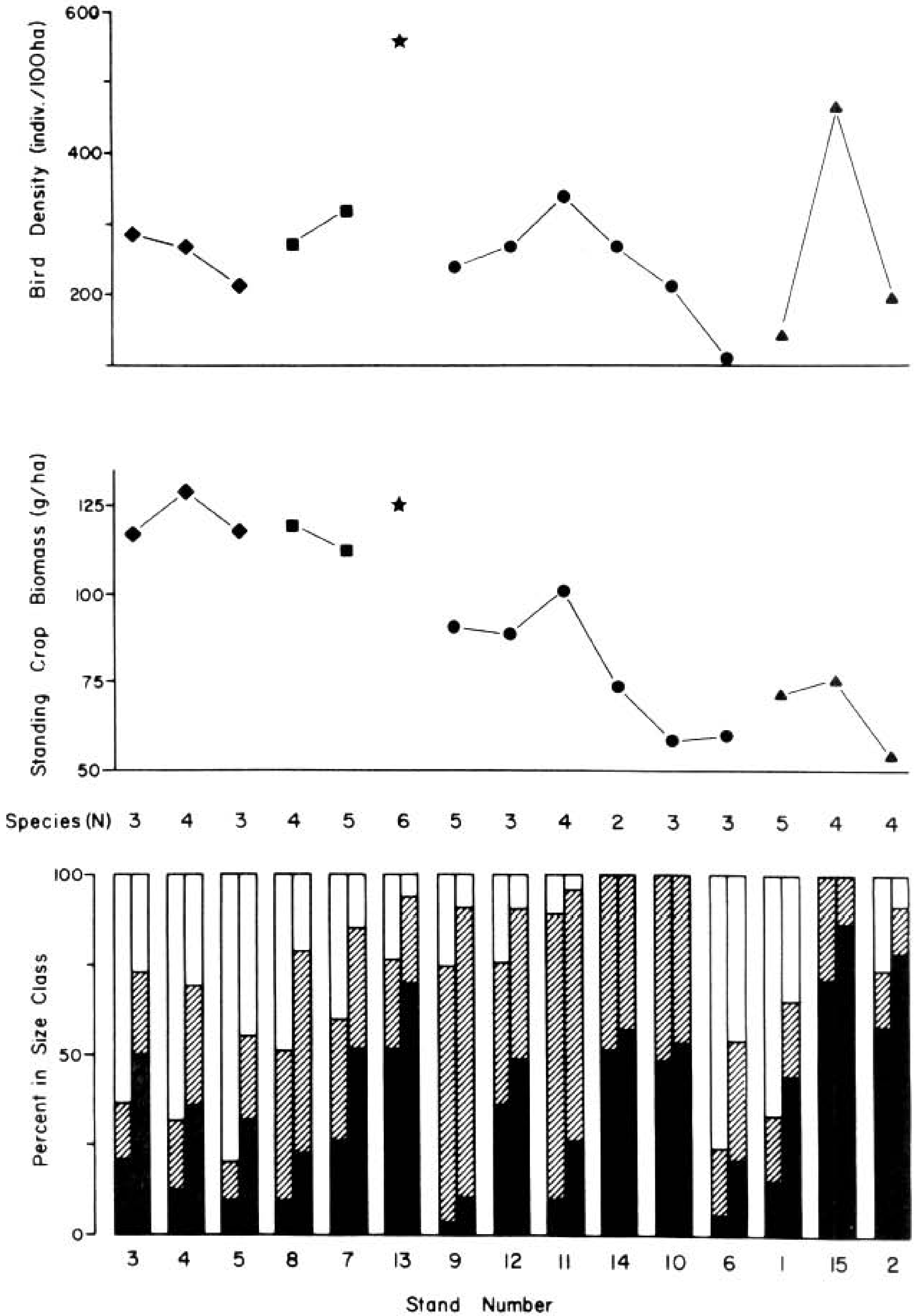

Fig. 7. Partitioning of biomass by size classes in 15 grassland and shrub-steepe study plots. For each stand, the first vertical bar is calculated according to individuals, the second according to biomass. For each, the proportion of the total contributed by small (<25g) species (black), medium (25-50g) species (cross-hatched,), and large (>80g) species (white) is presented. The Pawnee sites are numbered as in Fig. 1.

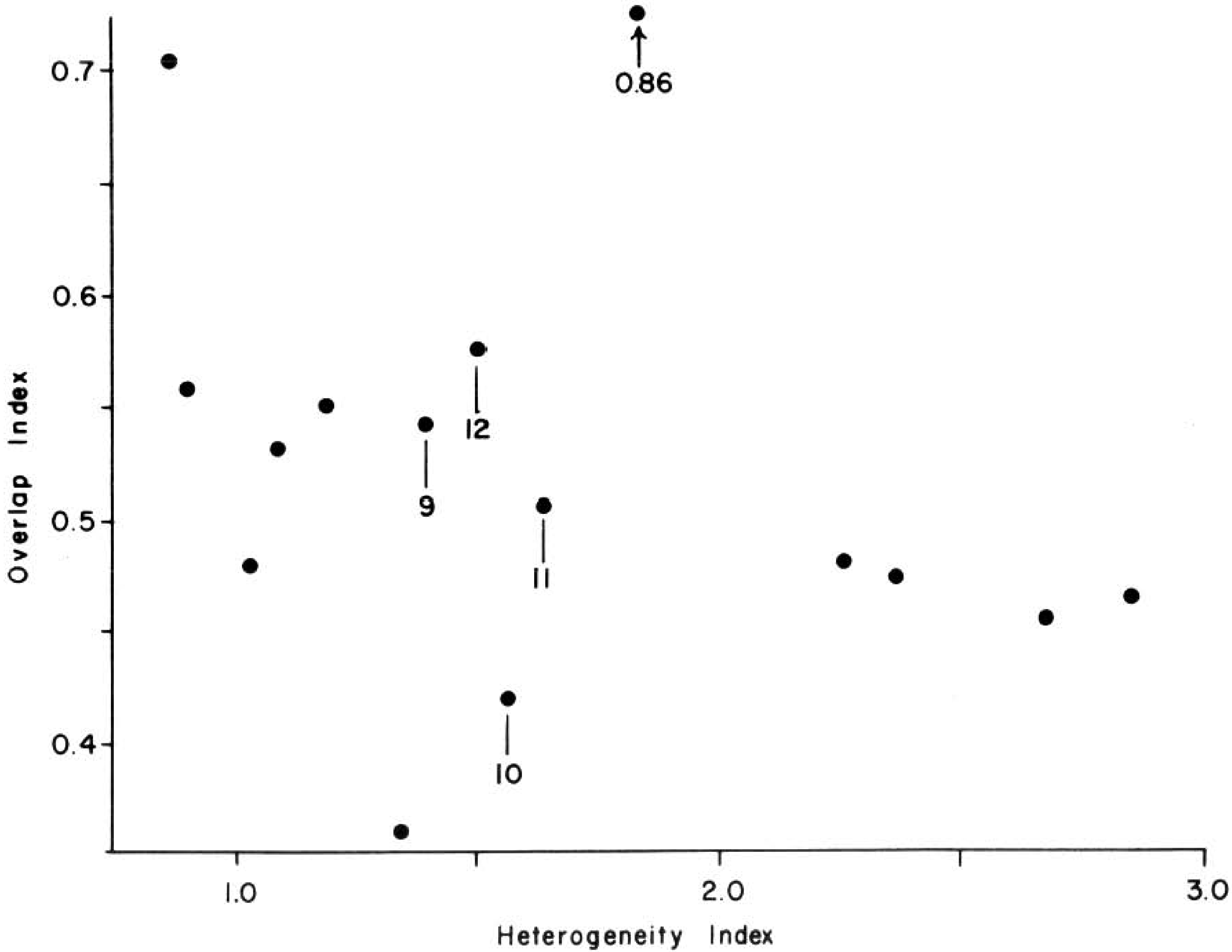

Fig. 8. The extent of interspecific spatial overlap (in a horizontal plane), as measured by an overlap index (see text), as related to plot heterogeneity. The Pawnee sites are indicated.

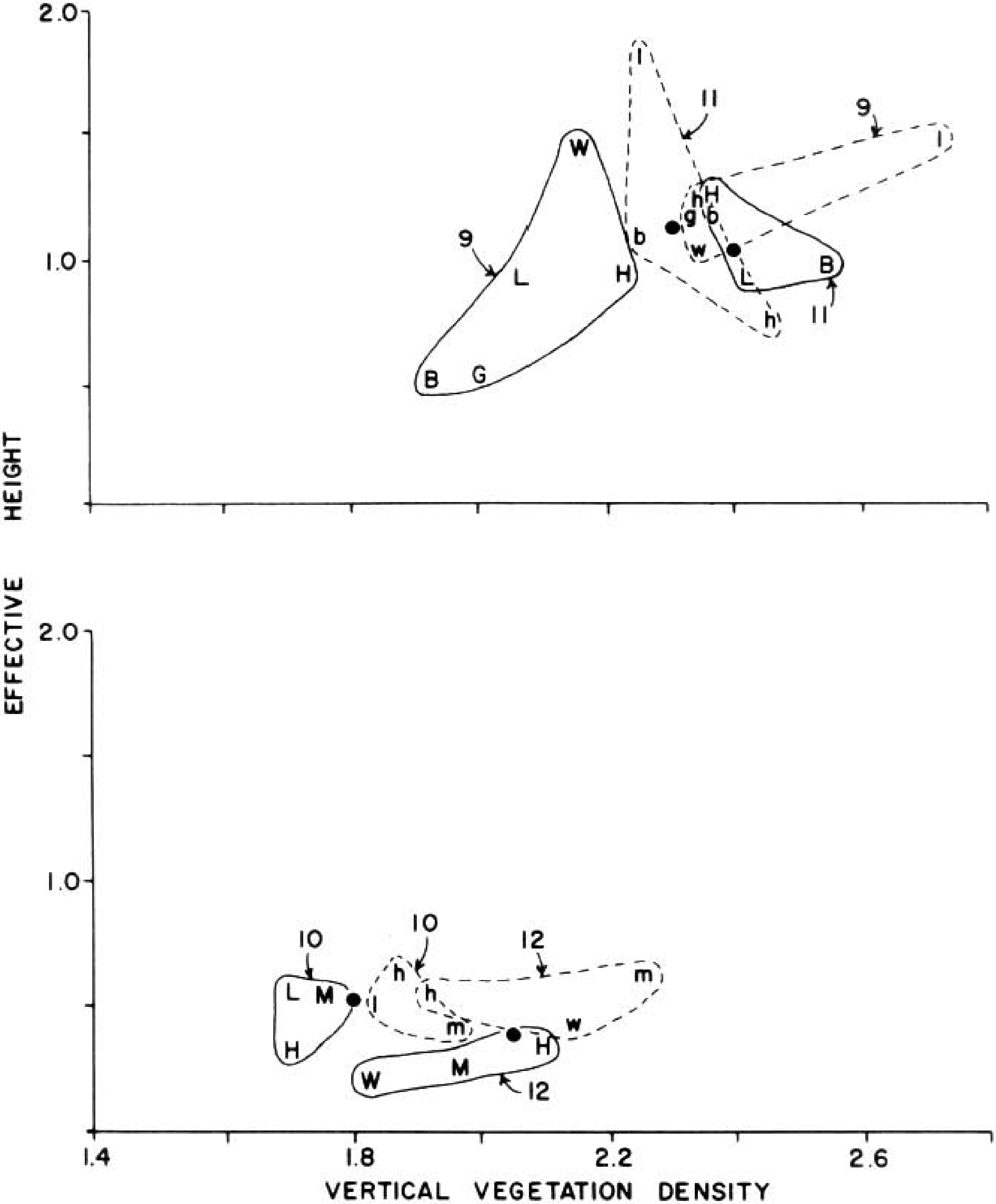

Fig. 9. Mean effective vegetation height vs. mean total vertical vegetation density at the Pawnee study plots. Capital letters denote mean values for areas occupied by each species; lower case letters denote mean values for unoccupied areas; dots mean values for the entire study plots. Values for each sampling are enclosed by lines. Key to study plots: 9 = Pawnee HW68, 10 = Pawnee HS68, 11 = Pawnee HW69, 12 = Pawnee HS69. Key to species: H = Horned Lark, W = Western Meadowlark, L = Lark Bunting, G = Grasshopper Sparrow, B = Brewer's Sparrow, and M = McCowan's Longspur.

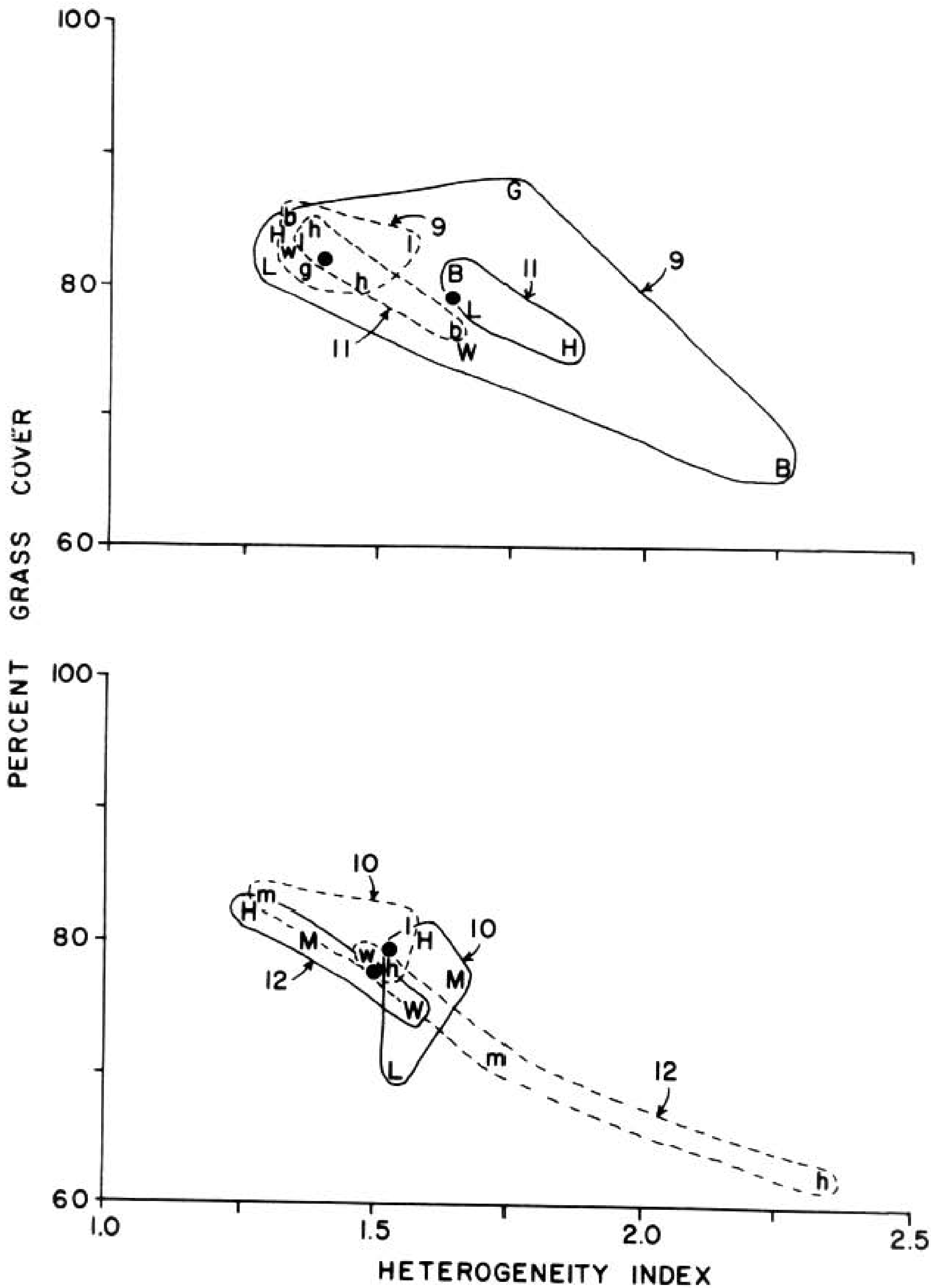

Fig. 10. Mean grass coverage vs. vegetational heterogeneity at the Pawnee study plots. Symbols as in Fig. 9.