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ECOLOGICAL RELATIONSHIPS AMONG GRASSLAND BIRDS DURING WINTER

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ECOLOGICAL RELATIONSHIPS AMONG GRASSLAND BIRDS DURING WINTER

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

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JOSEPH ANTHONY GRZYBOWSKI

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ECOLOGICAL RELATIONSHIPS AMONG

GRASSLAND BIRDS DURING WINTER

APPROVED BY

DISSERTATION COMMITTEE

PREFACE

This dissertation is prepared in the formats of three manuscripts to be submitted to refereed journals. The first paper will be submitted to the *Condor*, the second to *Ecology*, and the third to the *Auk*.

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POPULATION STRUCTURE IN GRASSLAND BIRD COMMUNITIES DURING WINTER.

JOSEPH A. GRZYBOWSKI

ABSTRACT.--Mid-winter populations of open-grassland birds were examined at 20 sites of varied grazing pressure and cultivation practices in Oklahoma and Texas from December 1975 through January 1979. The number of non-raptorial bird species observed on all sites was 23. Of these, only 14 were present on more than 2 of 53 censuses. Except for the meadowlarks and Sprague's Pipit, these species are granivorous. Regional distinctions in species composition of 10-degree latitude-longitude blocks occur along north-south and east-west axes in the south-central United States.

A cluster analysis of sites grouped them primarily on the basis of their most abundant species. Similar grazing treatments were generally placed into the same cluster. However, moderately grazed grassland sites in Oklahoma were divided between two clusters dominated by species of either heavily or lightly grazed grasslands.

The highest estimates of bird biomass were obtained on northern Oklahoma and southern Texas sites. Biomass estimates were higher on heavily grazed than lightly grazed grasslands in Oklahoma and western Texas. In contrast, moderately grazed grasslands in southern Texas supported significantly more bird biomass than heavily grazed sites. Total granivore biomass was correlated with seed abundance (r=0.78).

Annual changes in bird biomass were generally consistent among treatments (and also species) in central Oklahoma. The year 1976 was a drought year and fewer birds were present the winter of 1976-77 than in other winters. Reductions in Savannah Sparrows and increases of Smith's Longspurs accompanied the coldest winter (1978-79) with unusually high snowfall. The highest population estimates in southern Texas occurred in the year of record rainfall (1976-77).

Intensive studies of population dynamics and the role of birds as consumers in grassland ecosystems have been conducted during the breeding season (Allen 1938, Allen and Sime 1939, Mickey 1939, 1940, 1941, Mitchell 1961, Finzel 1964, Zimmerman 1965, 1966, 1967, Spiers and Orenstien 1967, Fiest 1968, Owens and Myres 1973, Wiens 1973, 1974a, 1974b, Raitt and Pimm 1976). Detailed analyses of grassland bird populations at other seasons, however, are limited in scope (Quay 1947, Finzel 1964, Webster 1964, Emlen 1972, Raitt and Pimm 1976) and some are restricted to counts of birds from roadway routes (Wiens et al. 1972, 1974, Risser 1980). As Wiens (1974a) and Wiens and Dyer (1975) indicated, we are hampered in our analysis of grassland bird communities by the nearly total lack of quantitative population studies conducted during non-breeding periods. This is unfortunate, since most temperate passerines spend only a few months a year in breeding activities, and many leave their breeding grounds immediately after nesting. Much of the structure of breeding avifaunas may be determined by winter resources (Fretwell 1972, Pulliam and Enders 1971, Wiens 1974a, Raitt and Pimm 1976) and by climatic factors influencing birds during the winter.

In temperate grasslands, the winter season differs from the breeding season in several important ways for grassland birds. Many species occupy different geographical ranges, are subjected to different climatic conditions (often more severe in winter), and utilize different food resources. Social associations may vary with season; for example, species which are territorial during the breeding season may form into flocks or become solitary when not breeding.

The resources for many temperate passerine species during winter consist primarily of seeds, which can be quite abundant (Johnston and Odum 1956); the abundance of seed resources is established at the time of the first frost, and decreases as the season progresses. The days are shorter in winter and afford less time for all activities. Competition may be heightened by increased overlap in ranges (of many species), and by the initial high postbreeding population levels which include many young birds.

Grasslands can undergo radical changes from year to year, as well as through the same season. Climatic instability can create perturbations in productivity and plant species composition (Albertson and Weaver 1944) and thus alter physiognomic structure. Productivity is reduced in arid, dry years compared to normal and wet years (Weaver and Albertson 1940, 1956), and xeric conditions can further affect grasslands by intensifying grazing pressure. Furthermore, a substantial percentage of the grasslands in the Great Plains are utilized to produce various crop monocultures. Agricultural practices can completely change the nature of a grassland site in a short period.

This paper is one of a series (Grzybowski 1976, 1980a, b) dealing with resource utilization and population structure in grassland bird communities during the winter. The purposes of this study are to: (1) determine the abundance and distribution of grassland bird species during winter in several regions of Oklahoma and Texas; (2) evaluate patterns of avian population structure on grassland sites with varied grazing pressure or cultivation practices within and among regions; (3) assess annual variation in grassland bird populations; and (4) evaluate the relation of observed patterns in bird abundance to various factors which may influence them.

METHODS

Population estimates were made at 20 sites in Oklahoma and Texas from December 1975 through January 1979. These sites included 2 in northern Oklahoma (Noble and Pawnee counties), 10 in central Oklahoma (Cleveland, Grady and McClain counties; Table 1), 4 in western Texas (Muleshoe National Wildlife Refuge, Bailey County), and 4 on the Rob and Bessie Welder Wildlife Refuge (San Patricio County) in southern coastal Texas (Fig. 1). Sites were selected on the basis of their uniformity, absence of trees or shrubs, and large size (permitting adequate sampling and minimal edge effect involving other habitats). The size of the sites ranged from about 30 ha on the smallest in southern Texas to greater than 100 ha. About 5% shrub cover occurred on two of the four southern Texas sites. Otherwise tree and shrub cover was absent or comprised less than 0.5% cover. In most cases, this cover consisted of isolated individual plants never exceeding

3 m in height.

Sites were classified on the basis of grazing pressure or cultivation. A site was considered a lightly grazed grassland (LG) when the dominant palatable grasses had uniformly grown to heights approaching their maximum potential height (Fig. 2A). When these dominant grasses occurred in distinct clumps, the site was considered a moderately grazed grassland (MG; Fig. 2B). When the dominant palatable grasses typical of the region were absent or present only in widely scattered clumps, and/or grazed to near ground level, the site was considered a heavily grazed grassland (HG). The only cultivated sites evaluated were planted with winter wheat (Triticum aestivum) in central Oklahoma. A cultivated site left fallow for a portion of the growing season was considered a successional grassland (SG) the following winter. A site in western Texas (MIX) included, in part, a prairie dog town, and, in part, a LG.

OKLAHOMA SITES

Oklahoma localities are in the region classified as bluestem-grama prairie (Andropogon-Bouteloua) by Kuchler (1964). Table 1 identifies sites by location and treatment. The dominant palatable grass on the Oklahoma sites was little bluestem (Schizachyrium scoparium; Figs. 2A and 2B). I used this species to gauge grazing pressure, as it occurs in decreasing abundance from LGs to HGs (P.G. Risser, pers. comm.). Forb cover, primarily common ragweed (Ambrosia artemisiifolia) and broom-snakeroot (*Gutierrezia sarothrae*), increased from LGs to HGs.

On one LG (site 1a; Fig. 2A), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*) were dominant species. These species are considered typical of prairie regions in central (Brunner 1931, Prier 1923) and northeastern Oklahoma (Buck and Kelting 1962). These dominant grasses were present on site 1b, but not as abundantly as on site 1a. The dominant grasses attained heights of 1.5 to 2.0 m on site 1a (LG), and 1.0 to 1.5 m on site 1b. Forbs were much less evident in LGs, occurring primarily in shallow soils on rock outcrops, along vehicle tracks, and in isolated patches, usually on ridge tops.

As grazing pressure increased, patches of three-awn (*Aristida* spp.), silver beardgrass (*Andropogon saccharoides*), and broom-snakeroot appeared and became larger and more in evidence. Ridge-top areas at some sites, considered MGs, contained large patches of three-awn. On many of the MGs, blue grama grass (*Bouteloua gracilis*) and *Panicum* spp. were also conspicuous. One MG (site 2a) contained a large patch (about 16 ha) of weeping lovegrass (*Eragrostis curvula*). Height of little bluestem on MGs was about 1 m.

HGs were dominated by three-awn, silver bluestem, ragweed and broom-snakeroot. Little bluestem was present in only small isolated clumps, or in small patches of clumped individuals. Plants were diminutive in stature, sometimes only 10 cm tall. Vegetation heights on HGs were less than 0.5 m.

Cultivated sites which I selected were similar. On three sites (in four of the years sampled) crops of sorghum (Sorghum bicolor) had preceded the fall plantings of winter wheat. Vegetation height (or litter depth) on cultivated sites was less than 5 cm.

Various amounts of heterogeneity were inevitable. Hilltops often had patches of three-awn in what was otherwise a MG. Also, MGs sometimes had dense patches of little bluestem. Trampled or eroded places, or areas of exposed rock, introduced heterogeneity in LGs and MGs. Gulleys, which dissected some sites (and are typical of grassland areas in the region), introduced fingers of scattered brush (Rhus sp. and Robinia sp.). The areas of tall trees were avoided, but sometimes the presence of such areas delimited a grassland site and restricted transects to ridge lines. Even the sites (3a, 4a and 4b) with the least relief (i.e., less then 5 m difference in elevation from highest to lowest points) had low wet pockets which added to their within-site heterogeneity.

Few sites remained the same from year to year. Grazing, agricultural practices, and variation in rainfall changed the character of several sites (Table 1). On site 1a, average vegetation height was 61.5 cm (SD=21.9; n=264) in December 1975 and 29.4 cm (SD=17.6) in December 1976; relative vegetation density was 65.5 vegetation contacts per grid-sample (SD=25.1; Grzybowski 1980a) in December 1975, and 40.3

contacts (SD=27.3) in December 1976. Drought conditions in 1976 reduced vegetation height and density at all grazed sites in Oklahoma. For example, average vegetation height on a HG (site 3a) was 26.2 cm (SD=8.6) in December 1975, and 22.1 cm (SD=8.5) in December 1976; relative vegetation density was 48.5 contacts (SD=23.6) in December 1975 and 42.4 contacts (SD=20.5) in December 1976. Many of the cattle had been removed from site 3a in the fall of 1975 so that this site was in the first year of partial recovery in 1976. In February 1977, this site was plowed and planted in cotton (*Gossypium herbaceum*). While the status at sites 2a and 2c (MGs) did not change, heavily grazed patches dominated by three-awn became progressively larger and more prominant with each passing year.

Cultivated site 4a was planted into winter wheat in early November of 1975, but not until early January in 1977. In November and December 1976, unharvested sorghum was present. This site was planted in cotton the following year. Another cultivated site (4b) was planted in winter wheat in 1976-77. A sorghum crop had been harvested just prior to this planting in 1976. In 1977, one-half of the field (i.e., a quarter section) was planted in maize (*Zea mays*), while the other half was left fallow allowing Johnson grass (*Sorghum halapense*) and bermuda grass (*Cynodon dactylon*) to dominate. The vegetation structure of the fallow portion (a SG) approached that of a MG.

WESTERN TEXAS SITES (MULESHOE NATIONAL WILDLIFE REFUGE)

The sites in western Texas are located in the grama-buffalo grass plains (Bouteloua-Buchloe) of Kuchler (1964). Dominant grass species on LGs were dropseed (Sporobolus sp.), blue grama and side-oats grama (Bouteloua gracilis and B. curtipendula), tobosa grass (Hilaria mutica), and hairy tridens (Erioneuron pilosum), with vegetation heights being less than 0.5 m. Dominant forbs were broom-snakeroot and paint-brush (Castilleja sp.). In the prairie dog towns and on HGs, false buffalo grass (Munroa squarrosa), three-awn, and tumbleweed (Salsola sp.) were dominant plant species. On more alkaline soil, sea-blite (Sueda sp.) was present.

On one LG (site 5a) in western Texas, 20% of the transect route passed through an active prairie dog town. This site (also referred to as MIX) was analyzed separately. A second LG (site 5b) included a portion of a prairie dog town which had not been active since 1973 (three years before the first year of my study). The abandoned prairie dog area was characterized by small patches of three-awn and remnants of old burrows. Both of these sites were grazed only in the summer. Another site (5c), considered a LG, was ungrazed beginning in 1976. A fourth site (5d) was heavily grazed. Cattle were removed from site 5d in 1978, and three-awn began to invade. Yucca (Yucca glauca) were present on a small section of this site. Vegetation heights on site 5d and the prairie dog town (at 5a) were generally less than 5 cm.

SOUTHERN TEXAS SITES (WELDER WILDLIFE FOUNDATION)

Weaver and Clements (1938) characterized the grasslands of this region as belonging to _Andropogon saccharoides_-_Stipa leucotricha_ associations though changes towards brushlands have occurred in the last 25 years (Box and Chamrod 1966). Grasslands in this region were dominated by little bluestem and _Andropogon_ species. Switchgrass was also present on several sites.

Site 6a was moderately grazed and located on well-drained sandy soil. Vegetation heights were generally between 1 and 2 m, but mowed fire breaks crossed the sites. A second MG (site 6b) was the wettest of my study areas with standing water in evidence each year. Vegetation heights on site 6b were about 0.5 to 1 m. Huisache (_Acacia farnesiana_) was an invading brush species which covered about 5% of the total area of sites 6b (MG) and 6c (HG), and was present, although less frequently, at another HG (site 6d). Heights of the brush patches were generally less than 1 m during the 1976-77 winter, but by January 1979, some brush patches exceeded 2 m in height. Grass heights on site 6c were less than 0.5 m; vegetation heights of site 6d were less than 0.5 m.

The impact of grazing increased on site 6a during my study. This site was lightly grazed in 1976-77, but was moderately grazed in 1978 and 1979. Vegetation heights ranged from 1 to 2 m in 1976-77 and between 0.5 to 1.5 m in 1978-79. In contrast, site 6c was HG in 1976-77 and MG in January 1978 and 1979. Grass heights approached 1.5 m in some patches in 1978-79.

CENSUS TECHNIQUES

Population estimates, in most cases, are based on counts made along transect routes and converted to density values by applying a coefficient of detectability (C.D.) for each species--the percentage of the total population in a strip of standard width that is detected (Emlen 1971, 1977). Transect lines were walked through the grasslands from 0.5 to 4 h after sunrise. The period just after sunrise was avoided because it appeared to be a time of heightened activity during which detectability was higher. At least three or four replicate transects, often walked over a period of several days, were used to obtain each estimate. On the smaller southern Texas sites, up to eight replicates were used for each estimate.

The location of each bird observed was recorded in relation to its perpendicular distance from the transect line. When groups were encountered, the distance of the individual farthest from the transect line was used and the group size recorded (cf. Emlen 1977). Coefficients of detectability were calculated for each species on each treatment and region from the data collected in March 1975, and between 15 November and 12 March of 1975-76 and 1976-77. These coefficients were used in calculating densities directly from counts in subsequent years. Only January estimates (or those for late December in 1975 and 1976 on the northern Oklahoma and southern Texas sites, respectively) are reported here.

Individuals in groups of five or fewer were treated as single birds in the calculations of population estimates and C.D. values. Since the Emlen technique assumes a random distribution of individuals, one can treat groups as individuals, assuming that they too are randomly distributed (Emlen 1977). However detectability of groups is higher than that of individuals, and separate C.D. calculations were made for groups (comprised of 6 to 30 individuals) of each species. Population estimates of grouped individuals were added to those for "ungrouped" individuals of a species to obtain a total density estimate. These adjustments were necessary in some cases for Horned Larks (see Appendix for scientific names), Eastern and Western meadowlarks, and Smith's and Chestnut-collared longspurs. For some highly gregarious species (Lapland and Smith's longspurs), population estimates of larger groups were made by counting the largest number of individuals in the air at one time, dividing by the area of the site, and adjusting this figure for 100 ha.

To evaluate similarities in bird communities among the various treatments, years, and regions, a cluster analysis, using standardized population estimates of species from censuses, was performed. Species occurring on only one census were deleted from this analysis. NT-SYS (Numerical Taxonomy Systems), a series of multivariate computer programs developed by F.J. Rohlf, J. Kishpaugh, and D. Kirk, was employed. Product-moment correlation coefficients were calculated between all pairs of censuses. Clusters were formed with the unweighted pair-group method, using arithmetic averages, and summarized in dendrograms. The cophenetic correlation was computed between the original correlation matrix and the cophenetic values of the cluster analysis to assess the amount of distortion in the dendrogram (Sokal and Rohlf 1962). A similar analysis, using sites as characters, was employed to evaluate similarities among species' occurrences.

To obtain a biomass estimate for a species, the average weights for up to 10 individuals (five males and five females) were multiplied by the population estimate. I used weights of specimens obtained on the sites, or housed in the Stovall Museum (University of Oklahoma) and obtained during the winter months (see Appendix). For analysis of biomass, each species was assigned to one of the following foraging guilds on the basis of species' size and the primary food consumed: doves; granivores; insectivores (other than meadowlarks); and meadowlarks (see Appendix for guild assignments).

An index of numerical dominance ($\underline{D}$) was calculated for each site ($\underline{S}$) using the formula:

$$\underline{D}_{\underline{S}} = \sum_{\underline{i}=1}^{\underline{m}} (\underline{n}_{\underline{i}}/\underline{n}_{\underline{t}})^2 \qquad (1)$$

where $\underline{n}_{\underline{i}}$ is the number of individuals of species $\underline{i}$, $\underline{n}_{\underline{t}}$ is the total number of individuals of all species, and $\underline{m}$ is total number of species (Pielou 1973). This value measures the probability that two individuals selected at random from a community will belong to the same species.

Seed samples were obtained in January of 1978 and 1979 on 10 of the sites. I randomly selected 20 to 30 locations on a site and brushed debris from the surface of areas 10 x 10 cm into a container. Seeds were sorted into size classes and counted. I transformed frequency data to a seed volume (*SV*) estimate with the formula,

$$SV = \sum_{i=1}^{n} (4/3)(\pi r_i^3 Y_i X_a) \qquad (2)$$

where r_i is radius of mean seed size in the *i*th class, *n* is number of classes, Y_i is the number of seeds in the *i*th class, and X_a is a correction factor to adjust seed volume to cubic millimeters of seeds per square meter for sample *a*. This provided a general index of seed availability in mid-winter. A similar sampling procedure was employed by Pulliam (1975).

Physiognomic structure of vegetation was measured in detail at seven of the sites (twice at two of these) to characterize grazing treatments. A total of 264 point samples spaced 15 m apart were taken in a strip 1000 m long and 60 m wide at each site. Details of this sampling are described in Grzybowski (1980a).

Results of Christmas Bird Counts (CBC; C.E. Bock, pers. comm.), compiled by the National Audubon Society, were used to evaluate bird species distributions at the regional level. These data are represented as the number of birds (of a species) seen per man-hour of observation time within a 10-degree latitude-longitude block (Fig. 3). I averaged annual results from these censuses for a 10-year period

(1962-71) to reduce the effect of inconsistencies in observer effort and skill (Bock and Lepthien 1974). The average frequencies within grid-blocks were converted to the proportion of total observations for each species. I divided the 15 grid-blocks (Fig. 3) into four quarters (NW, SW, NE, SE), four grid-blocks per quarter (except for the SW, which had three). The proportion occurrence of species in grid-blocks were summed for each quarter and used to regionally assess equitability of species distributions. I divided values for the SW quarter by 0.75 to adjust for the missing grid-block. Patterns of distribution among grassland bird species were assessed with a cluster analysis of grid-blocks, using proportion occurrence of species as variables.

RESULTS

Table 2 provides population estimates of non-raptorial species (in birds per 100 ha) occurring in Oklahoma grasslands during December or January from 1975-76 through 1978-79. Treatment types are identified for each sampling, as are total bird biomass, granivore biomass, and dominance. Tables 3 and 4 provide similar estimates for western Texas and southern Texas sites, respectively, for the winters of 1976-77 through 1978-79.

Tables 2, 3 and 4 indicate that the number of wintering grassland bird species is small in all areas studied. A total of 23 species (excluding raptors and shrikes) occurred on the 20 sites (based on 53 censuses); six of the species were found on only one census--Common Snipe, Common Flicker, American Robin, Yellow-rumped Warbler, Cardinal, and American Goldfinch. None of these were common, or would be considered typical of open grassland habitats. An additional three species occurred on only two censuses--the Common Ground Dove and Lincoln's Sparrow in southern Texas, and Baird's Sparrow in western Texas. Common Ground Doves and Lincoln's Sparrows have previously been reported in low numbers on the grassland areas at Welder Wildlife Foundation (Emlen 1971). Baird's Sparrows are typical of grasslands, but are rare (Bent 1968). This leaves only 14 species which occurred on more than two mid-winter censuses on all Texas and Oklahoma sites. Except for the meadowlarks and Sprague's Pipit, these species are granivorous.

REGIONAL COMPARISONS

Distribution of species at the regional level and equitability in species distributions were evaluated from CBC data. Table 5 gives proportion occurrence of most passerine species which occurred on two or more censuses by grid-block. Tree and Lincoln's sparrows, more typical of non-grassland habitats (Bent 1968), are not included; the Snow Bunting (*Plectrophenax nivalis*), a species of open habitats in the northern plains (Bent 1968) is included. The average proportion occurrence of species in the northwestern quarter is 0.07, while the averages for the southwestern and southeastern quarters are 0.39 and 0.37, respectively. The average for the northeastern quarter is 0.27.

A cluster analysis of grid-blocks, using proportion occurrence of species as variables (Table 5), is shown in Fig. 4. The cophenetic correlation is 0.888, indicating little distortion in representing the original correlation matrix. A regional cluster is found for the four northwestern grid blocks. This zone is dominated by one species, the Horned Lark. Blocks 13 and 14 are the northernmost in the east. The Snow Bunting is typical of this area. The eastern blocks 24 and 34 are similar. LeConte's Sparrows are more concentrated in this area. Species composition changes along a north-south axis from blocks 13 to 23 to 43. Snow Buntings typify block 13, Lapland and Smith's longspurs block 23, and Savannah Sparrows and Sprague's Pipits block 43. A distinct east-west separation occurs between blocks 12, 22, 23, 33, and 42, and blocks 13, 23, 24, 34, and 43, respectively. This analysis demonstrates the regional character of grassland bird distribution in the southern Great Plains.

SITE COMPARISONS

A cluster analysis (Fig. 5), using population estimates from the 52 censuses (Tables 2, 3 and 4; excluding site 5c in 1979 when no birds were present), shows that sites are generally associated on the basis of the dominance of one species. In the dendrogram (Fig.5; cophenetic correlation=0.893), sites in group 1 were dominated by Savannah Sparrows. LeConte's Sparrow was co-dominant on sites 1a in 1976 and 6b in 1977 of this group (see Fig. 5). All samples for sites 6a and 6b (group 1) were very similar indicating low species turnovers from year to year. In 1979, both of these sites were lightly to moderately grazed. The second group in the cluster analysis includes four sites dominated by meadowlarks, and represents an assortment of treatment types. Meadowlarks were present on most sites so this cluster represents absence of other species and/or a high number of meadowlarks relative to other species. Unlike other grassland bird species, meadowlarks undergo local movements to adjacent shrubby habitats, which affect estimates of their abundance in open grassland (unpubl. data); these local movements may have contributed to this clustering. Group 3 includes HGs in southern Texas where Sprague's Pipits were present. On site 6c in 1979, I found Sprague's Pipits in numbers similar to other years, but, because of increases in Savannah Sparrows, this site for 1979 was placed with the first group. Group 4 is the largest group and includes heavily to moderately grazed sites in central Oklahoma where Smith's Longspurs were dominant. Three of the censuses in this group (2c in 1977 and 1978, and 3a in 1977) had high numbers of Chestnut-collared Longspurs relative to Smith's Longspurs (see Table 2). Smith's Longspurs on these three sites were less common than on the other sites in this group. Group 5 includes cultivated sites dominated by Lapland Longspurs. This species occurred only sporadically and in low numbers on other sites. Localities included in the last group are dominated by Horned

Larks; this group includes site 4c, a cultivated field from which Lapland Longspurs were absent, and most sites in western Texas. The correlation of species' abundances between sites 5b in 1979 and 5c in 1978 is 0.66 (Fig. 5). Both had very low density estimates for all species present (see Table 2). Site 2a in 1976 and 1978 (Fig. 5; between groups 3 and 4) was dominated by Tree Sparrows. Densities were also low at these sites. Site 1b in 1977 (Fig. 5) had low density estimates of meadowlarks and LeConte's Sparrows only.

The cluster analysis shows that MGs overlapped two extremes of habitat; the first, which was more lightly grazed, was dominated by Savannah Sparrows (and sometimes also LeConte's Sparrows), and the second, which was more heavily grazed, was dominated by Smith's Longspurs. The size of suitable habitat patches on a site influences a species' abundance. Regional differences in species composition are evident for groups 1 and 3 which are primarily composed of southern Texas sites, and group 6 composed mainly of western Texas sites.

A cluster analysis of species (Fig. 6; cophenetic correlation=0.759) further supports the generally weak relations among most of the species. The most closely associated species are Common Ground Dove, Lincoln's Sparrow and Bairds's Sparrow. The first two are uncommon on MGs in southern Texas; the latter is a rare western Texas species. These associations are based on similarities in non-occurrence for species found on only two censuses each. Thus, none of the 17 species are similar in their response to particular site characteristics.

TREATMENT COMPARISONS

Table 6 provides mean biomass estimates for granivores, meadowlarks, insectivores (other than meadowlarks) and doves organized by region; dominance values are also included. Table 7 shows the results of Duncan's multiple range test (Kramer 1956) for total, granivore and meadowlark biomass between different treatments within and between regions.

In central Oklahoma, a trend towards increasing biomass is seen from LGs to HGs (Table 6). However, few of the treatments were significantly different ($P<.05$; Table 7) HGs had significantly higher granivore biomass than MGs or LGs ($P<.05$). Biomass estimates for cultivated sites are high, but extremely variable. The biomass estimate for the HG (site 3b) in northern Oklahoma is the highest of any estimate on any site. The Smith's Longspur (Table 2) dominated this site, comprising 97% of all individuals.

The highest population estimates for western Texas sites occur on site 5a (MIX; Table 6), which was a lightly grazed area partially traversing a prairie dog town. MIX had significantly higher ($P<.05$) estimates of granivore and total biomass then LGs in western Texas. Granivore biomass was higher on MGs than HGs ($P<.05$) in southern Texas. Total biomass also increased from HGs to MGs ($P<.05$).

Insectivores (other than meadowlarks) were inconsequential on the Oklahoma and western Texas sites (Table 6). Meadowlarks were absent from the northern Oklahoma sites. Insectivores were more abundant on southern Texas sites than on those in Oklahoma, as were doves (which were absent in Oklahoma grasslands). However, the presence of doves in southern Texas was irregular (Table 4). Sprague's Pipit was the only obligate insectivore consistently appearing on some southern Texas sites (sites 6c and 6d; Table 4), although meadowlarks in southern Texas were entirely carnivorous in the winter (unpubl. data). No significant differences ($\underline{P}>.05$) were noted for any of the treatment comparisons within regions for meadowlarks.

Biomass for all foraging groups was higher on MGs in southern Texas than in central Oklahoma (Tables 6 and 7). Western Texas and central Oklahoma sites did not differ in biomass ($\underline{P}>.05$). Biomass estimates for all groups are considerably greater on the LG in southern Texas than for LGs in central Oklahoma or western Texas (Table 6). While HGs in southern Texas, central Oklahoma, and western Texas (including MIX) did not differ in total biomass, HGs in southern Texas have significantly fewer granivores and significantly more meadowlarks than HGs in other regions ($\underline{P}<.05$; Tables 6 and 7). However, large numbers of granivores did occur on MGs nearby (in southern Texas).

Dominance ranged from 0.849 and 0.951 on northern Oklahoma sites to 0.25 on a MG in central Oklahoma (Tables 2, 3 and 4). HGs in southern Texas had the lowest mean for any treatment (0.342, SD=0.078), but were not significantly different ($\underline{P}$>.05) from HGs in central Oklahoma and western Texas and from MGs in southern Texas. The mean number of species on HGs in southern Texas was 3.6 (SD=0.55). The mean treatment dominance value of 0.342 approaches that of complete eveness; i.e., the expected dominance value if all species were equally common (in this case, 0.280). These HGs were the only sites in the study where an insectivore (Sprague's Pipit) was regularly present.

Dominance values approached their minimum on several other censuses, but were not consistently low for any other treatment type or region. Dominance values are expected to be low when the total number of individuals is very low. In a few cases, dominance was low with moderate numbers of individuals present (site 3a, 1977; site 2a, 1976-78; site 4d, 1977; see Table 2).

ANNUAL VARIATION

All Oklahoma sites censused showed decreases in total bird biomass and granivore biomass for the winters of 1975-76 to that of 1976-77 (Table 2). The year 1976 was dry with 45.9 cm of rainfall compared to a mean of 80.0 cm (Natl. Ocean. Atmos. Admin. 1978). Standing crop biomass (as measured by vegetation contacts) was lower on the sites in December 1976 than in December 1975.

Some cultivated sites showed substantial increases in bird biomass (Table 2; sites 4b and 4d) between January 1977 and January 1978. On site 4d, the increase in biomass was due to a large number of meadowlarks.

Several MGs in Oklahoma show increases in granivore biomass from 1977-78 to 1978-79 (Table 2). This was due to the incursion of Smith's Longspurs. In fact, much of the annual variation in granivore biomass in MGs and HGs is attributable to this species (Table 2). Normally Smith's Longspurs winter in high numbers in north-central and northeastern Oklahoma, as indicated by estimates at sites 3b and 2d (and unpubl. data). The winter of 1978-79 was the coldest on record (mean January temperature -3.2 ^{o}C; 30-year mean, 2.8 ^{o}C; Natl. Ocean. Atmos. Admin. 1978), and Smith's Longspurs were abundant on many sites in central Oklahoma. However, Smith's Longspurs are habitat specialists (Grzybowski 1980a) and occupy patches of dense three-awn grass which occur in heavily grazed areas. Patches of three-awn on many sites grew larger during the period of study, and this may have resulted in more Smith's Longspurs using these sites.

Savannah Sparrow numbers were low in the winter of 1978-79 on the grassland sites in central Oklahoma (Table 2); only a few scattered individuals could be found at some locations. Heavy mortality of Savannah Sparrows may have occurred in the severe winter of 1977-78 (unpubl. data), when snow covered the ground for a record 38 days in central Oklahoma (Natl. Ocean. Atmos. Admin. 1978). Savannah Sparrows were very abundant on a first-year successional field in 1977-78 and were present on most sites in 1975-76 and 1976-77.

In western Texas, temperature and rainfall were similar in the different years of my study (unpubl. Muleshoe National Wildlife Refuge weather summary). Site 5b underwent a gradual decline in biomass from January 1977 to January 1979 (Table 3). A slight increase in biomass occurred at the MIX site (site 5a) but the changes in granivore and meadowlark components were compensatory; in January 1978, Horned Larks were much less abundant than in other years, while meadowlarks were more abundant (Table 2). On the HG (site 5d), biomass estimates were high in 1979 (Table 3) after removal of cattle. The site was recovering from overgrazing, and seed abundance had increased slightly. In general (all western Texas sites combined), Horned Larks were less common in January 1978 than in other years. The ungrazed grassland (site 5c) contained very few birds.

Some general trends were apparent on the southern Texas sites. The year 1976 was the wettest on record (305 cm; mean, 87 cm). Granivore biomass peaked in 1976-77, being extremely high on site 6b (MG), because of the large numbers of Savannah and LeConte's sparrows (Table 4). Site 6b had clay soils and was wet in all years of the study, in contrast to site 6a (also MG), located on well-drained sandy soils. Granivore biomass generally decreased on the MGs from 1976-77 to January 1979, but increased slightly on the HGs over this period (Table 4). Savannah Sparrows were a consistently abundant element of the granivore biomass. Meadowlarks gradually increased on site 6a (MG); at the same time, grazing pressure was increasing. At site 6b (MG), meadowlarks were most abundant in 1976-77 and equally common in 1978 and 1979. Doves were present on southern Texas sites (Table 2) and formed a significant portion of the total biomass (20.4 kg/100 ha; 44%) on site 6a in January 1978. Meadowlarks were generally more abundant on the HGs than on the MGs (Table 4). Bobwhites (Colinus virginianus) were occasionally noted on the MGs, but were not recorded on any of the morning transects. Turkeys (Meleagris gallopavo) were also observed traversing site 6a.

Seed abundance was measured on several sites in January of 1978 and 1979. Figure 7 shows granivore biomass plotted against the log of seed volume. A correlation of 0.78 was obtained, but when the two outliers were removed, the correlation was reduced to 0.44. This analysis implies that seed abundance is a factor on seed rich sites, but that other factors also determine granivore population sizes on sites of intermediate to low food abundance. The sites with the highest seed abundance had the highest granivore biomass, and those with very low seed abundance supported very low granivore biomass (Fig. 7). Site 4b was left fallow in the winter of 1977-78, and the abundant seed crops of invading grasses and weeds attracted large numbers of Savannah Sparrows (Table 2).

MGs in southern Texas, which had higher seed densities, supported more granivores than the moderately grazed sites in Oklahoma. In southern Texas, HGs had very low seed densities compared to HGs in Oklahoma. In Oklahoma, seed abundance was higher in HGs than in MGs. In western Texas, LGs had very low seed densities, and HGs were only slightly higher; seed abundance was highest in prairie dog towns.

DISCUSSION

Birds occupying grasslands in Oklahoma and Texas are primarily winter residents. Of 11 species occurring in Oklahoma grasslands and 9 species in western Texas, only the Horned Lark and Eastern and Western meadowlarks breed in the southern plains region. Most individuals of these species migrate from breeding localities further north (Sutton 1967). However, solitary meadowlarks could be observed singing in November and sporadically through to February, and these individuals may be resident throughout the year (unpubl. data). Of 14 species in southern Texas, only Mourning Doves, Common Ground Doves, Eastern Meadowlarks and Cardinals breed in the region; only the Mourning Dove and Eastern Meadowlark were present on more than two of my censuses. Thus species turnover is nearly complete for grassland bird communities from summer to winter. Raitt and Pimm (1976) showed a large influx of seed-eaters in winter at their grassland site in southern New Mexico. Wiens and Dyer (1975) provided data from roadside counts which indicate high species turnovers from fall to winter and winter to spring (72-95%) for three "true prairie" sites. One of these localities (Osage) is near my northern Oklahoma sites.

Many grassland birds are habitat specialists in winter

(Grzybowski 1976, 1980a). Cluster analysis showed sites grouped on the basis of the dominance of one or two species. Lapland Longspurs preferred cultivated sites; LeConte's Sparrows occurred primarily on lightly grazed areas. Smith's Longspurs may be the most specialized, occupying heavily grazed patches of three-awn (Grzybowski 1980a). Meadowlarks were less specialized, appearing on all site types, sometimes in large numbers. Savannah Sparrows also appeared on all grazing treatment types in Oklahoma and southern Texas, but were rare in western Texas. Species composition is consistent on treatment type within regions.

Climatic tolerances also influence distribution of birds. CBC data show north-south gradients in distribution for eastern plains regions (Fig. 8) similar to distribution patterns during the breeding season. Thus, the passerine species breeding furthest north--the Snow Bunting--has the most northerly wintering distribution (Godfrey 1966). The Smith's and Lapland longspurs are tundra species (Godfrey 1966) whose winter distributions typify the central-northeastern grid-blocks (Fig 8A). Many sparrow species breeding in northern plains grasslands (Bent 1968) winter along the southern border of the United States (Fig. 8).

Smith's and Lapland longspurs never occurred on the same census on any of my sites; they prefer different habitats on their wintering grounds just as they do on their breeding grounds (Bent 1968, Jehl 1972). The Smith's Longspur is typically abundant in north-central and northeastern Oklahoma.

In 1978-79, an unusually cold winter in Oklahoma (Natl. Ocean. Atmos. Admin. 1979), larger than normal numbers appeared in central Oklahoma. Snow cover may also have been instrumental in determining the winter distribution of this species (unpubl. data).

Climatic factors also may affect east-west changes in distribution. Horned Larks were most common in western regions and dominated grasslands in western Texas. Colorado studies (Wiens 1974a) during the breeding season showed it was commoner in dry years. The preference of Horned Larks for arid conditions may be manifest in their east-west distribution patterns (Fig. 8C). Species turnover is highest between shortgrass areas of the high plains and the mid-grass and tallgrass areas of eastern regions. Southwestern regions are typified by Baird's Sparrows, and McCown's and Chestnut-collared longspurs; southeastern regions by LeConte's and Savannah sparrows, and Sprague's Pipits (Fig 8). These regional patterns may have been associated with historical habitat distributions. Some mixing from east and west occurs, yet no open field granivores that occupy sparsely vegetated areas occur in heavily grazed habitats in southern Texas. Some Horned Larks and Chestnut-collared Longspurs were observed during the study in sandy dry areas (blowouts) on the coast, and in some large cultivated fields (unpubl. data).

While habitat may influence which species occupy a particular site and climate can influence regional distributions, grassland birds exhibit opportunistic utilization of concentrated food sources. Abundance of individuals was related to food abundance. Savannah Sparrows were very common on a succesional field in central Oklahoma where seed density was very high. High densities were present at MGS in southern Texas in 1976-77 when a record rainfall may have produced abundant seed crops. In southern New Mexico, Raitt and Pimm (1976) noted the clumped distribution of seeds; these authors indicated that movements of birds in flocks were probably adapted to exploit these localized seed-rich patches. This opportunism has been implicated in other studies (Pulliam and Enders 1971, Cody 1971). Many grassland species are gregarious (Grzybowski 1980b) and may undergo local movements that permit exploitation of patchily distributed foods. Such behavior could minimize site tenacity, and could result in erratic fluctuations in population distributions of these species at the local level. I noted local fluctuations in Lapland Longspurs and Eastern Meadowlarks (unpubl. data).

In central Oklahoma and western Texas, trends of increasing abundance from LGs to HGs were significant in only a few cases. All samples were combined for a treatment, and annual variation may have overshadowed treatment effects. LGs generally have the lowest seed abundance. These sites have stable perennial grass species where reproduction is more K-selected (Emlen 1973). Grasses with high seed production are more prevalent in HGs, or recently cultivated (and thus disturbed) areas left fallow. The MIX site had the highest seed densities of any habitat in western Texas. Thus the observation of increasing bird biomass from LGs to HGs may be a trend influenced by the reproductive strategies of dominant plant species.

Avian biomass estimates of summer studies in mid-grass prairie (Wiens and Dyer 1975) were generally higher than estimates during winter in central Oklahoma. The mid-grass prairie estimates given by Wiens and Dyer (1975) for the breeding season were 9.95 kg/100 ha (SD=3.42); my winter estimates were 6.86 kg (SD=6.06). My estimates for the northern Oklahoma sites were much higher (89.48 kg in HG and 23.93 kg in MG). Biomass estimates for short-grass plains sites were higher in summer (10.28 kg; SD=3.35) than in winter (5.86 kg; SD=4.62) in western Texas. On cultivated sites, biomass estimates were lower in summer (6.91 kg; SD=4.92) than in winter (9.54 kg; SD=8.66) in central Oklahoma. Biomass estimates for southern Texas sites were much higher than in other regions.

Since 1850, grasslands have undergone dramatic changes. The large herds of bison have been replaced by large numbers of cattle. Prairie dogs, once forming extensive and widespread colonies, are now very localized in much of the plains region. What was once continuous grassland is now dissected by fencelines into patches subjected to differing grazing pressure. Some of the most productive areas are intensively cultivated as large monocultures. Many ungrazed areas are regularily mowed for hay. These practices and uses must have affected grassland bird populations.

Some grassland birds appear to have diminished in numbers as a result of the reduction and alteration of natural grassland. These include species such as the Baird's Sparrow and Sprague's Pipit (Bent 1950, 1968). Even an open grassland species of sparsely vegetated areas, the McCown's Longspur, has undergone drastic reductions in its range (Bent 1968). Others, such as the Horned Lark, have expanded their range in response to open agricultural conditions (Hurley and Franks 1976). Lapland Longspurs are abundant in agricultural areas. During winter in central Oklahoma, Lapland Longspurs occur mainly on cultivated plots, particularily those on which sorghum was the fall crop.

Box and Chamrod (1966) indicated a major replacement of coastal prairie by brush species in southern Texas during the past 25 years due to a change in grazing practices and fire control. Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*) has suffered major habitat losses from this reduction of grassland (Lehman 1968). Species such as LeConte's Sparrows may also be affected.

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LITERATURE CITED

Albertson, F.W., and J.E. Weaver. 1944. Effects of drought, dust and intensity of grazing on cover and yield of short-grass pastures. Ecol. Monogr. 14:1-29.

Allen, P.F. 1938. Breeding bird census, short-grass plains. Bird-Lore (Suppl.) 40:365.

Allen, P.F., and P.R. Sime. 1939. Breeding bird census, short-grass plains. Bird-Lore (Suppl.) 41:18.

Bent, A.C. 1950. Life Histories of North American wagtails, shrikes, vireos, and their allies. U.S. Natl. Mus. Bull. 197.

Bent, A.C. 1968. Life Histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

Brunner, W.E. 1931. The vegetation of Oklahoma. Ecol. Monogr. 1:99-188.

Bock, C.E., and L.W. Lepthien. 1974. Winter patterns of bird species diversity and abundance in the United States and Canada. Am. Birds 28:556-562.

Box, T.W., and A.D. Chamrod. 1966. Plant communities of the Welder Wildlife Refuge. Welder Wildl. Foun. Contr. No. 5, Ser. B., 28p.

Buck, P., and R.W. Kelting. 1962. A survey of the tall grass prairie in northeastern Oklahoma. Southwest. Nat. 7:163-175.

Cody, M.L. 1971. Finch flocks in the Mohave Desert. Theor. Pop. Biol. 2:142-158.

Emlen, J.M. 1973. Ecology: An evolutionary approach. Addison-Wesley Publ. Co., Reading, Massachusetts.

Emlen, J.T. 1971. Population densities of birds derived from transect counts. Auk 88:323-342.

Emlen, J.T. 1972. Size and structure of a wintering avian community in southern Texas. Ecology 53:317-329.

Emlen, J.T. 1977. Estimating breeding season bird densities from transect-counts. Auk 94:455-468.

Feist, F.G. 1968. Breeding bird populations on sagebrush-grassland habitat in central Montana. Audubon Field Notes 22:691-695.

Finzel, J.E. 1964. Avian populations of 4 herbaceous communities in southeastern Wyoming. Condor 66:496-510.

Fretwell, S. 1972. Populations in a seasonal environment. Princeton Univ. Press., Princeton, New Jersey.

Godfrey, W.E. 1966. The birds of Canada. Natl. Mus. Canada, Bull. No. 203, Biol. Ser. No. 73.

Grzybowski. J.A. 1976. Habitat selection among some grassland birds wintering in Oklahoma. Ann. Okla. Acad. Sci. 6:176-182.

Grzybowski, J.A. 1980a. Niche relations of grassland birds during winter. Auk. (MS).

Grzybowski, J.A. 1980b. Sociality and space use of grassland birds during winter. Ecology. (MS).

Hurley, R.J., and E.C. Franks. 1976. Changes in the breeding ranges of two grassland birds. Auk 93:108-115.

Jehl, J.R., Jr. 1968. The breeding biology of Smith's

Longspur. Wilson Bull. 80:123-149.

Johnston, D.W., and E.P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37:50-62.

Kramer, C.Y. 1956. Extension of multiple range tests to group means with unequal numbers of replication. Biometrics 12:307-310.

Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society, New York.

Lehman, V.W. 1968. The Attwater Prairie Chicken, current status and restoration oportunities. Trans. N.A. Wildl. Conf. 33:398-407.

Mickey, F.W. 1939. Breeding bird census, original prairie. Bird-Lore (Suppl.) 41:17.

Mickey, F.W. 1940. Breeding bird census, original prairie. Bird-Lore (suppl.) 42:477.

Mickey, F.W. 1941. Breeding bird census, original prairie. Bird-Lore (suppl.) 43:484.

Mitchell, M.J. 1961. Breeding bird populations in relation to grassland succession on the Anoka sand plain. Flicker 33:102-108.

National Oceanic and Atmospheric Administration. 1978. Local climatological data: Oklahoma City, Oklahoma. National Climatic Center, Ashville, North Carolina.

National Oceanic and Atmospheric Administration. 1979. Local climatological data: Oklahoma City, Oklahoma. National

Climatic Center, Ashville, North Carolina.

Owens, R.A., and M.T. Myres. 1973. Effects of agriculture upon populations of native passerine birds of an Alberta fescue grassland. Can. J. Zool. 51:697-713.

Pielou, E.C. 1975. Ecological diversity. John Wiley and Sons, New York.

Prier, C.W. 1923. Fall grasses of Cleveland County, Oklahoma. Proc. Okla. Acad. Sci. 3:85-87.

Pulliam, H.R. 1975. Coexistence of sparrows: A test of community theory. Science 189:474-476.

Pulliam, H.R., and F. Enders. 1971. The feeding ecology of five sympatric finch species. Ecology 52:557-566.

Quay, T.L. 1947. Winter birds of upland plant communities. Auk 64:382-388.

Raitt, R.J., and S.L. Pimm. 1976. Dynamics of bird communities in the Chihuahuan Desert, New Mexico. Condor 78:427-442.

Risser, P.G. (Ed.). 1980. The true prairie ecosystem. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Sokal, R.R., and F.J. Rohlf. 1962. The comparison of dendrograms by objective methods. Taxon 11:33-40.

Spiers, J.M., and R. Orenstein. 1967. Bird populations in fields of Ontario County, 1965. Can. Field Nat. 81: 175-183.

Sutton, G.M. 1967. Oklahoma birds. Univ. Oklahoma Press., Norman.

Weaver, J.E., and F.W. Albertson. 1940. Deterioration of grassland from stability to denudation with decrease in soil moisture. Bot. Gaz. 101:598-624.

Weaver, J.E., and F.W. Albertson. 1956. Grasslands of the Great Plains. Johnson Publ. Co., Lincoln, Nebraska.

Weaver, J.E., and F.E. Clements. 1938. Plant ecology. McGraw-Hill, New York.

Webster, J.D. 1964. Winter bird population study. No. 23, Short-grass prairie; No. 24, Shrub desert. Breeding bird census No. 31, Short-grass prairie; No. 34, Shrub desert. Audubon Field Notes 18:404-405,563,564.

Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1-93.

Wiens, J.A. 1973 Pattern and process in grassland bird communities. Ecol. Monogr. 43:237-270.

Wiens, J.A. 1974a. Climatic instability and the "ecological saturation" of grassland bird communities in North American grasslands. Condor 76:385-400.

Wiens, J.A. 1974b. Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. 91:195-213.

Wiens, J.A., and M.I. Dyer. 1975. Rangeland avifaunas: Their composition, energetics, and role in the ecosystem. Proc. Symp. Manage. Forest and Range Habitats of Nongame Birds. USDA Forest Serv. Gen. Tech. Rep. WO-1:146-182.

Wiens, J.A., J.T. Rotenberry, and J.F. Ward. 1972. Avian populations at IBP grassland biome sites: 1971. US/IBP

Grassland Biome Tech. Rep. No. 205.

Wiens, J.A., J.T. Rotenberry, and J.F. Ward. 1974. Bird populations at Ale, Pantex, Osage, and Cottonwood, 1972. US/IBP Grassland Biome Tech. Rep. No. 267.

Zimmerman, J.L. 1965. Breeding bird census, grassland. Audubon Field Notes 19:614.

Zimmerman, J.L. 1967. Breeding bird census, grassland. Audubon Field Notes 20:665.

Zimmerman, J.L. 1967. Breeding bird census, grassland. Audubon Field Notes 21:667.

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FIGURE 1. Census locations. Number of sites evaluated at each regional location are given in parentheses.

FIGURE 2. Treatment types in Oklahoma. (A) Lightly grazed grassland (site 1a in December 1975) where heights of dominant palatable grasses (bluestems [*Andropogon gerardi* and *Schizachyrium scoparium*] and indiangrass [*Sorghastrum nutans*]) are maximal and uniform. (B) Moderately grazed grassland (site 2d in March 1978) where little bluestems are formed into clumps by grazing.

FIGURE 3. South-central United States showing 10-degree latitude-longitude blocks used in summarizing results of Christmas Bird Count data.

FIGURE 4. Correlation phenogram of Christmas Bird Count grid-blocks based on an unweighted pair-group method of cluster analysis using arithmetic averages (see text). Block numbers correspond to those in Fig. 3.

FIGURE 5. Correlation phenogram of censuses based on an unweighted pair-group method of cluster analysis using arithmetic averages. Region symbols are: COK=central Oklahoma, NOK=northern Oklahoma, STEX=southern Texas, WTEX=western Texas; Site and treatment symbols as in Tables 1, 3 and 4; January date for year of winter season is used.

FIGURE 6. Correlation phenogram of species based on an unweighted pair-group method of cluster analysis using arithmetic averages. See Appendix for species symbols.

FIGURE 7. Relation of granivore biomass to seed abundance (of seeds 1-4 mm in length).

FIGURE 8. Proportion occurrence of species (see text) along west-east and north-south axes for Christmas Bird Count data in south-central United States.

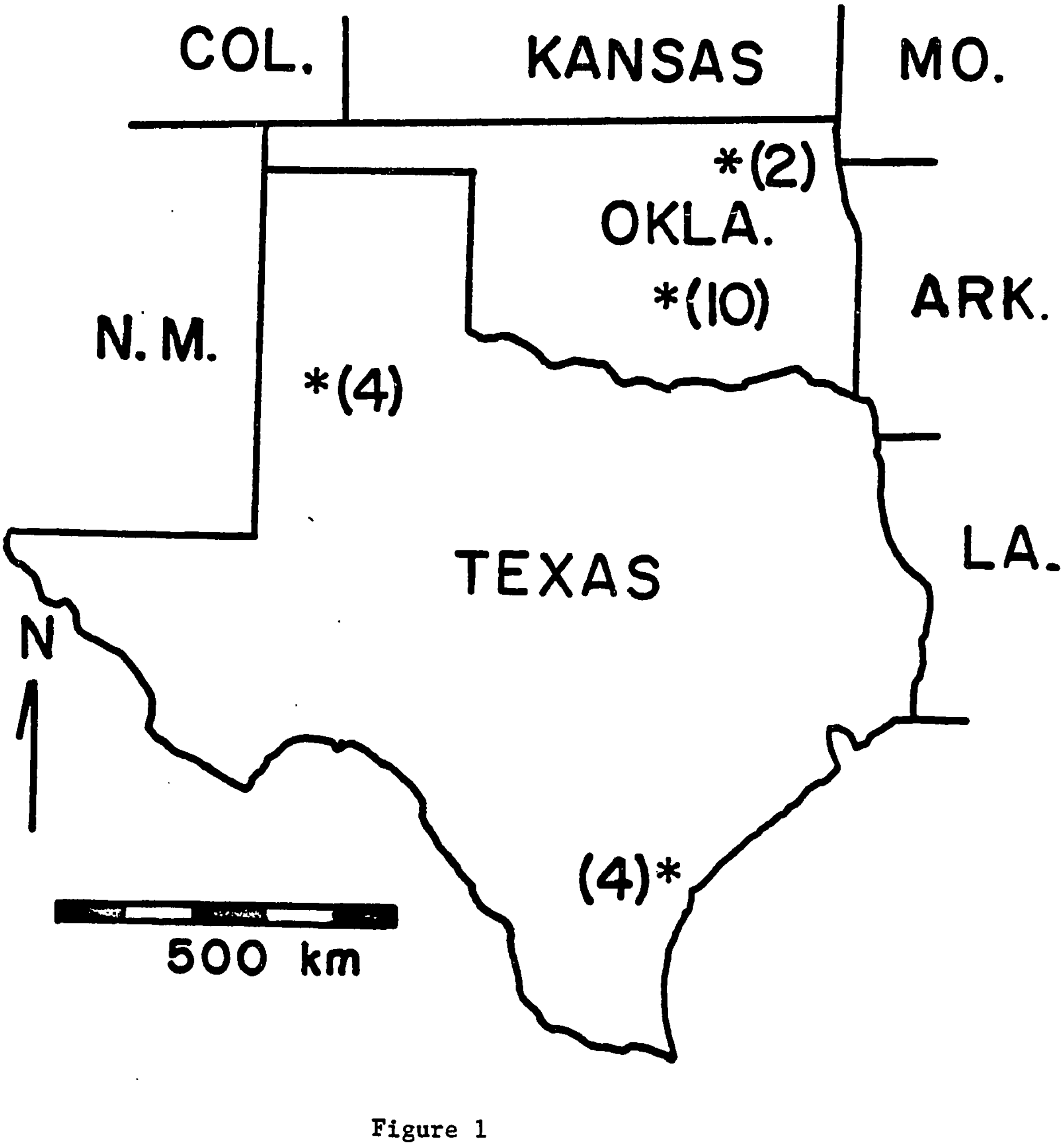
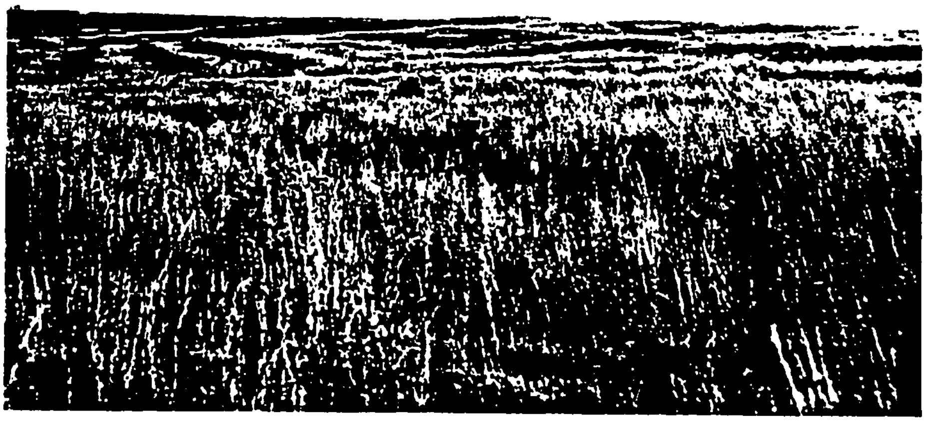


Figure 1

A



B

Figure 2

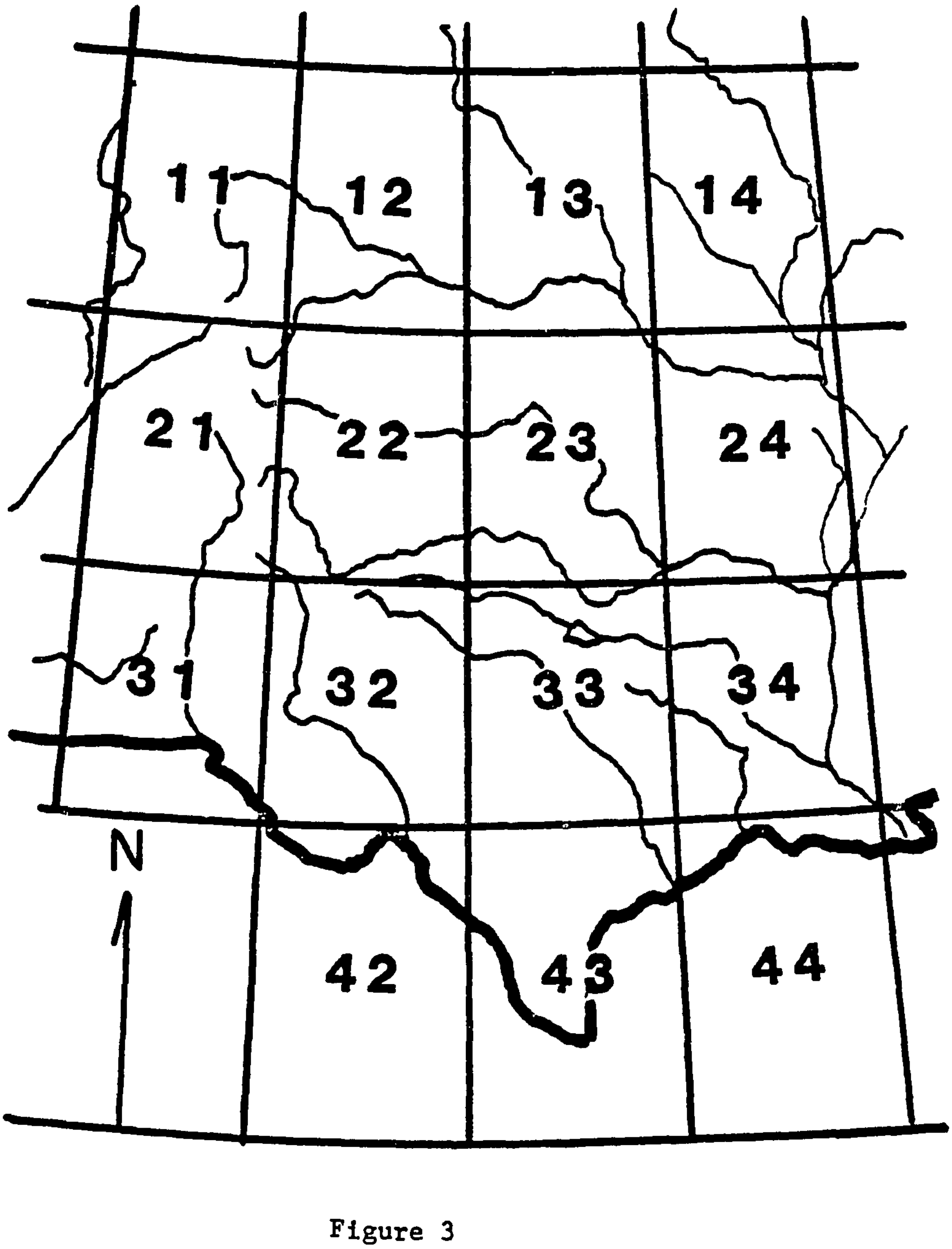


Figure 3

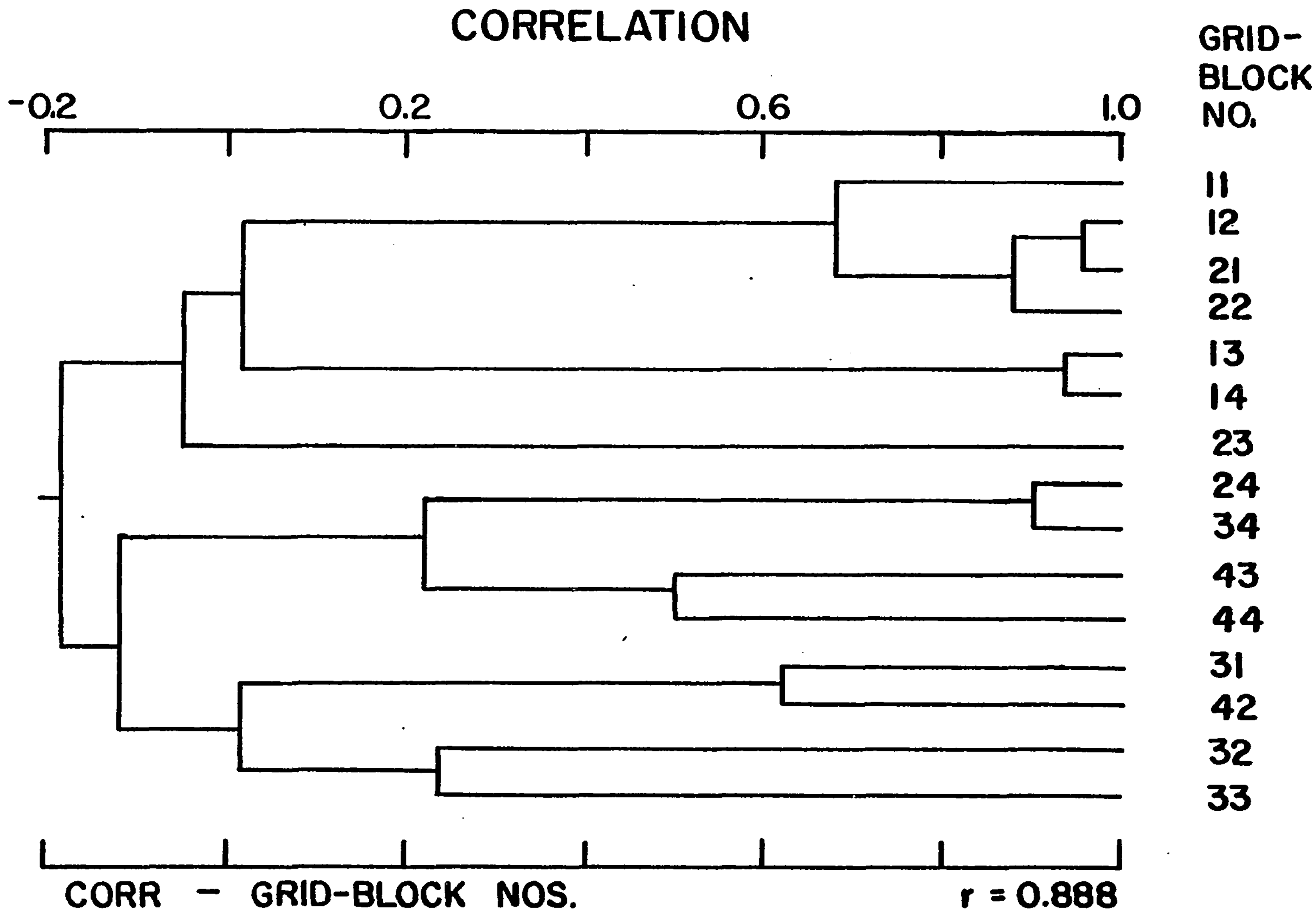

CORRELATION
-0.2
0.2
0.6
1.0
GRID-BLOCK NO.
11
12
21
22
13
14
23
24
34
43
44
31
42
32
33
CORR - GRID-BLOCK NOS.
r = 0.888

Figure 4

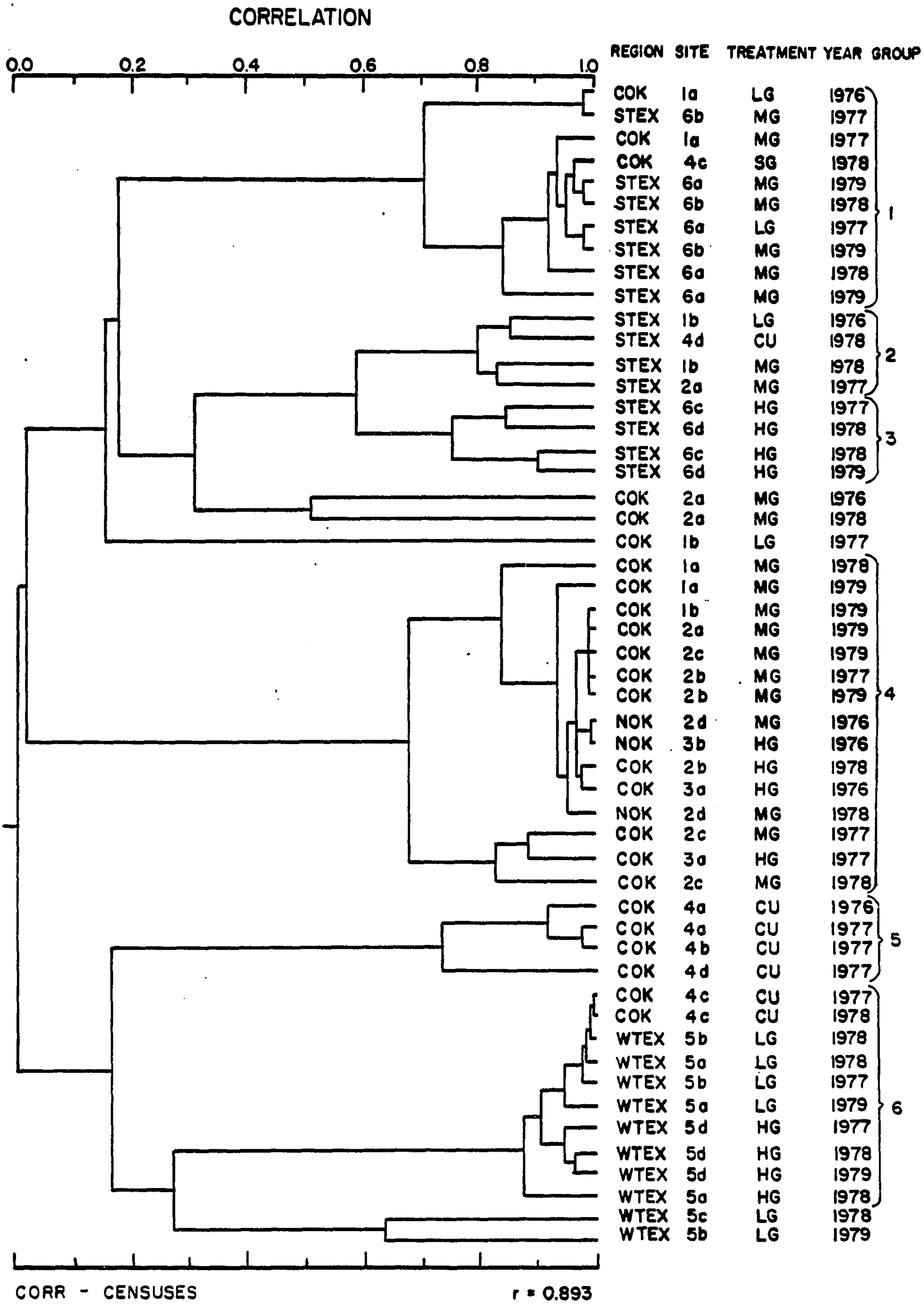

CORRELATION
0.0
0.2
0.4
0.6
0.8
1.0
REGION SITE TREATMENT YEAR GROUP
COK 1a LG 1976
STEX 6b MG 1977
COK 1a MG 1977
COK 4c SG 1978
STEX 6a MG 1979
STEX 6b MG 1978
STEX 6a LG 1977
STEX 6b MG 1979
STEX 6a MG 1978
STEX 6a MG 1979
1
STEX 1b LG 1976
STEX 4d CU 1978
STEX 1b MG 1978
STEX 2a MG 1977
2
STEX 6c HG 1977
STEX 6d HG 1978
STEX 6c HG 1978
STEX 6d HG 1979
3
COK 2a MG 1976
COK 2a MG 1978
COK 1b LG 1977
COK 1a MG 1978
COK 1a MG 1979
COK 1b MG 1979
COK 2a MG 1979
COK 2c MG 1979
COK 2b MG 1977
COK 2b MG 1979
NOK 2d MG 1976
NOK 3b HG 1976
COK 2b HG 1978
COK 3a HG 1976
NOK 2d MG 1978
COK 2c MG 1977
COK 3a HG 1977
COK 2c MG 1978
4
COK 4a CU 1976
COK 4a CU 1977
COK 4b CU 1977
COK 4d CU 1977
5
COK 4c CU 1977
COK 4c CU 1978
WTEX 5b LG 1978
WTEX 5a LG 1978
WTEX 5b LG 1977
WTEX 5a LG 1979
WTEX 5d HG 1977
WTEX 5d HG 1978
WTEX 5d HG 1979
WTEX 5a HG 1978
6
WTEX 5c LG 1978
WTEX 5b LG 1979
CORR - CENSUSES
r = 0.893

Figure 5

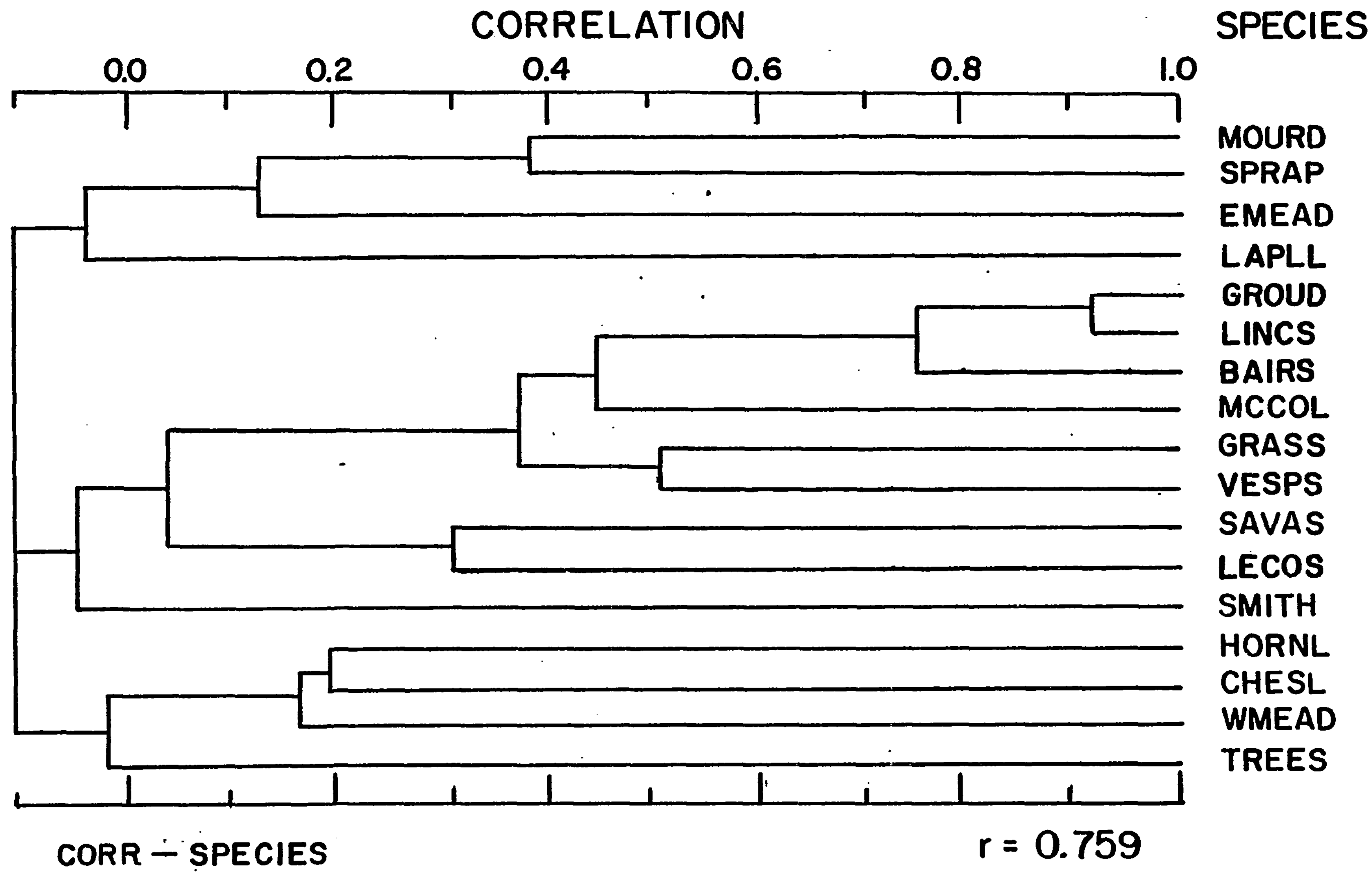

CORRELATION
SPECIES
0.0
0.2
0.4
0.6
0.8
1.0
MOURD
SPRAP
EMEAD
LAPLL
GROUD
LINCS
BAIRS
MCCOL
GRASS
VESPS
SAVAS
LECOS
SMITH
HORNL
CHESL
WMEAD
TREES
CORR — SPECIES
r = 0.759

Figure 6

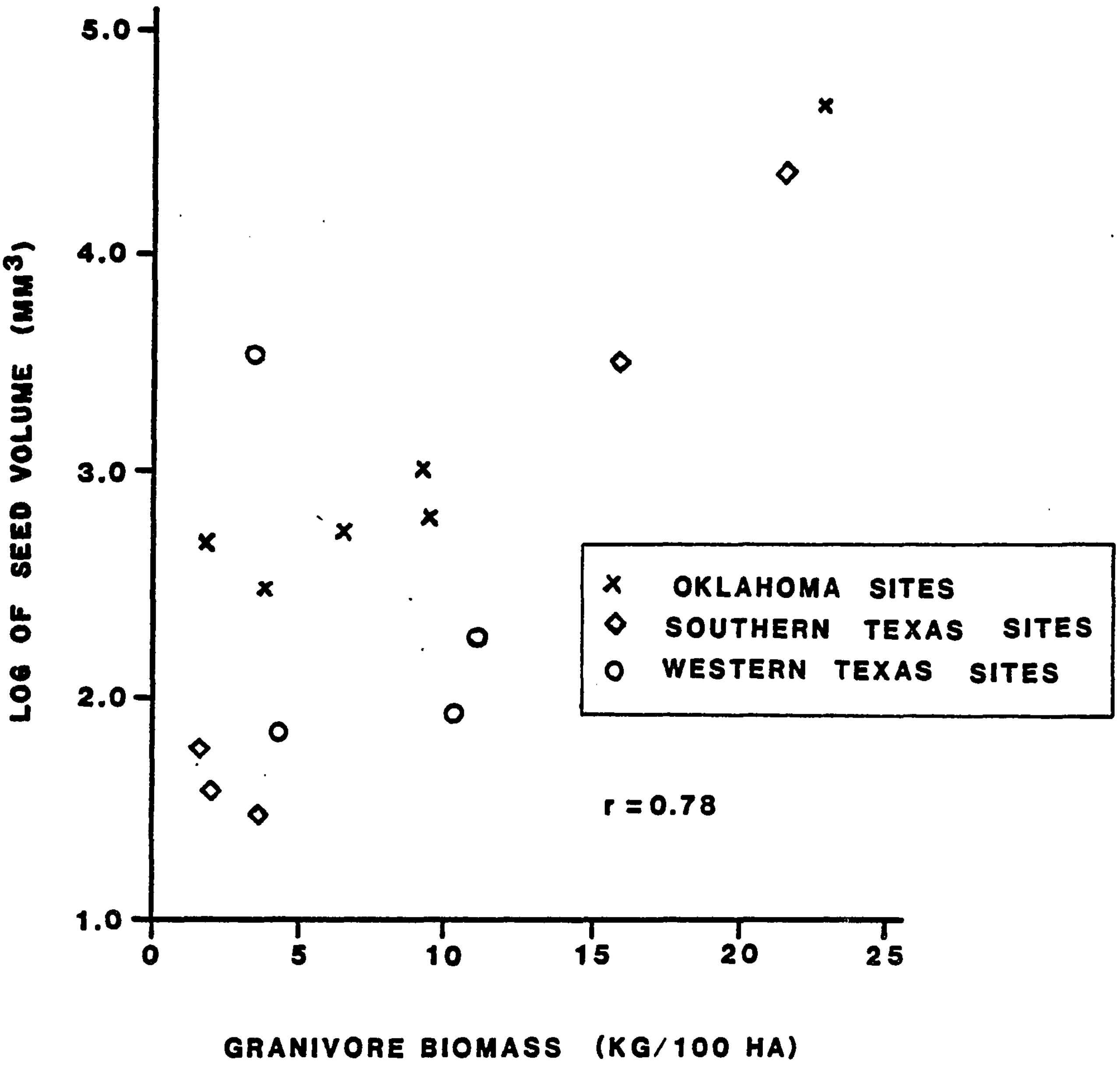
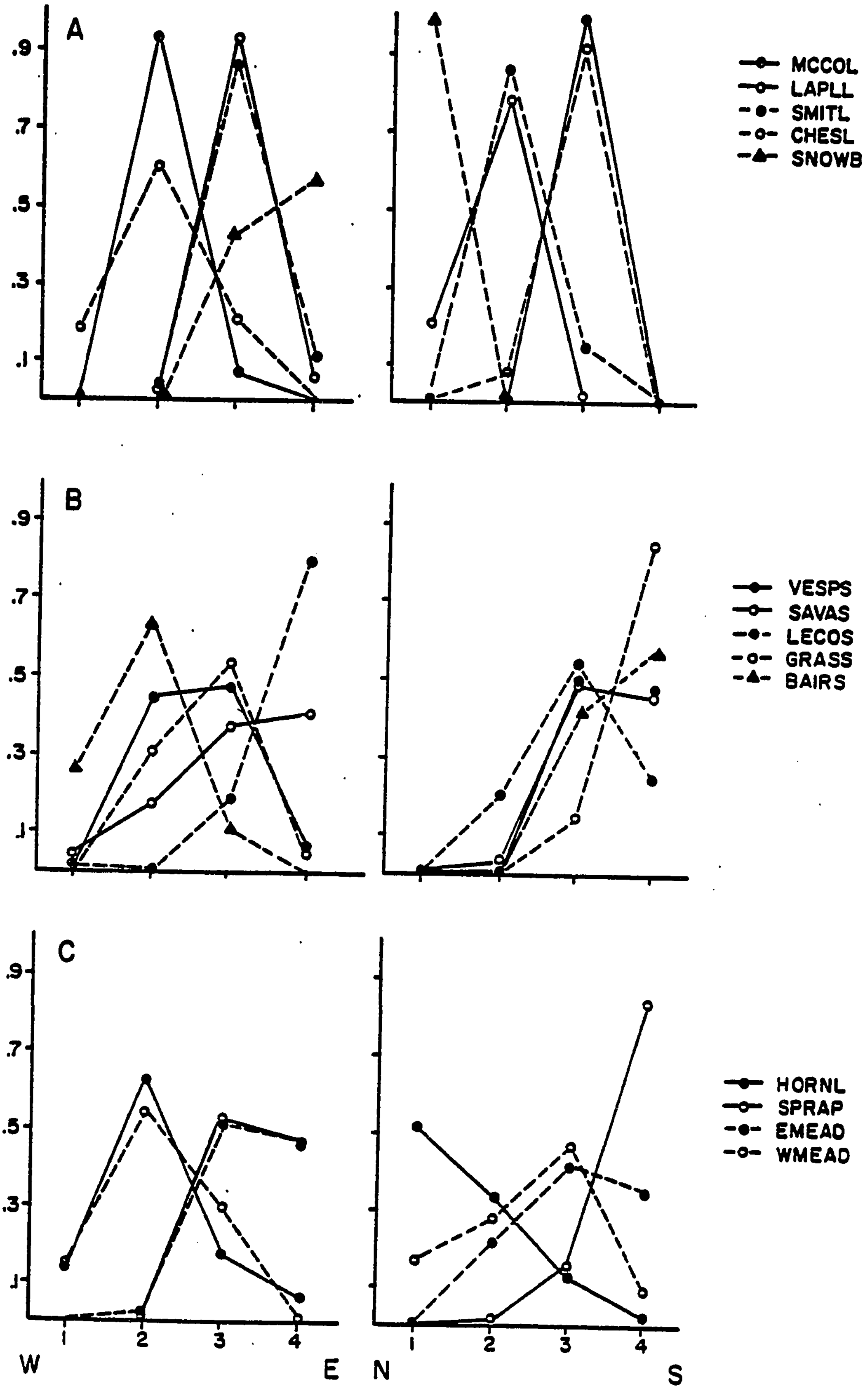

LOG OF SEED VOLUME (MM3)
5.0
4.0
3.0
2.0
1.0
0
5
10
15
20
25
GRANIVORE BIOMASS (KG/100 HA)
× OKLAHOMA SITES
◇ SOUTHERN TEXAS SITES
○ WESTERN TEXAS SITES
r = 0.78

Figure 7


A
B
C
.9
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.3
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MCCOL
LAPLL
SMITL
CHESL
SNOWB
VESPS
SAVAS
LECOS
GRASS
BAIRS
HORNL
SPRAP
EMEAD
WMEAD
1
2
3
4
W
E
N
S

Figure 8

TABLE 1. Location and treatment status of Oklahoma study sites from 1975 through 1979.[a]

Region	County	Locality	Symbol	Winter 1975-76	1976-77	1977-78	1978-79
Central	McClain	Goldsby	1a	LG	MG	MG	MG
Central	Grady	Vincent	1b	LG	LG	MG	MG
Central	Grady	Middleburg	2a	MG	MG	MG	MG
Central	Cleveland	Norman	2b	-	MG	HG	HG
Central	Grady	Tabler	2c	-	MG	MG	MG
Northern	Noble	Red Rock	2d	MG	-	MG	-
Central	Cleveland	Norman	3a	HG	HG	-	-
Northern	Pawnee	Red Rock	3b	HG	-	-	-
Central	Cleveland	Norman	4a	CU	CU	-	-
Central	Cleveland	Norman	4b	-	CU	SG	-
Central	Cleveland	Liberty	4c	-	CU	CU	-
Central	Cleveland	Liberty	4d	-	CU	CU	-

[a] LG=Lightly grazed grassland; MG=Moderately grazed grassland; HG=Heavily grazed grassland; CU=Cultivated; SG=Succesional grassland; -=not sampled.

TABLE 2. January population estimates, total and granivore biomass, and dominance for grassland bird communities in Oklahoma. Population estimates given as birds/100 ha.

Species	Goldsby(1a)[a]				Vincent(1b)				Middleburg(2a)			
	LG[b] 1976	BG 1977	MG 1978	HG 1979	LG 1976	LG 1977	MG 1978	BG 1979	MG 1976	BG 1977	MG 1978	MG 1979
Common Flicker	0	0	0	16	0	0	0	0	0	0	0	0
Horned Lark	0	0	0	49	0	0	6	29	7	5	7	16
Sprague's Pipit	0	0	0	0	0	0	0	0	0	0	0	0
Eastern Meadowlark	3	4	16	20	16	8	8	12	17	14	15	15
Western Meadowlark	0	1	2	8	0	0	0	0	0	0	0	2
Savannah Sparrow	46	23	19	0	0	0	0	0	10	5	5	0
Leconte's Sparrow	43	0	0	0	0	22	0	0	0	0	0	0
Tree Sparrow	0	4	17	32	0	0	0	0	22	1	25	0
Lapland Longspur	0	0	0	0	0	0	0	0	0	0	0	3
Smith's Longspur	0	0	48	150	0	0	0	169	0	0	0	120
Chestnut-collared Longspur	0	0	0	0	0	0	0	0	0	5	37	0
Total Biomass (kg/100 ha)	1.75	1.05	3.85	11.50	1.74	1.16	1.07	6.96	2.69	1.82	2.64	5.79
Granivore Biomass (kg/100 ha)	1.42	0.50	2.00	6.41	0	0.29	0.20	5.65	0.84	0.29	1.01	3.94
Dominance	0.47	0.55	0.31	0.39	1.00	0.61	0.51	0.67	0.29	0.30	0.29	0.61

Species	Norman(2b)			Tabler(2c)			Red Rock(2d)		Norman(3a)		Red Rock(3b)
	MG 1977	MG 1978	MG 1979	MG 1977	BG 1978	MG 1979	MG[c] 1976	BG[d] 1978	MG 1976	MG 1977	MG[c] 1976
Common Flicker	0	0	0	0	0	0	0	0	0	0	0
Horned Lark	0	22	18	28	11	23	19	25	0	0	0
Sprague's Pipit	0	0	0	5	0	0	0	0	0	0	0
Eastern Meadowlark	25	15	15	52	52	23	0	0	50	38	0
Western Meadowlark	0	0	0	0	7	5	0	0	0	0	0
Savannah Sparrow	0	23	0	18	6	0	0	0	56	16	0
Leconte's Sparrow	0	0	0	0	0	0	0	0	0	0	0
Tree Sparrow	0	0	0	0	0	0	0	0	0	0	0
Lapland Longspur	0	0	0	0	0	0	10	0	0	0	0
Smith's Longspur	305	280	320	103	52	181	803	174	690	49	1,182
Chestnut-collared Longspur	0	0	0	69	18	5	41	46	35	46	83
Total Biomass (kg/100 ha)	11.14	10.54	11.07	11.35	8.71	8.92	23.93	6.60	26.25	7.12	89.88
Granivore Biomass (kg/100 ha)	8.41	8.90	9.44	5.56	2.30	5.88	23.93	6.60	20.80	2.98	89.48
Dominance	0.86	0.69	0.83	0.25	0.28	0.60	0.85	0.55	0.70	0.25	0.95

Species	Norman(4a)		Norman(4b)		Liberty(4c)		Liberty(4d)	
	CU 1976	CU 1977	CU 1977	SG 1978	CB 1977	CB 1978	CB 1977	CB 1978
Common Flicker	0	0	0	0	0	0	0	0
Horned Lark	79	21	0	12	32	8	62	56
Sprague's Pipit	0	0	0	14	0	0	0	0
Eastern Meadowlark	53	65	48	41	0	0	19	200
Western Meadowlark	0	2	0	0	0	0	0	0
Savannah Sparrow	0	0	0	1,060	0	0	0	0
Leconte's Sparrow	0	0	0	0	0	0	0	0
Tree Sparrow	0	0	0	0	0	0	0	0
Lapland Longspur	184	131	127	0	0	0	51	99
Smith's Longspur	0	0	0	0	0	0	0	0
Chestnut-collared Longspur	0	0	0	166	0	0	0	0
Total Biomass (kg/100 ha)	13.68	11.73	8.83	27.80	1.09	0.27	5.68	25.51
Granivore Biomass (kg/100 ha)	7.91	4.43	3.60	22.58	1.09	0.27	3.61	4.72
Dominance	0.41	0.46	0.60	0.74	1.00	1.00	0.17	0.82

[a] Site symbols as in Table 1.
[b] Treatment symbols as in Table 1.
[c] Censused 20-21 December 1975.
[d] Censused 6 March.

TABLE 3. January population estimates, total biomass, and dominance of grassland bird communities in western Texas (Muleshoe National Wildlife Refuge). Population estimates given as birds/100 ha.

	5a (MIX)[a]			5b			5c		5d		
Species	LG[b] 1977	LG 1978	LG 1979	LG 1977	LG 1978	LG 1979	LG 1978	LG 1979	HG 1977	HG 1978	HG 1979
Horned Lark	231	82	256	182	38	3	0	0	86	108	213
Eastern Meadowlark	0	26	0	3	0	0	0	0	0	0	0
Western Meadowlark	3	31	10	23	2	4	4	0	21	6	8
Savannah Sparrow	0	6	0	0	0	0	0	0	0	0	0
Baird's Sparrow	14	0	0	20	0	0	0	0	0	0	0
McCown's Longspur	0	0	62	0	0	0	0	0	0	13	17
Lapland Longspur	0	0	13	0	0	0	0	0	0	0	0
Chestnut-collared Longspur	16	30	5	14	0	3	0	0	22	35	122
Total biomass (kg/100 ha)	8.77	9.67	11.97	9.63	1.50	0.59	0.43	0	5.63	5.13	11.10
Granivore biomass (kg/100 ha)	8.45	3.53	10.90	6.85	1.29	0.16	0	0	3.39	4.49	10.25
Dominance	0.77	0.30	0.58	0.58	0.91	0.34	1.00	-	0.50	0.50	0.47

[a] See text for description of sites.

[b] Treatment symbols as in Table 1.

TABLE 4. January[a] population estimates of grassland bird communities in southern Texas (Welder Wildlife Foundation; birds/100 ha).

Species	6a[b]			6b			6c			6d	
	LG[c] 1977	MG 1978	MG 1979	MG 1977	MG 1978	MG 1979	HG 1977	HG 1978	HG 1979	HG 1978	HG 1979
Common Snipe	0	0	0	0	0	13	0	0	0	0	0
Mourning Dove	38	155	39	0	0	9	60	0	0	0	0
Common Ground Dove	25	43	0	0	0	0	0	0	0	0	0
American Robin	0	0	0	0	0	223	0	0	0	0	0
Sprague's Pipit	0	0	4	0	0	0	90	28	42	80	64
Yellow-rumped Warbler	4	0	0	0	0	0	0	0	0	0	0
Eastern Meadowlark	18	43	69	218	75	75	102	202	62	53	145
Cardinal	6	0	0	0	0	0	0	0	0	0	0
American Goldfinch	17	0	0	0	0	0	0	0	0	0	0
Savannah Sparrow	1,228	685	665	1,580	876	919	54	101	141	62	63
Grasshopper Sparrow	47	71	95	0	201	0	0	0	0	0	0
LeConte's Sparrow	237	95	47	1,888	67	263	0	0	51	0	48
Vesper Sparrow	119	213	36	0	0	0	0	0	0	0	0
Lincoln's Sparrow	24	0	0	36	0	0	0	0	0	0	0
Total biomass (kg/100 ha)	38.46	45.91	27.94	78.46	28.93	52.30	21.55	24.58	11.09	8.92	20.16
Granivore biomass (kg/100 ha)	30.86	20.84	15.64	54.70	20.76	20.63	1.01	1.88	3.29	1.16	1.78
Dominance	0.53	0.33	0.51	0.44	0.55	0.57	0.27	0.47	0.32	0.34	0.31

[a] Censuses indicated for January 1977 were actually obtained 21-23 December 1976.

[b] See text for description of sites.

[c] Treatment symbols as in Table 1.

TABLE 5. Proportion occurrence of grassland bird species by 10-degree latitude-longitude grid-blocks. Data from 1962-72 Christmas Bird Counts (see text).

Species	Grid-block														
	11	12	13	14	21	22	23	24	31	32	33	34	42	43	44
Horned Lark	0.04	0.40	0.06	0.02	0.08	0.14	0.10	0.02	0.02	0.09	0.01	0.01	T[a]	0.01	0.01
Sprague's Pipit	0	0	0	0	0	0	0.01	T	0	T	0.05	0.11	0	0.47	0.37
Eastern Meadowlark	0	0	0.02	0.01	0	0	0.12	0.09	T	0.01	0.23	0.18	0	0.14	0.20
Western Meadowlark	0.06	0.05	0.05	T	0.04	0.07	0.16	0.02	0.04	0.38	0.05	T	0.05	0.04	T
Savannah Sparrow	0	0	T	T	0	T	0.02	0.01	0.04	0.16	0.12	0.18	0.02	0.24	0.22
Grasshopper Sparrow	0	0	0	0	0	0	0	0	0	0.06	0.07	0.02	0.25	0.58	0.03
Baird's Sparrow	0	0	0	0	0	0	0	0	0.26	0.16	0	0	0.48	0.11	0
LeConte's Sparrow	0	0	0	0	0	0	0	0	0.26	0.16	0	0	0.48	0.11	0
Vesper Sparrow	0	0	0	T	T	T	0.01	T	0.02	0.26	0.18	0.05	0.19	0.29	0.01
McCown's Longspur	0	0	T	0	0	0.01	T	0	0	0.92	0.07	0	0	0	0
Lapland Longspur	T	0.01	0.16	0.04	T	T	0.78	0.01	T	T	T	0.01	0	0	0
Smith's Longspur	0	0	0	0	0	0	0.84	0.02	0	0.01	0.02	0.10	0	0	0
Chestnut-collared Longspur	0	0	T	0	T	0.07	0.02	0	0.18	0.54	0.20	0	0	0	0
Snow Bunting	0.01	T	0.39	0.51	T	0	0	0	0	0	0	0	0	0	0

[a] T= trace (<.005).

TABLE 6. Mean biomass (kg/100 ha) and dominance estimates for various treatment groupings in different regions of Oklahoma and Texas. Standard Deviation (SD) given in parenthesis. Treatment symbols as in Tables 2 and 3.

		Biomass					
Treatment	N	Total	Granivore	Meadowlark	Insectivore	Dove	Dominance
Northern Oklahoma							
MG	1	23.93	23.93	0	0	0	0.849
HG	1	89.48	89.48	0	0	0	0.951
Central Oklahoma							
LG	3	1.55	0.57	0.98	0	0	0.693
		(0.34)	(0.75)	(0.71)			(.275)
MG	12	5.50	3.04	2.44	0.01	0	0.450
		(3.84)	(2.76)	(1.82)	(0.03)		(.213)
HG	5	13.30	9.71	3.18	0.41	0	0.572
		(7.45)	(6.71)	(1.65)	(0.92)		(.238)
CU	7	9.54	3.66	6.02	0	0	0.614
		(8.66)	(2.51)	(7.52)			(.272)
SG	1	27.50	22.58	4.47	0.35	0	0.737
Western Texas							
LG	5	2.43	1.66	0.77	0	0	0.566
		(4.06)	(1.95)	(1.14)			(.411)
MIX	3	10.13	7.63	2.51	0	0	0.553
		(1.65)	(3.75)	(3.17)			(.236)
HG	3	7.28	6.04	1.24	0	0	0.489
		(3.31)	(3.68)	(0.87)			(.018)
Southern Texas							
LG	1	38.46	30.86	1.96	0.005	5.59	0.525
MG	5	46.71	26.51	10.46	4.53	5.20	0.479
		(20.67)	(15.91)	(7.57)	(10.07)	(8.70)	(.099)
HG	5	17.26	1.82	12.99	1.50	1.44	0.342
		(6.86)	(0.90)	(6.73)	(0.64)	(3.22)	(.078)

TABLE 7. Multiple-range test comparisons of biomass for treatments within and among regions.

Central Oklahoma				Southern Texas		Western Texas		
LG[a]	MG	HG	CU	MG	HG	LG	MIX	HG
				Total Biomass				
AA[b]	AA		AA			AA		AA
		BB	BB		BB		BB	BB
				CC				
				Granivore Biomass				
AA	AA		AA		AA	AA		AA
		BB					BB	BB
				CC				
				Meadowlark Biomass				
AA	AA	AA	AA			AA	AA	AA
			BB	BB				
				CC	CC			

[a] Treatment symbols as in Tables 1 and 3.

[b] Treatments with same letters are not significantly different (*P*>.05).

APPENDIX. Systematic list of species occurring on censuses with ecological category designations and mean weights.

Common name	Scientific name	Species symbol	Category[a]	Mean Wt. (g)
Common Snipe	*Capella gallinago*	COMMS	I	104.0
Mourning Dove	*Zenaidura macroura*	MOURD	D	120.0
Common Ground Dove	*Columbina passerina*	COMMD	D	41.4
Common Flicker	*Colaptes auratus*	COMMF	I	128.7
Horned Lark	*Eremophila alpestris*	HORNL	G	34.1
American Robin	*Turdus migratorius*	AMERR	I	95.0
Sprague's Pipit	*Anthus spragueii*	SPRAP	I	24.8
Yellow-rumped Warbler	*Dendroica coronata*	YELLW	I	13.1
Eastern Meadowlark	*Sturnella magna*	EMEAD	M	109.0
Western Meadowlark	*Sturnella neglecta*	WMEAD	M	106.7
Cardinal	*Cardinalis cardinalis*	CARDI	G	45.8
American Goldfinch	*Carduelis tristis*	AMERG	G	13.8
Savannah Sparrow	*Passerculus sandwichensis*	SAVAS	G	18.7
Grasshopper Sparrow	*Ammodramus savannarum*	GRASS	G	17.7
Baird's Sparrow	*Ammodramus bairdii*	BAIRS	G	18.2

LeConte's Sparrow	*Ammospiza leconteii*	LECOS	G	13.0
Vesper Sparrow	*Pooecetes gramineus*	VESPS	G	26.1
Tree Sparrow	*Spizella arborea*	TREES	G	18.8
Lincoln's Sparrow	*Melospiza lincolni*	LINCS	G	17.5
McCown's Longpsur	*Calcarius mccownii*	MCCOL	G	27.6
Lapland Longspur	*Calcarius lapponicus*	LAPLL	G	28.4
Smith's Longspur	*Calcarius pictus*	SMITL	G	27.6
Chestnut-col. Longspur	*Calcarius ornatus*	CHESL	G	20.7

[a] D--doves; G--granivores; I--insectivores (other than meadowlarks); M--meadowlarks.

SOCIALITY AND SPACE USE OF GRASSLAND BIRDS DURING WINTER.

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Abstract: Sociality and space use of passerine birds occupying open grasslands of the south-central United States were evaluated during winter in relation to various ecological attributes. Passerine birds in temperate grasslands are primarily granivorous during winter. Of the granivores, sparrows were more sedentary, tended to be solitary and occupied the taller and denser grasslands; the highly mobile longspurs and horned larks were more gregarious and occupied the sparser and shorter grasslands. However, savannah sparrows, when at moderate to high densities in suitable habitat, formed groups of widely-spaced individuals. When disturbed, these individuals would aggregate and move along predictable circular paths.

Measures of sociality (group size, individual distance, and percent of individuals solitary) were highly correlated with habitat variables (vegetation height and density) for all granivores, but not for sparrows, or longspurs and horned larks separately. No solitary species occupied sparse, exposed habitats, but one longspur species, the Smith's

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Longspur, occurred in flocks in dense but short grass. For sparrows, bird density increased with seed density; group size increased with both bird and seed density. Group size was positively correlated with seed density for longspurs. No association of bird density with seed density was found in this group.

A solitary strategy is favored in grasslands where concealment from predators is good, bird density (which might attract predators) is low, and few perches for aerial predators are present. Solitary species were generally found in low densities in comparison to other species. LeConte's sparrows were always solitary and occupied grasslands with the densest and tallest vegetation. Lapland longspurs, in contrast, were highly gregarious and preferred cultivated fields (in central Oklahoma) devoid of vegetation cover.

Key words: Alaudidae; flush distance; Fringillidae; grasslands; habitat density; meadowlarks; Motacillidae; Oklahoma; predation; sociality; space use; Texas; winter.

INTRODUCTION

Spatial relations of birds are the result of natural selection acting to maximize an individual's fitness. Flocking may enhance the efficiency of food exploitation (Crook 1965, Morse 1970, Cody 1971). Environmental features, such as nesting or roosting sites, or the amount of cover, can also influence sociality and space use of individuals (Davis 1973, Post 1974, Snapp 1976, Pulliam and Mills 1977, Pleasants 1979). Spacing patterns and gregariousness can aid in predator avoidance and afford protection (Bertram 1978, Murton et al. 1963, Kenward 1978, Pulliam 1973).

Pulliam (1973) and Powell (1974) suggested that advantages of enhanced food exploitation and predator detection may interact in foraging flocks. An individual joining a flock can benefit from another group member's detection of predators; it could thus reduce its time scanning for predators and increase its foraging time without incurring a decrease in its probability of avoiding predation. However, Goss-Custard (1970) and Caraco (1979) pointed out that group membership may have disadvantages, such as increasing susceptibility to disease or parasites, foraging interference, and increasing costs associated with intraspecific aggression. Sociality of birds reflects a balance of selective forces acting both to draw organisms together and spread them apart.

This paper deals with the spatial relations of passerine birds occupying open grasslands in temperate regions during winter. These habitats are relatively simple in structure compared to scrub and woodland habitats and often occur in large homogeneous tracts. Granivory is the primary and almost exclusive foraging mode of grassland birds, further simplifying the system. Climatic severity and reduced winter daylength necessitate effective exploitation of food resources.

While most passerines are territorial during the breeding season, many gather into flocks during the non-breeding periods. Longspurs (*Calcarius* spp.), with flocking habits (Bent 1968), are characteristic of many open grasslands; yet solitary species, particularily of the genera *Ammodramus* and *Ammospiza*, can also be found in grasslands (Murray 1969, Pulliam 1975). Grasslands provide a simple homogenous setting in which factors affecting extremes in sociality can simultaneously be assessed. In the present study, I evaluate space use and sociality in relation to various resource attributes, bird density, and predator avoidance strategies.

METHODS

Grasslands of varied grazing pressure or cultivation practices in several regions of Oklahoma and Texas were used. Data were collected at 14 sites from the winters of 1975-76 through 1978-79. The sampling period began 15 November and ended 15 February for each season. One Oklahoma site was also sampled in January and February 1975. The sites included seven in central Oklahoma (Cleveland, Grady, and McClain counties), three in western Texas (Muleshoe National Wildlife Refuge, Bailey County), and four on the Rob and Bessie Welder Wildlife Refuge (San Patricio County) in southern coastal Texas (Fig. 1). The size of sites ranged from about 30 ha on the smallest sites in southern Texas to greater than 100 ha. Sites were characterized by their uniformity and large size, thus minimizing edge effect with other habitats. Two of the southern Texas sites contained about 5% shrub cover. Otherwise tree or shrub cover were absent or comprised less than 0.5% cover, consisting of isolated individual plants less than 3 m in height.

Sites were classified on the basis of grazing pressure or cultivation practices. A site was considered a lightly grazed grassland (LG) when the dominant palatable grasses had uniformly grown to heights approaching their maximum potential heights. For LGs in Oklahoma and southern Texas, maximum vegetation heights ranged from 1 to 2 m. In western Texas, maximum grass heights of LGs were about 0.5 m. When dominant palatable grasses occurred in distinct clumps, the site was designated a moderately grazed grassland (MG). Vegetation heights of MGs were up to 1 m in Oklahoma, and 1.5 m in southern Texas. When the dominant palatable grasses were absent, or present only in widely scattered clumps and/or grazed to near ground level, the site was considered a heavily grazed grassland (HG). Vegetation heights in HGs were less than 0.5 m on all sites. The cultivated sites were planted with winter wheat (<u>Triticum aestivum</u>); these sites had been harvested of a sorghum (<u>Sorghum bicolor</u>) crop in fall. On one cultivated site, only the heads of the sorghum were removed; the field was left fallow in this condition for the winter observation period. More detailed site descriptions are given in Grzybowski (1980a).

Habitat variables used were vegetation height (HHT) and vegetation density (HDEN). Vegetation height for a 15 meter-square block was the average of four point samples about 1 m apart, and measured to the nearest centimeter. HDEN is:

$$HDEN = \sum_{m=1}^{4} \sum_{k=1}^{25} x_{km} \qquad (1)$$

where x_{km} is the number of vegetation contacts made with the tip of a wire passed through the vegetation for 30 cm at the *k*th height (at 10-cm intervals from 5 to 240 cm), and *m*th point (of four).

Habitat preferences were determined in the 1975-76 and 1976-77 seasons for each species on each specific grazing treatment (Grzybowski 1980b). Strips 1,000 X 60 m were established on each site, and these divided into 15 meter-square blocks. Frequency occurrence of bird species in the blocks was recorded during visits to each treatment type. The species preferred habitat on a given site was determined by averaging the HHTs and HDENs of blocks in which the species was observed. Each block used by a bird species was weighted by the frequency occurrence of that species in the block.

Additional habitat sampling was conducted to characterize preferred horned lark and chestnut-collared longspur habitats on a HG in western Texas during the 1977-78 and 1978-79 seasons. Thirty samples, measured as above, were obtained at locations from which these species were flushed, and averaged to provide preferred habitat values.

Seed samples were obtained in January of 1978 and 1979 on 9 of the 14 sites. Areas occupied by a species (as characterized through the space-use data and general impressions of occupied habitat) were sampled. Seed samples within these habitats were obtained by brushing debris from the surface of 15 to 30 randomly selected points, each 10 X 10 cm, into a container. Seeds from these samples were sorted into size classes and counted. Frequency data for seeds were transformed to a volume estimate with the formula:

$$SDEN = \sum_{i=1}^{n} (4/3)(\pi r_i^3 Y_i X_a), \qquad (2)$$

where r_i is the radius of mean seed size in the *i*th class, *n* is the number of classes, Y_i is the number of seeds in the *i*th class, and X_a is the correction factor to standardize seed volume (to cubic millimeters of seeds per square meter for sample *a*). This provided a relative index of seed availability among the sites in mid-winter.

Estimates of bird densities were obtained for sites from November through February by the Emlen (1971) strip method. January population estimates (December 1976 on southern Texas sites) for each species were used in the analysis; these estimates represent a mid-winter period when species composition appeared most stable (unpubl. data). One extremely high estimate of LeConte's sparrow is treated separately. November estimates for horned larks were used to avoid the beginning of the reproductive period (Bent 1942).

Two types of data characterizing sociality were collected: (1) individual distance (IDIS); and (2) group size (GSIZ). The IDIS was estimated for pairs of individuals encountered on the ground or recently flushed: (a) in body lengths for distances less than 1.5 m; (b) to the nearest 0.5 m for distances less than 5 m; and (c) to the nearest meter for distances greater than 5 m. For each individual for which the IDIS was obtained, the distance and the species' name were recorded. When the nearest individual was not a conspecific, the distance to the nearest conspecific was also obtained (if less than 25 m) through direct observation, or by walking spirally around the bird's flush point to 25 m. For solitary species, special attempts were made to locate the nearest conspecific to as far as 100 m. Distance estimates were obtained by pacing when greater than 5 m. A marker was placed at the flush point of solitary individuals to act as a reference when a second individual was encountered.

The GSIZ was the number of individuals of a species which responded similarily to disturbance by the observer, or were observed foraging together as a unit distinct from other individuals. Groups which flushed from locations within 30 m of each other and later joined in flight (as in longspurs), were considered separate from each other. Individuals in proximity of each other which flew in different directions (as did occasionally happen with some sparrow species) were considered separate from each other. Only observations made on the first pass through a site on each visit were used. The IDIS and GSIZ of individuals known to be moving ahead of the observer (and of birds which these individuals joined) were recorded only once in any site visit. Observations of single individuals occurring with larger groups of other species are ignored in the GSIZ analysis. From data on GSIZs, the percent of solitary individuals (SOL) of a species was calculated. This variable estimates the proportion of individuals acting independently of any other individuals of their own or other species. Data on GSIZ and IDIS were collected from 0.5 h after sunrise to 1.5 h before sunset to avoid effects of behavior associated with roosting.

To evaluate responses of birds to potential predators, flush distances to the observer were obtained. Flush distance was the distance (to the nearest meter) a bird would allow the observer walking at a moderate pace to approach. Maps were made of several of the sites, and the flushing and landing points of individuals recorded for up to 10 consecutive flushes to evaluate horizontal space use. I made estimates of the distance a bird would fly when flushed; however, this proved difficult for longspurs and horned larks. On some occasions, responses of birds to various aerial predators were also recorded.

Measures of sociality, flush distance, and bird density were averaged over winter seasons and within grazing treatments to provide a value for each species. Habitat preferences were determined for a species occupying a particular grazing treatment (within a region) during the 1975-76 and 1976-77 seasons. Seed densities obtained on sites during the 1977-78 and 1978-79 seasons were used to characterize seed availability in habitats.

Distinctions were made in western Texas among HGs grazed by cattle and those grazed primarily by prairie dogs (PD). Observations made in January 1979 were separated from those made in the 1976-77 through 1977-78 seasons for a HG in western Texas; the site was ungrazed in 1978 and was in its initial stages of recovery in January 1979. Observations of LeConte's Sparrows on a LG in southern Texas were also separated from the others for analysis.

Data were divided into those for granivorous species and those for insectivorous species. Two behavioral subsets of granivores were analyzed: (1) flyers, which included those species regularily observed moving between grasslands, and (2) sparrows, which included more sedentary species never observed flying high over grasslands. Of the flyers, longspurs were dealt with separately. These distinctions are shown in Table 2.

To evaluate similarities in sociality among the species occurring on various treatments and regions, a cluster analysis was performed. NT-SYS (Numerical Taxonomy Systems), a series of multivariate computer programs developed by F.J. Rohlf, J. Kishpaugh, and D. Kirk, was employed. Product-moment correlation coefficients were calculated between all pairs of species. Clusters were formed with the unweighted pair-group method, using arithmetic averages, and summarized in dendrograms. The cophenetic correlation was computed between values in the correlation matrix and the cophenetic values of the cluster analysis to assess the amount of distortion in the dendrogram (Sokal and Rohlf 1962).

RESULTS

Mean values of social and ecologic variables for each species by grazing treatment and region are given in Table 1. All three sociality measures were significantly correlated with each other ($P<.001$) for the major groupings (granivores and insectivores). As GSIZ increased, IDIS and SOL decreased ($r=-0.79$ and -0.78, respectively for the granivore data; $r=-0.77$ and -0.83, respectively for the insectivore data). Correlations of IDIS with SOL were 0.84 for the granivore data and 0.95 for the insectivore data. The ecological measures of HDEN and HHT were also significantly correlated ($r=0.94$ and 0.92 for the granivore and insectivore data, respectively; $P<.001$). SDEN was weakly but significantly correlated with BDEN ($P<.05$) for granivores ($r=0.61$) and sparrows ($r=0.83$), but not for flyers ($r=0.20$; $P>.05$).

Correlations of ecologic variables with GSIZ, IDIS, and SOL are given in Table 2. For granivores, GSIZ, IDIS, and SOL were significantly correlated with HDEN and HHT ($P<.01$). As HDEN (or HHT) increases, GSIZ decreases and IDIS and SOL increase. IDIS and SOL decrease with increases in BDEN

(*P*<.05). Densities of LeConte's Sparrows on one site in southern Texas (December 1976) were very high; more than seven times higher than the next highest estimate (Grzybowski 1980a), and far above what previous investigators had encountered (Emlen 1971; G. Blacklock, pers. comm.). With this observation included, the correlation of SOL with BDEN for granivores is non-significant (*r*=-0.35; *P*>.05).

For insectivores, GSIZ increases with BDEN (*r*=0.67; *P*<.05). Correlations of IDIS and SOL with any ecologic measures are not significant (*P*>.05; Table 2). Insectivores included meadowlarks (*Sturnella* spp.) and one sample for Sprague's pipit. This latter species was solitary in all encounters included here and at all other localities where observed (unpubl. data). When this species was removed, the correlations of BDEN with GSIZ increased to 0.81 (*P*<.01), -0.73 (*P*<.05) with IDIS, and -0.85 (*P*<.05) with SOL. Densities of meadowlarks were low in open grasslands compared to peripheral and adjacent areas where some scrub was present, and along roads (unpubl. data). Meadowlarks were normally found in groups in these areas.

When the two granivore subgroups (i.e., sparrows and flyers) were analyzed separately, the correlations of GSIZ, IDIS or SOL with HDEN and HHT became non-significant (*P*>.05; Table 2). Among the sparrows, mean GSIZ never exceeded 4.2 individuals, and was 3.0 or less in all other cases (Table 1). The highest GSIZ values for sparrows occurred for savannah sparrows at very high densities (1,228 birds/100 ha). HDEN was never below 30 vegetation contacts per grid sample for sparrow habitats. However, longspurs and horned larks usually occurred in groups of much greater than five individuals, and almost always occurred at vegetation densities of less than 30 vegetation contacts.

GSIZ was correlated with SDEN for sparrows (r=0.88; P<.001) and for flyers (r=0.72; P<.01), but not for both taken together (Table 2). The correlation of GSIZ with SDEN for longspurs was significant (r=0.94; P<.01). For sparrows, GSIZ increased less in relation to SDEN than for longspurs (Fig. 2).

Higher values of GSIZ in sparrows may have been the result of increased BDEN. BDEN was significantly correlateed with SDEN (r=0.75; P<.05) for sparrow habitats. Correlations of GSIZ with BDEN was 0.82 (P<.01). All the variation on GSIZ was recorded within savannah sparrows. As BDEN of savannah sparrows increased, individuals were closer together, and, at high densities, tended to respond together. GSIZ was significantly correlated with BDEN for savannah sparrows (r=0.95; P<.01).

SOL was inversely correlated with SDEN for sparrows (r=-0.80; P<.01). SOL was associated with BDEN (r=-0.76; P<.01). Three of the five sparrow species (LeConte's sparrow, grasshopper sparrow, and Baird's sparrow) were always solitary and occurred in relatively seed-poor habitats (Table 1).

For longspurs, the correlation of IDIS with SDEN was -0.90 (P<.01). Lapland longspurs occurred in habitats with high SDEN compared to Smith's longspurs (Table 1). IDIS was lower among lapland than Smith's longspurs. Chestnut-collared longspurs maintained the highest IDIS of all the longspurs in habitats with the lowest SDEN.

A cluster analysis, using the four ecologic and three sociality measures above, and also the flush responses, as variables, summarizes similarities of species by treatment and region (Fig. 3). Three groups are thus distinguished: one composed of sparrows, where the species are solitary and occupy tall and dense habitats; one containing horned larks and lapland longspurs where the species are highly gregarious in sparse habitats; and a group with intermediate habitat and sociality characteristics. When sociality measures were removed in the cluster analysis, the results were very similar. Thus, ecologic characteristics are an indicator of sociality.

SPACE USE

Space use patterns exhibited by grassland birds are depicted in Fig. 4. Each square represents an area which is large relative to the individual bird. Space use patterns vary from those of the LeConte's sparrow (Type 1), where individuals appear territorial, to those of species like lapland longspurs (Type 4b), where individuals utilize large continuous areas, but where the distribution of individuals at any time is highly clumped. Patchy use of grassland habitats is exhibited by gregarious species (Type 4a) and solitary species (Type

2b). Each type is discussed below.

LeConte's sparrows were solitary. On a LG in central Oklahoma, they could regularly and predictably be located within particular 15-m grid-blocks. Their locations, made from plots of their flush routes taken from December 1975 through February 1976 (Fig. 5), strongly implicate active spacing mechanisms, and perhaps territoriality. For each pair of "territories" in Fig. 5 which border each other, the two birds were flushed within several minutes of each other on at least one occasion. On four occasions, when LeConte's sparrows flushed a second time returned in the direction of their original flush, a second sparrow was flushed just beyond the first bird's landing point. Boundaries for bird movements were difficult to assess for one area (delimited by dashed lines in Fig. 5) occupied by at least four, but perhaps eight, individuals. Many of their flush paths crossed each other. On one southern Texas site which supported a very high density of LeConte's sparrows, spacing patterns were so regular in some patches, that as many as 12 to 17 different birds (three occasions) were flushed, one every five to seven steps, but no closer. These latter observations further suggest active spacing mechanisms in this species.

Baird's and grasshopper sparrows were also solitary on LGs in western and southern Texas, respectively. Few observations of these species were made but they appeared to exhibit spacing patterns of type 2a (Fig. 4). Distances flushed by Baird's sparrows were more than triple those for other solitary species. Of 14 initial flushes of Baird's Sparrows, three birds flew to landing positions beyond the resolution of the observer watching with 7X35 binoculars. Birds were observed in two of three locations from which an individual was earlier removed. On one occasion, a Baird's sparrow landed within 5 m of a second sparrow. Both flushed in opposite directions as was the case with LeConte's and grasshopper sparrows flushed from adjacent locations.

Savannah sparrows were variable in the use of space. They exhibited type 2b spacing patterns (Fig. 4) on a LG in central Oklahoma where distinct patches (With lower vegetation height and density than the site means; Grzybowski 1980b) were regularily utilized. Only 1 bird/patch occurred in the smallest patches. Birds in patches occupied by more than one individual were normally solitary, but flew near each other when disturbed. On MGs in Oklahoma, where patchiness of habitat was not distinctive, birds exhibited type 2a spacing patterns similar to Baird's sparrows in western Texas.

On some sites, where savannah sparrow densities were high, the type 3 spacing pattern (Fig. 4) was observed. Savannah sparrows were widely spaced when first encountered, but often joined in groups when disturbed. On areas where moderate to high densities occurred, these groups would continue to grow in numbers as I progressively chased birds about the area. The groups would travel circular paths within certain bounds. Fig. 6 shows areas occupied by groups of sparrows on an Oklahoma site. Boundaries of areas utilized by groups were much less well defined on a southern Texas site where densities were very high. Unlike the Oklahoma-site birds, the paths of groups in southern Texas overlapped and could not clearly be defined.

That savannah sparrows on southern Texas sites formed persistent social units is doubtful. If a sparrow was flushed while other birds were in the air, it would join them, even if it meant flying in a path around, rather than away from, the observer. However, indiviudals flushed at a time when no other birds were in the air usually flew ahead of the observer, even if this direction was away from already grouped savannah sparrows. Birds flushed subsequently, but while the first bird was still airborne, would join this first individual. The direction of travel of subsets of potentially larger groups could change in this manner. However, location calls of an individual or individuals on the ground often attracted a newly flushed bird. Little synchrony among individuals in a group was evident. Birds on the ground at the hind edge of a group often flushed forward in subgroups of one to 20 individuals. Groups of up to 65 and 75 birds were observed on the southern Texas and Oklahoma sites.

On one Oklahoma site, about 30 savannah sparrows which formed into a group could be chased to the edge of their cover, where they circled back and dispersed as solitary birds. A repeat performance occurred in 0.5 h, when all birds were dispersed singly. This behavior was noted over and over again on my other visits to the site. Basically, savannah sparrows on this site maintained solitary behavior except when disturbed.

Smith's and chestnut-collared longspurs were gregarious but frequented specific patches of a grassland site (Type 4a; Fig. 4). Fig. 7a and 7B shows space use by Smith's and chestnut-collared longspurs, respectively, on a HG site in central Oklahoma. Chestnut-collared longspurs were much more common on this site in November, before Smith's longspur arrived; Smith's was more abundant in mid-winter. Use by Smith's appears to favor particular patches which were characterized by dense growth of three-awn (Aristida sp.) and silver beardgrass (Andropogon saccharoides; unpubl. data); chestnut-collared longspurs occur mostly in pockets of sparser, but similar vegetation (Table 1; Grzybowski 1980b) between areas used by Smith's longspurs (Fig. 7A and B). Smith's longspurs observed on two other sites also favored dense patches of three awn and silver beardgrass (unpubl. data). Chestnut-collared longspurs observed on MGs, where no other longspur species occurred, used particular areas extensively during one winter season (unpubl. data). When disturbed in these circumstances, these species would move in a group to another similar patch.

Lapland longspurs and horned larks are generally gregarious. They exhibited type 4b spacing patterns (Fig. 4). Lapland longspurs on most cultivated sites in central Oklahoma, and horned larks on a prairie dog town in western Texas occupied extensive and continuous areas of their site.

However, at any one time their distribution was clumped. IDIS for these species was low (Table 1). They were often observed flying overhead from most grassland sites, and often from non-grassland sites in loosely spaced groups.

In western Texas, seed densities were generally lower than in Oklahoma. In two years of the study, chestnut-collared longspurs were widely scattered during the day (0830-1600 h). Single birds were located. One very widely spaced group of 16 was located (in 19 days of observation), in addition to other groups of five, seven, and 11. All other observations were of one or two birds. Seed abundance was low compared to other sites, and may account for the solitary foraging behavior of these birds. These birds exhibited type 2c spacing patterns (Fig. 4). In January 1979, one or two groups of chestnut-collared longspurs (numbering about 18 to 30) were located on a heavily grazed site in patches where three-awn was conspicuous; they exhibited type 4a spacing patterns (Fig. 4). SDEN was also higher in these patches than in other areas where single birds occurred.

PREDATOR AVOIDANCE

Predator avoidance may also influence sociality, and may be responsible for some of the patterns observed. Solitary species occurred only in the grasslands with high HDEN. Gregarious species occurred in habitats with low or intermediate HDEN. Solitary passerines never occurred in sparsely vegetated grasslands.

Concealment could be an effective method of avoiding predators for LeConte's, grasshopper, and Baird's sparrows. They occur in the densest habitats in their region, and have very low flush distances (2.0, 4.5, and 3.4 m, respectively). LeConte's sparrows were reluctant to flush consecutive times when chased. Of 320 attempts, 144 could be flushed twice and only 29 of these 144 were flushed three times. None could be flushed four consecutive times. Their short flush distances help them avoid predators, since dense grass makes the probability of detection low. Ground predators can be detected by sound in dense grass. Because observability of predators by sparrows is also hampered, a sparrow flushing too soon may fly towards a predator. In open grassland, aerial predators have few perches from which to observe activities, further enhancing predator avoidance for sparrows.

However, for high HDEN to be used most effectively in predator avoidance, BDEN also needs to be low. Just as BDEN is correlated with SDEN, so would we expect the relation of predators with their sparrow prey. High BDEN increases the chances of a predator encountering a prey. The habitats in Oklahoma and western Texas with the densest and tallest vegetation have the lowest seed densities (Table 1). Thus, these habitats are predictably food sparse. Persistent solitary habits for species occupying these habitats may have evolved in response to this condition (even though exceptionally high densities were recorded on one site). BDEN would be higher in adjacent habitats, attracting predators to these relatively bird-rich areas.

Smith's longspurs occurred in dense patches of three-awn and silver beardgrass. The vegetation in these grasslands is not as tall as habitats of LeConte's and grasshopper sparrows, but were generally seed-rich compared to adjacent microhabitats. Higher seed densities will attract more birds. Since BDENs will also be higher, bird predators could potentially move profitably from patch to patch. Smith's longspurs are gregarious. When disturbed, their groups fly up calling. The response of the group may serve to distract predators' attention from any one individual, and thus serve in predator avoidance (Vine 1971, Kenward 1978). A solitary strategy may not be as successful for this species. Because one individual would elicit a group flush response (pers. obs.), flocking aids in earlier detection of predators for most group members.

Flocking can enhance predator detection as well as create distraction tactics against predators in sparsely vegetated habitats. Lapland longspurs and horned larks occur in sparse habitats with almost no cover. Lapland longspurs form large groups, and horned larks in November (pre-breeding) were primarily flockers. Chestnut-collared longspurs observed in migration in plowed fields were also seen in large groups. I observed prairie falcons (_Falco mexicanus_) attempting to capture these species on four occasions; the falcons flew low toward a flock. These longspurs and larks all flew up in response to a falcon, forming into a tight group. Horned

Larks responded similarily to burrowing owls (Athene cunicularia) accidently flushed by the observer into the flocks.

Some sexual differences in response to the observer were noted in chestnut-collared longspurs. The strikingly colored males tended to move behind grass clumps when approached. When observed in a cultivated field, males would actively move into furrows not aligned with the observer. However, the few females observed (11) would generally be still, even if exposed to the observer.

Motionless behavior was also typical of Smith's longspur. To observe flocks of Smith's longspurs on the ground, it was necessary to know where a group had landed and approach very slowly to within 20 m of this location. Then, the observer would need to wait 10 to 20 min before a bird, often unobstructed from view, would move its head. Thus, Smith's longspurs and female chestnut-collared longspurs may use their camouflage in preference to flushing to avoid detection of potential predators.

Savannah sparrows were once observed feeding among a flock of chestnut-collared longspurs when a loggerhead shrike (Lanius ludovicianus) flew over. Every longspur flew up into a tight flock; every savannah sparrow (about 15 individuals) held its ground, indicating that this latter species depends on camouflage to avoid detection of aerial predators.

Sprague's pipits were solitary and occurred in habitats with low vegetation height (14.1 cm, SD=13.2) and moderate vegetation densities (29.7 vegetation contacts per grid sample, SD=13.2). Pipits were fairly common on some HGs in southern Texas. They behaved like savannah sparrows on the ground, moving away from the observer when approached. They could be approached to about 20 m when stalked slowly; flush distance was 12 m. However, when flushed, a Sprague's pipit would fly high, often giving a loud alarm call as do longspurs. It would often fly up to considerable heights, hover and then drop quickly to a safe location. Occasionally other Sprague's pipits would flush at distances much greater than 50 m from the observer after a flushed individual gave its alarm call. This behavior may be used to observe potential predators from a safe location, and may also serve to alert other pipits of the potential predator's presence. Responses of Sprague's pipits to aerial predators were not noted.

DISCUSSION

Cody (1971) indicated that flocking in desert sparrows is an adaptation to food supplies of low density and high dispersion. In wet years, when food is abundant, birds are widely dispersed in small flocks. However, in dry years when food is sparse, desert sparrows formed into large flocks. Cody generated a model to explain the course, amount of circularity, and rate of travel of these species. The model predicts that birds return to an area after the seed resources have been replenished through runoff-dependent ripening rates.

In contrast, Raitt and Pimm (1976) presented the argument that flocking is a response to the concentration of food resources by desert rains. Flocks search for the seed bonanzas.

In grasslands, a continuum exists from solitary bird species occupying seed-sparse habitats with good cover to flocking species occupying seed-rich areas with or without cover. Flocking was associated with patch use in Smith's and chestnut-collared longspurs. However, lapland longspurs and horned larks also occurred in flocks on open cultivatd sites where seeds were abundant, and more evenly distributed. Savannah sparrows, on some areas exhibiting type 2 spacing patterns (Fig. 4), formed into groups when disturbed. Flocking appears useful for predator avoidance in open habitats or where birds utilized seed-rich habitats. Flocking may serve for early detection of predators, and may also enhance evasion tactics of birds in open habitats.

The tallest ungrazed or lightly grazed areas in grasslands typically contain perennial grass species. For these plant species, the strategy is K-selected (Emlen 1973). Individual plants compete for space and are thus expected to divert their resources toward increasing individual size, as opposed to seed production. Risser (1980) showed seed production on LGs is much lower than on HGs. Low seed production for LGs was recorded in the present study (Table 1). LeConte's and Baird's sparrow habitats were seed-sparse compared to habitats of savannah sparrows. Low SDEN would support low BDEN. Solitary species could evolve with this system. Spacing would insure that individuals had enough of the limiting resource to survive. Predator avoidance is enhanced by dense habitat, low BDEN, and the small size of the species occupying these tall habitats.

I observed a high density of LeConte's sparrows in south Texas during December 1976 and February 1977. SDEN was not measured that season, but four times the mean rainfall (305 cm; mean, 87 cm) probably produced a bumper seed crop. Even though BDEN was extremely high, LeConte's sparrows remained solitary. Johnson (1956) reported a field occupied by about 200 LeConte's sparrows in his study in central Oklahoma. High densities of LeConte's sparrows have also been noted by D.S. Wood (pers. comm.) and me during migration in central and western Oklahoma. However, low densities were more often found for LeConte's, Baird's and grasshopper sparrows in this study, and for Baird's and grasshopper sparrows by Pulliam and Mills (1977) and Emlen (1972).

At moderate to high densities, savannah sparrows were spaced apart, but utilized only part of the suitable habitat at any time (Fig. 4, Type 3). Predators, potentially attracted to higher BDEN, may have presented a positive clustering effect. However, the data of first-disturbed birds indicate that savannah sparrows have evolved spatial and social habits which take advantage of spacing birds apart, yet still have positive group effects.

BDEN was significantly correlated with SDEN for sparrows. High densities of savannah sparrows were recorded at the highest SDEN. Savannah sparrows were absent from one site where they (and SDEN) were very high the following year (Grzybowski 1980a), indicating total recruitment in response to SDEN. In contrast to sparrows, BDEN was not significantly correlated with SDEN for longspurs. This may indicate that sparrows track their environments more closely than longspurs. However, longspurs were often seen flying over sites. The actual area utilized per bird may be closely correlated with SDEN for longspurs. Because longspurs forage from patch to patch, and could easily have utilized sites nearby, calculations of birds per area, or birds per SDEN would not be valid. Longspurs may very closely track SDEN.

Resources other than seeds may have influenced space use of grassland birds. Water was certainly one. Longspurs were observed at ponds in the early morning. Lapland Longspurs may depend on available water sources, and this factor may limit their geographic distribution. On days when ice covered ponds, flocks were observed pecking on the ice. Much of the local movement of longspur individuals in morning hours may have been due to longspurs travelling to water.

Pulliam and Mills (1977) presented evidence that space use by grassland sparrows may be affected by the presence of tree or shrub cover. According to these authors, competing species vie for positions near cover to enhance predator avoidance. Pulliam and Mills claimed that savannah sparrows are displaced from tree or shrub cover by vesper sparrows. In Fig. 6, however, only two of the four group ranges of savannah sparrows included cover greater than 1 m tall, in spite of the presence of this cover nearby and the absence of other sparrow species. In general Savannah sparrows avoided any but grass cover in almost all situations, unless they were disturbed repeatedly.

Caraco (1979, 1980) developed a model to predict group size in yellow-eyed juncos (*Junco phaeonotos*). Juncos in flocks can decrease their time scanning for predators, and increase their foraging effort as group size increases because of the increased probability of detecting a predator with more eyes watching. However, increased food density, which decreases requisite feeding time, allows more time for aggressive behavior between individuals, thus increasing the probability that a subordinate may be driven from a group.

In my study, increased food density was associated with increased bird density, and increased group size. This appears to conflict with Caraco's findings. However, Caraco's study dealt with one species in one environmental setting. I investigated a number of species with differing biologies. Caraco's model assumes that dominance hierarchies will form, driving subordinates from the group when dominants have more time for aggression. Dominance hierarchies may not be as prominant in grassland bird species as in juncos. Large numbers of individuals on grasslands with high seed densities, the high mobility of some species (especially longspurs), and a more even distribution of seeds on grasslands may reduce advantages of dominance.

Caraco's (1979, 1980) study emphasizes the dynamic nature of groups. However, if the establishment of dominance hierarchies is suppressed in grassland birds, groups may be more stable. Furthermore, juncos (in Caraco's study) fed in exposed areas, and moved to cover relatively safe from predators when not foraging. The lack of suitable cover, expecially in some open grassland habitats, may favor the maintenance of groups.

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LITERATURE CITED

Bent, A.C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. United States National Museum Bulletin 179.

Bent, A.C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. United States National Museum Bulletin 237.

Bertram, B.C.R. 1978. Living in groups: Predators and prey. In Krebs, J.R. and N.B. Davies (editors), Behavioral ecology, an evolutionary approach. pp. 64-96. Sinauer Associates, Inc., Sunderland, Massachusetts.

Caraco, T. 1979. Time budgeting and group size: A theory. Ecology 60:611-617.

Caraco, T. 1980. Stochastic dynamics of avian foraging flocks. The American Naturalist 115:262-275.

Cody, M.L. 1971. Finch flocks in the Mohave Desert. Theoretical Population Biology 2:142-158.

Crook, J.H. 1965. The adaptive significance of avian social organizations. Symposium of the Zoological Society of London 14:181-218.

Davis, J. 1973. Habitat preferences and competition of wintering juncos and golden-crowned sparrows. Ecology 54:174-180.

Emlen, J.M. 1973. Ecology: An evolutionary approach. Addison-Wesley Publishing Company, Reading, Massachusetts.

Emlen, J.T. 1971. Population densities of birds derived from transect counts. The Auk 88:323-342.

Emlen, J.T. 1972. Size and structure of a wintering avian community in southern Texas. Ecology 53:317-329.

Goss-Custard, J.D. 1970. Feeding dispersion in some overwintering wading birds. In J.H. Crook (editor) Social behavior in birds and mammals. pp. 3-34. Academic Press, London.

Grzybowski, J.A. 1980a. Population structure in grassland bird communities during winter. The Condor (MS).

Grzybowski, J.A. 1980b. Niche relations of grassland birds during winter. The Auk (MS).

Johnson, J.C., Jr. 1957. Habitat preferences among representative wintering and breeding birds of the central Oklahoma forest-prairie ecotone. Doctoral Dissertation, University of Oklahoma, Norman.

Kenward, R.E. 1978. Hawks and doves: Attack success and selection in goshawk flights at wood-pigeons. Journal of Animal Ecology 47:449-460.

Morse, D.H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs 40:119-168.

Murray, B.G., Jr. 1969. A comparative study of the LeConte's and sharp-tailed sparrows. The Auk 86:199-231.

Murton, R.K., A.J. Isaacson, and N. Westwood. 1963. The feeding ecology of the woodpigeon. British Birds 56:345-375.

Pleasants, B.Y. 1979. Adaptive significance of the variable dispersion pattern of breeding northern orioles. The Condor 81:28-34.

Post, W. 1974. Functional analysis of space-related behavior in the seaside sparrow. Ecology 55:564-575.

Powell, G.V.N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Animal Behaviour 22:501-505.

Pulliam, H.R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38:419-422.

Pulliam, H.R. 1975. Coexistence of sparrows: A test of community theory. Science 189:474-476.

Pulliam, H.R., and G.S. Mills. 1977. The use of space by wintering sparrows. Ecology 58:1393-1399.

Raitt, R.J., and S.L. Pimm. 1976. Dynamics of bird communities in the Chihuahuan Desert, New Mexico. The Condor 78:427-442.

Risser, P.G. (Editor). 1980. The true prairie ecosystem. Dowden, Hutchinson and Ross, Inc., Stroudsberg, Pennsylvania.

Snapp, B.D. 1976. Colonial breeding in the barn swallow (Hirundo rustica) and its adaptive significance. The Condor 78:471-480.

Sokal, R.R., and F.J. Rohlf. 1962. The comparison of dendrograms by objective methods. Taxon 11:33-40.

Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. Journal of Theoretical Biology 30:405-422.

FIG. 1. Locations of study sites in Oklahoma and Texas.

FIG. 2. Relation of group size to seed density for sparrows and longspurs.

FIG. 3. Correlation phenogram of species based on an unweighted pair group method of cluster analysis using arithmetic averaging for species and site attributes. Cophenetic correlation was 0.846. Species are BAIRS--Baird's sparrow, CHESL--chestnut-collared longspur, GRASS--grasshopper sparrow, HORNL--horned lark, LAPLL--lapland longspur, LECONS--LeConte's sparrow, SAVAS--savannah sparrow, SMITL--Smith's longspur, VESPS--vesper sparrow. Site designation are: LG--lightly grazed grassland, MG--moderately grazed grassland, HG--heavily grazed grassland, HG+--heavily grazed grassland in January 1979, and CU--cultivated field. Regions are: OKLA--Oklahoma; STEX--southern Texas; WTEX--western Texas.

FIG. 4. Diagramatic representation of spacing patterns exhibited by grassland birds during winter. Four types are identified. Each square represents an area which is large relative to the individuals. Individuals are represented by dots; six dots in each square are used for convenience. Solid circles surrounding dots represent use-areas to which enclosed individuals (dots) restrict

themselves. Circles formed with dashed lines represent temporary use areas. Three sizes of circles are used--the smallest for types 4a and 4b represent areas of individual distance; intermediate in types 1, 2b, and 3 represent "territories" or individual spacing units larger than individual distances; and the largest for type 3 represents an area of group activity. Ellipses (in types 2b and 4a) represent patches of preferred habitat. Arrows depict the magnitude of potential movements by individuals, including within "territories" (type 1), locally within site (type 2a), within and between patches (types 2b and 4a), within group activity areas (type 3), within site (types 2c and 4b), and between sites (types 2c, 4a, and 4b).

FIG. 5. Space use areas of LeConte's sparrows on a lightly grazed grassland in central Oklahoma during the winter of 1975-76. Activity areas of individuals are delineated by solid lines. The area delimited by dashed lines was occupied by four to eight sparrows. See text.

FIG. 6. Space use by groups of savannah sparrows (delimited by dashed lines) on a succesional grassland in central Oklahoma during the winter of 1977-78. See text.

FIG. 7. Space use areas of groups of (A) Smith's and (B) chestnut-collared longspurs during the winter of 1975-76

on a HG (site 1a) in central Oklahoma. Areas used by longspurs are enclosed by solid lines. Heavy use areas are designated by cross-hatching to the right within other enclosures (see text).

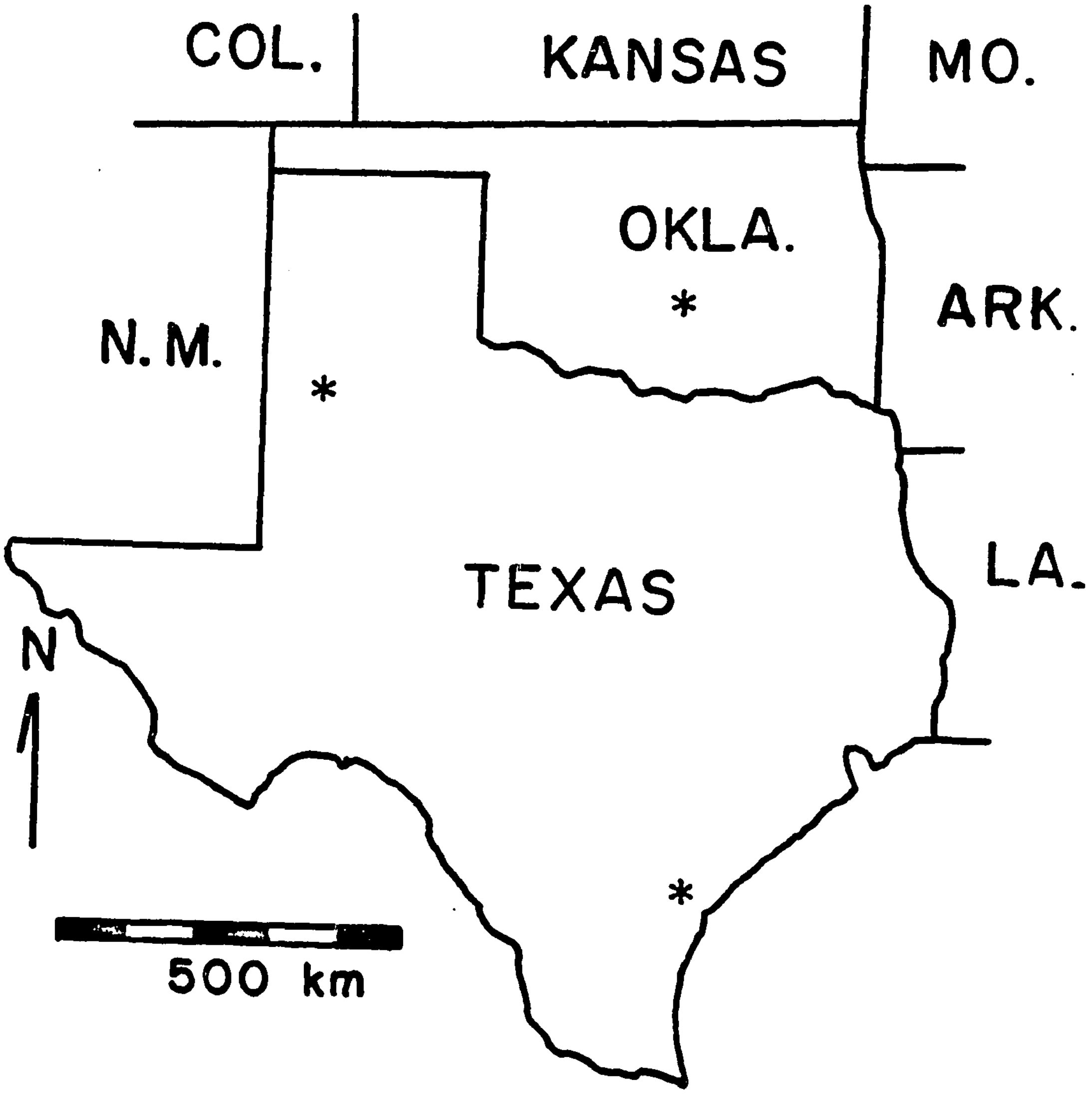


Figure 1

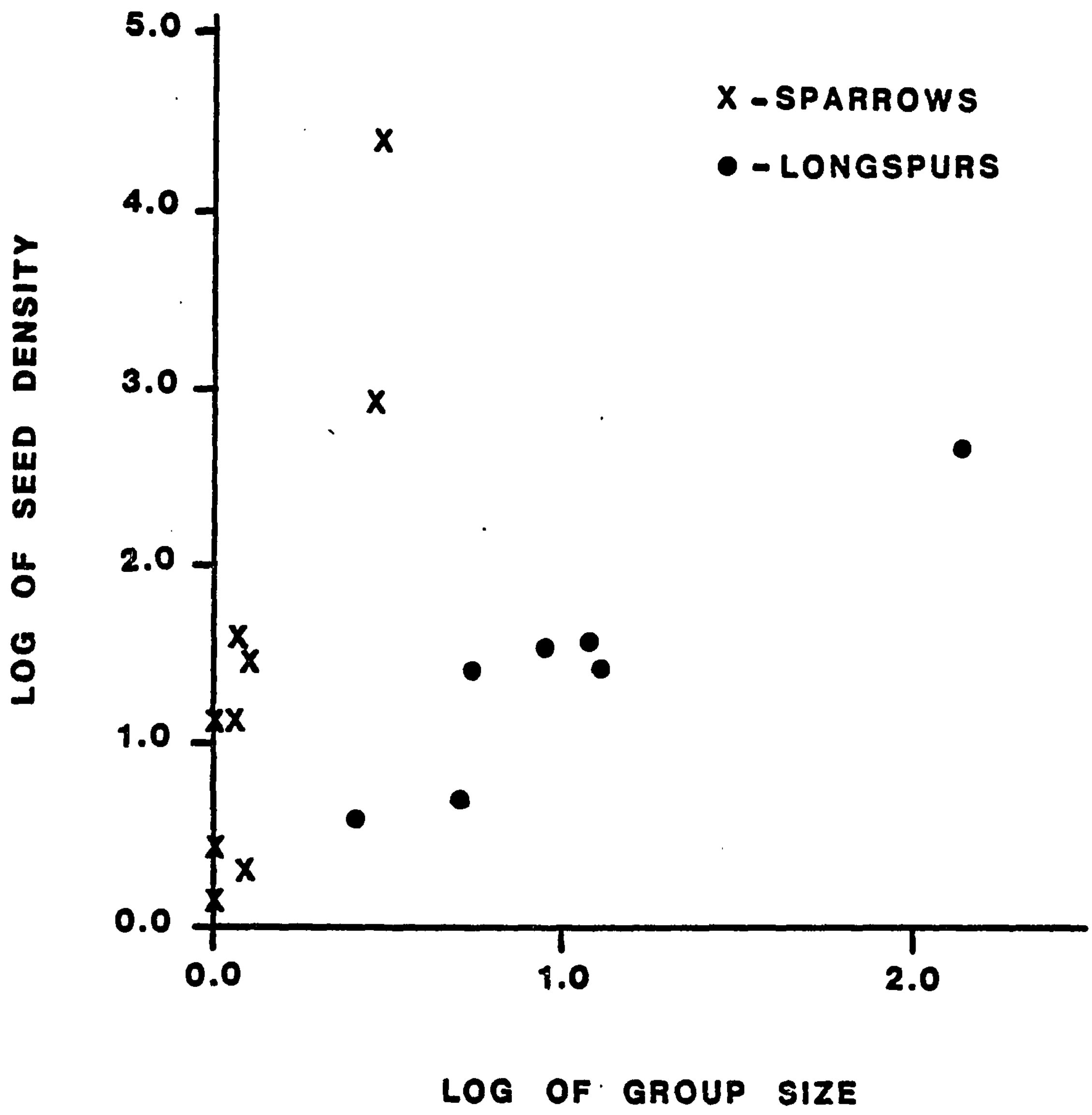

X - SPARROWS
● - LONGSPURS
5.0
4.0
3.0
2.0
1.0
0.0
LOG OF SEED DENSITY
0.0
1.0
2.0
LOG OF GROUP SIZE

Figure 2

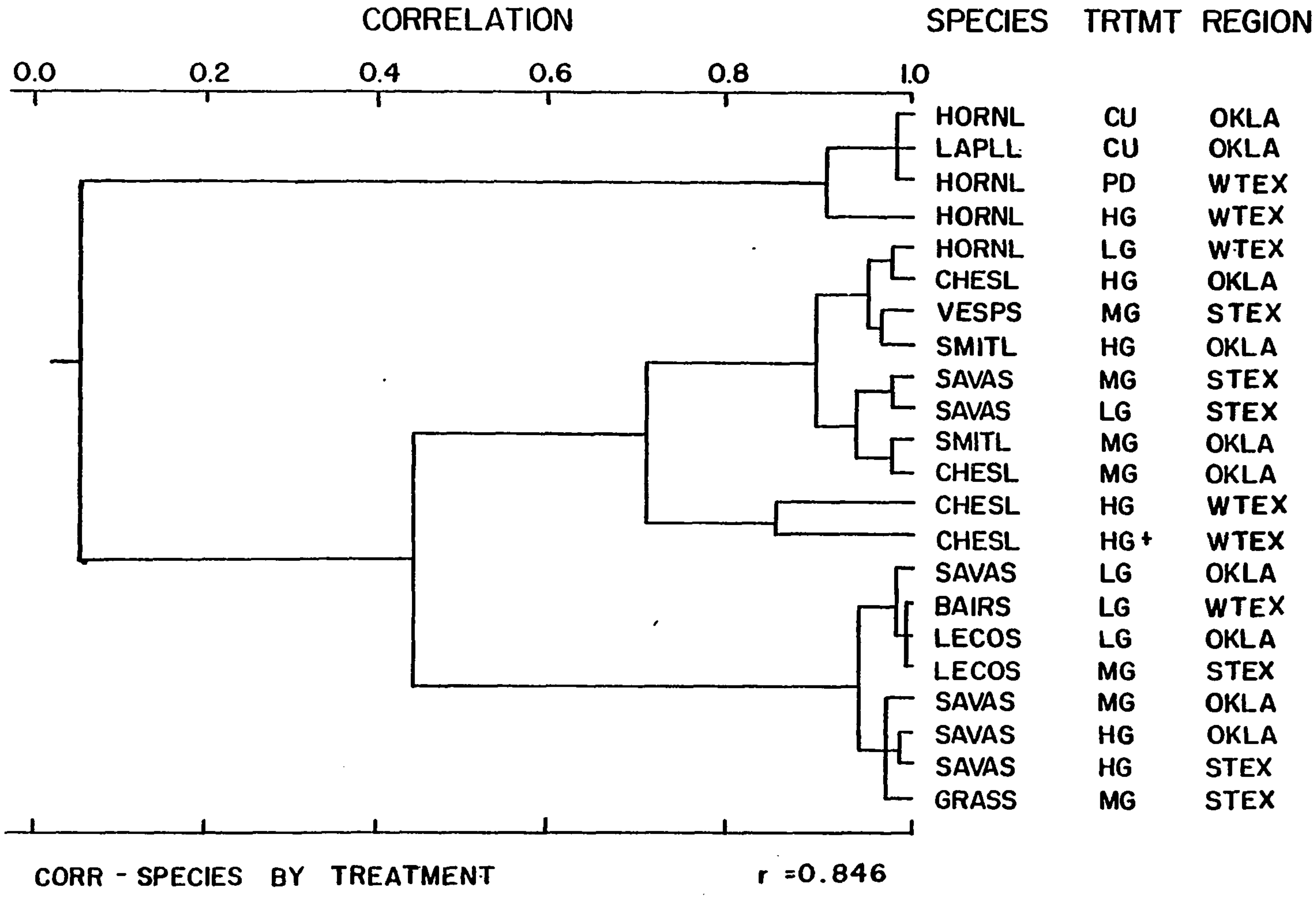

CORRELATION
SPECIES TRTMT REGION
0.0 0.2 0.4 0.6 0.8 1.0
HORNL CU OKLA
LAPLL CU OKLA
HORNL PD WTEX
HORNL HG WTEX
HORNL LG WTEX
CHESL HG OKLA
VESPS MG STEX
SMITL HG OKLA
SAVAS MG STEX
SAVAS LG STEX
SMITL MG OKLA
CHESL MG OKLA
CHESL HG WTEX
CHESL HG+ WTEX
SAVAS LG OKLA
BAIRS LG WTEX
LECOS LG OKLA
LECOS MG STEX
SAVAS MG OKLA
SAVAS HG OKLA
SAVAS HG STEX
GRASS MG STEX
CORR - SPECIES BY TREATMENT
r =0.846

Figure 3

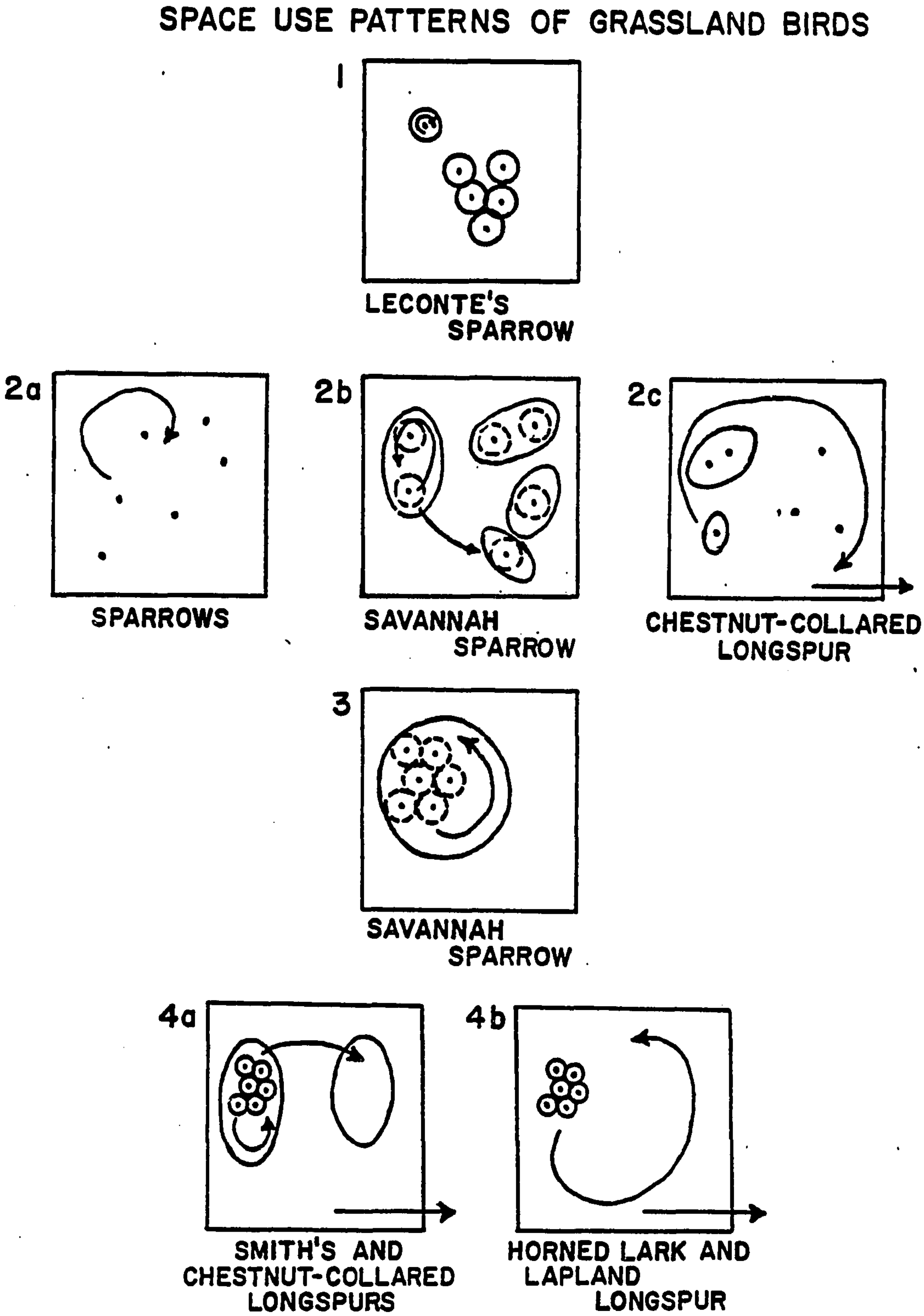
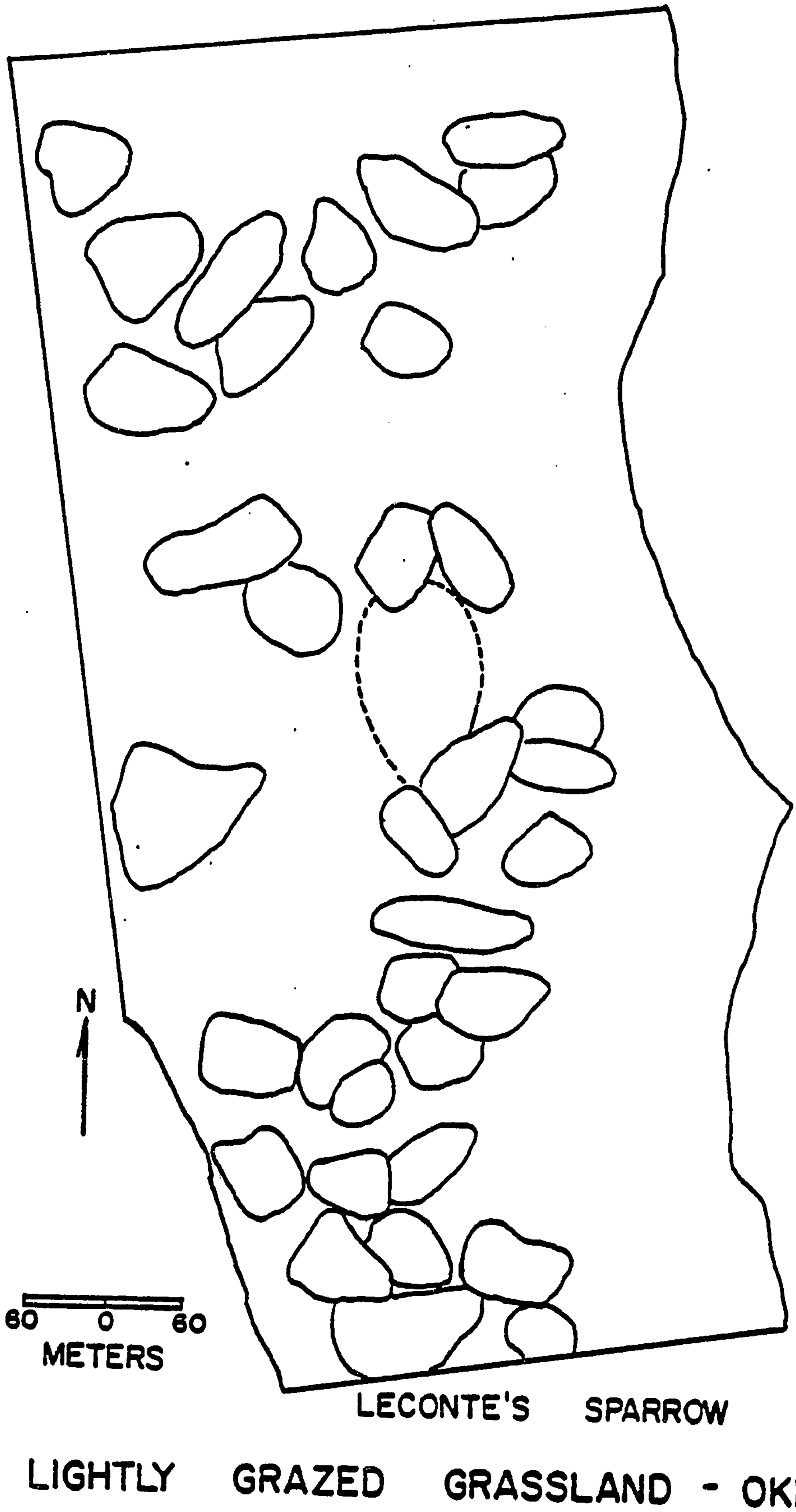

SPACE USE PATTERNS OF GRASSLAND BIRDS
1
LECONTE'S SPARROW
2a
SPARROWS
2b
SAVANNAH SPARROW
2c
CHESTNUT-COLLARED LONGSPUR
3
SAVANNAH SPARROW
4a
SMITH'S AND CHESTNUT-COLLARED LONGSPURS
4b
HORNED LARK AND LAPLAND LONGSPUR

Figure 4



LIGHTLY GRAZED GRASSLAND - OKLAHOMA

Figure 5

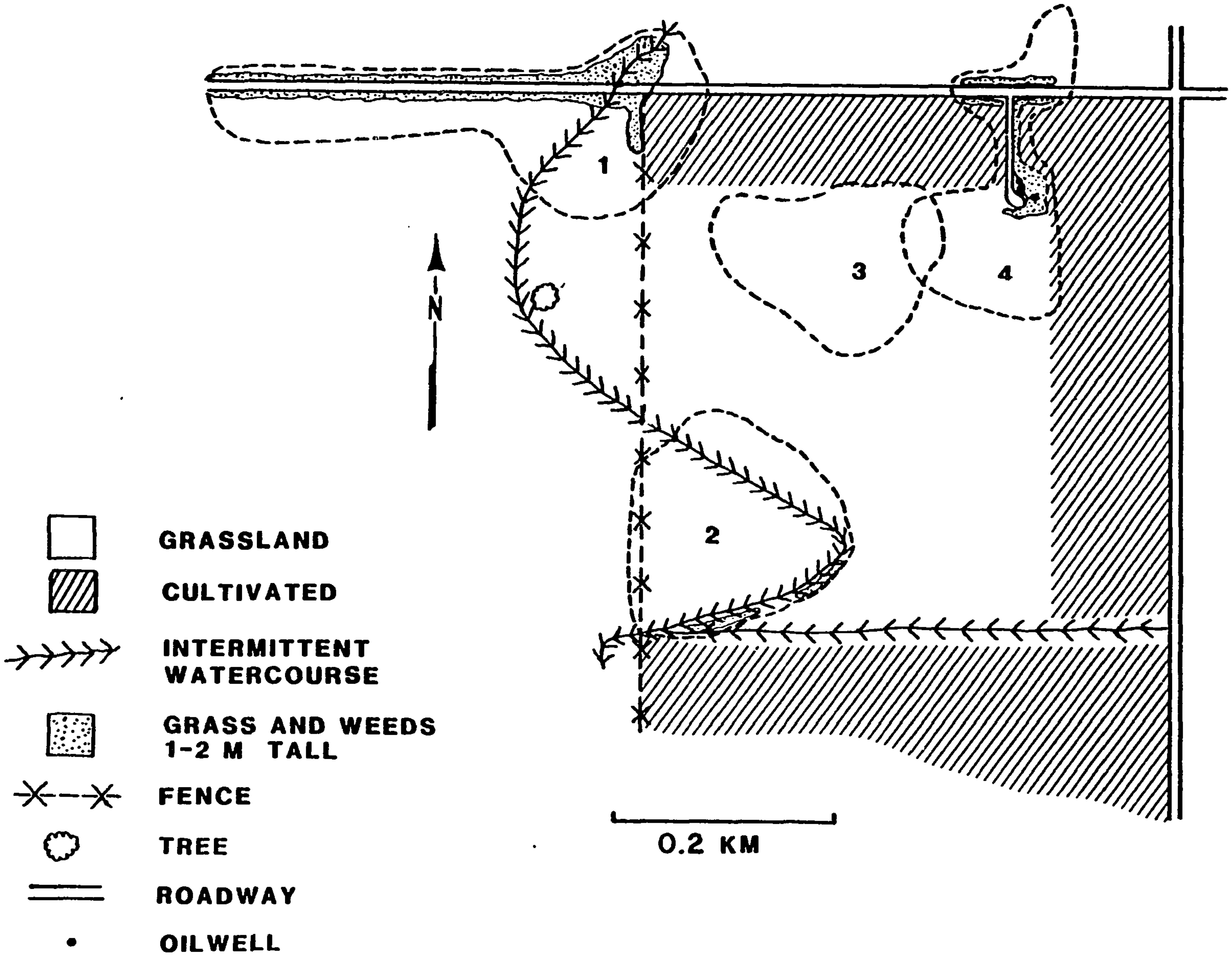
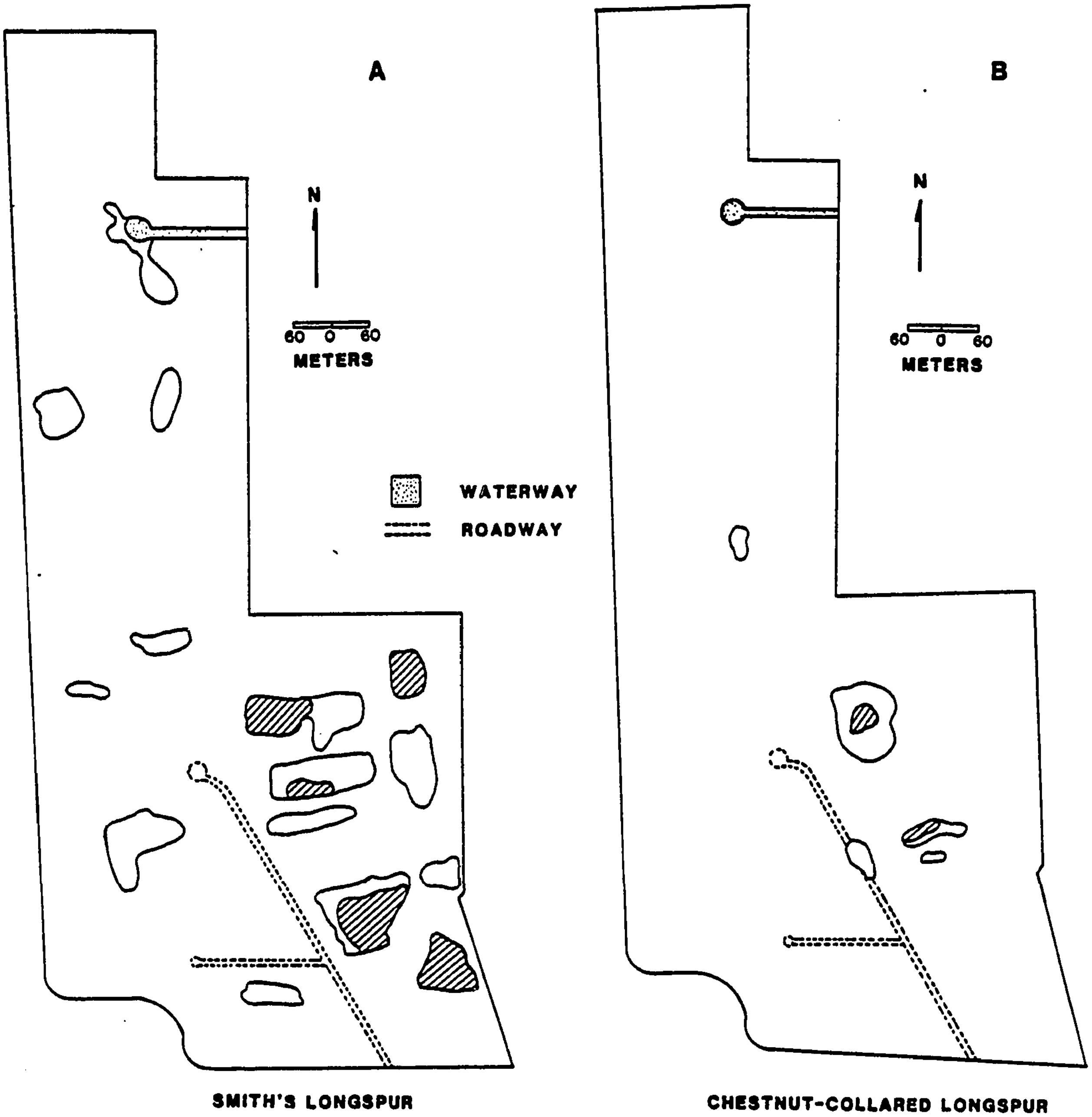

1
2
3
4
N
0.2 KM
GRASSLAND
CULTIVATED
INTERMITTENT WATERCOURSE
GRASS AND WEEDS 1-2 M TALL
FENCE
TREE
ROADWAY
OILWELL

Figure 6



HEAVILY GRAZED GRASSLAND - OKLAHOMA

Figure 7

TABLE 1. Social and ecologic attributes of grassland bird species.

Species	Treatment[a]	Region[b]	Social: Group size	Social: Individual distance	Social: Percent of individuals solitary	Ecologic: Habitat density	Ecologic: Habitat height	Ecologic: Bird density	Ecologic: Seed density[c]
Flyers[d]									
Horned Lark (Eremophila alpestris)	CU	Okla	6.1	1.7	3	0.8	0.8	102.3	2.71
	LG	WTex	8.5	1.8	3	30.8	21.6	132.0	0.10
	HG	WTex	8.1	2.2	2	10.0	7.5	102.0	0.66
	PD	WTex	15.0	1.6	1	4.4	3.5	734.0	2.08
Lapland Longspur (Calcarius lapponicus)	CU	Okla	146.9	1.5	0	0.6	1.0	118.8	2.71
Smith's Longspur (Calcarius pictus)	MG	Okla	11.6	2.9	3	33.5	39.0	139.7	1.59
	HG	Okla	12.8	2.9	1	37.7	21.2	279.8	1.46
Chestnut-collared Longspur (Calcarius ornatus)	MG	Okla	8.6	5.4	1	29.3	38.7	26.8	1.59
	HG	Okla	5.4	6.5	5	25.5	17.3	40.5	1.46
	HG	WTex	2.6	12.7	15	15.5	14.5	28.5	0.61
	HG[e]	WTex	5.1	7.6	4	17.6	14.5	122.0	0.71
Sparrows									
Savannah Sparrow (Passerculus sandwichensis)	LG	Okla	1.2	13.2	74	47.5	45.1	46.0	1.46
	MG	Okla	1.1	103.0	94	32.3	40.6	12.3	1.11
	HG	Okla	1.2	18.7	70	38.6	23.8	38.3	1.51
	LG	STex	4.2	6.9	8	52.0	60.1	1,228.0	--
	MG	STex	2.9	14.1	19	52.0	60.1	786.2	4.41
	HG	STex	1.3	12.2	57	28.4	23.3	84.2	0.29
Grasshopper Sparrow (Ammodramus savannarum)	MG	STex	1.0	19.5	100	68.8	63.6	71.0	1.11
Baird's Sparrow (Ammodramus bairdii)	LG	WTex	1.0	60.7	100	30.0	21.6	25.2	0.10
LeConte's Sparrow (Ammospiza lecontei)	LG	Okla	1.0	42.7	100	66.4	63.2	32.5	0.40
	LG	STex	1.0	11.1	100	--	--	1,888.0	--
	MG	STex	1.0	17.1	100	64.0	63.2	142.8	1.10
Vesper Sparrow (Pooecetes gramineus)	MG	STex	3.0	3.7	10	37.7	24.6	122.7	2.92
Insectivores									
Sprague's Pipit (Anthus spragueii)	HG	STex	1.0	59.1	100	29.7	14.1	60.8	--
Eastern Meadowlark (Sturnella magna)	LG	Okla	1.7	14.8	46	44.4	40.0	7.7	--
	MG	Okla	1.4	21.6	63	36.0	31.0	21.2	--
	HG	Okla	1.5	14.8	40	44.7	24.3	27.6	--
	CU	Okla	3.4	9.6	10	1.3	1.4	77.0	--
	MG	STex	2.1	11.4	12	68.0	45.0	96.0	--
	HG	STex	7.9	10.2	12	30.3	16.0	112.8	--
Western Meadowlark (Sturnella neglecta)	LG	WTex	1.0	100.0	100	30.0	21.6	8.3	--
	HG	WTex	1.0	100.0	100	--	--	11.7	--

[a] CU= cultivated; HG= heavily grazed; LG= lightly grazed; MG= moderately grazed; PD= prairie dog town.

[b] Okla= Oklahoma; STex= southern Texas; WTex= western Texas.

[c] Log of seed volume are given (see text).

[d] See text for category designations.

[e] Means from January 1979 when the site was recovering from being heavily grazed.

TABLE 2. Correlations of social and ecologic variables.

Variables[a]	Granivores (n=22)	Insectivores (n=10)	Sparrows (n=11)	Flyers (n=11)	Longspurs (n=7)
GSIZ-HDEN	-0.64***[b]	-0.16	-0.07	-0.33	-0.43
GSIZ-HHT	-0.55**	-0.20	-0.08	-0.26	-0.36
GSIZ-BDEN	0.39	0.67*	0.82**	0.46	0.40
GSIZ-SDEN	0.41	--	0.88***	0.72**	0.94**
IDIS-HDEN	0.57**	-0.15	-0.09	0.31	0.07
IDIS-HHT	0.57**	-0.17	0.01	0.37	0.10
IDIS-BDEN	-0.48*	-0.59	-0.69*	-0.61*	-0.69
IDIS-SDEN	-0.32	--	-0.52	-0.45	-0.90**
SOL-HDEN	0.63**	-0.10	0.20	0.12	-0.16
SOL-HHT	0.56**	-0.08	0.09	0.03	-0.16
SOL-BDEN	-0.44*	-0.62	-0.76**	-0.48	-0.64
SOL-SDEN	-0.39	--	-0.80**	-0.71**	-0.70

[a] See text for symbol designations.

[b] *--(*P*<.05); **--(*P*<.01); ***--(*P*<.001).

NICHE RELATIONS OF GRASSLAND BIRDS DURING WINTER

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ABSTRACT: Patterns of resource use were evaluated for passerine birds occupying open grassland habitats in Oklahoma and Texas. Of 11 species, the Eastern Meadowlark and the Savannah Sparrow were generalists, with broad niches, that occupied a broad range of habitats. Horned Larks and Lapland Longspurs were found in open habitats only, where they were abundant. LeConte's and Grasshopper sparrows were generally uncommon, and found only in tall and dense grasslands. Smith's and Chestnut-collared longspurs occurred in intermediate grassland habitats. These latter two species' niche widths were similar in magnitude to those of the Lapland Longspur and LeConte's Sparrow. Vesper Sparrows exhibited the narrowest niche width.

Stepwise discriminant function analysis showed percent grass cover to be the best variable for discriminating among the habitat preferences of grassland bird species. Vegetation height and percent forb cover, with percent grass cover, (taken in combination) were also important. This was not the

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case in the western Texas region where vegetation density at the 20-30 cm height interval, litter depth and percent litter cover were more important in discriminating the habitat preferences of grassland bird species. In a principal components analysis, vegetation height and density accounted for the most variation in the species' habitat preferences; litter depth and forb cover were of secondary importance.

Horned Larks dominated the western Texas sites, but occupied only a portion of the total range of grassland habitats available. Few individuals in western Texas occupied habitats characterized by taller vegetation. A paucity in use of taller and denser grassland habitats was also evident at several Oklahoma localities. This was not true on the southern Texas sites.

[INTRODUCTION]

In the past 20 years, much attention has been given to defining habitat preferences of birds, and evaluating resource division and methods of coexistence among members of bird communities (Cody and Diamond 1975). Bond (1957) and Beals (1960) evaluated the distribution of bird species along phytosociological gradients in a series of woodland communities; although several species showed little or no preference, several indiscrete groupings were identified on the basis of the bird species' preferences for tree species responding to soil moisture conditions. More recently, ordinations of various types have been employed to describe habitat partitioning of bird species along a few axes summarizing a larger number of often highly correlated variables (James 1971, Anderson and Shugart 1974, Whitmore 1975, 1977). Shugart and Patten (1974) developed a model for niche quantification, and used it to evaluate niche pattern of fringillid species.

I have evaluated resource use among grassland birds during winter. While Cody (1968) and Wiens (1969) investigated resource relations among grassland birds during the breeding season, neither these studies, or most others, consider resource use during non-breeding periods. Since most temperate passerines spend only a few months a year in breeding activities, and many leave their breeding grounds immediately after nesting, a substantial portion of their ecology has been neglected.

Winter seasons differ from summer seasons in that many bird species occupy different geographical ranges, are subjected to different environmental conditions, encounter different competitors, and utilize different food resources. Competition may be heightened in the winter, not only by increased southward overlap in ranges (of many species), but by recruitment of young, non-replenishing food supplies and reduced photoperiod (Fretwell 1972). Because food may be more limiting in winter, Fretwell (1972) suggested that species groupings may be more structured than in summer.

This paper is one of a series dealing with ecological relations among grassland birds during winter (Grzybowski 1976, 1980a, b). The purposes of my study are to (1) assess resource use of bird species occupying open grassland habitats during winter, (2) determine the elements important in structuring these bird communities, (3) describe the relationships of resource use between species, and (4) evaluate patterns of use within the grassland habitat resource spectrum among regions.

METHODS

Sites varying in grazing pressure or cultivation practices were selected for study in three regions of the southern plains. They encompass the range of variation in structural habitat characteristics for grasslands in the region, and include most of the avian species typical of open grassland. These sites included: four in central Oklahoma (one each of heaviliy grazed, moderately grazed, lightly grazed and cultivated); one in western Texas traversing, in part, a prairie dog town and, in part, a lightly grazed grassland; and two sites in coastal southern Texas (a lightly to moderately grazed and a heaviliy grazed grassland). The geographic locations of these sites are shown in Fig. 1.

Sites were selected on the basis of their uniformity, absence of trees or shrubs, and large size. About 5% shrub cover was present on a heavily grazed grassland in southern Texas; otherwise, shrub cover was absent or comprised less than 0.5%. In most cases, this cover consisted of isolated shrubs less than 3 m in height. The cultivated site used in central Oklahoma was planted in winter wheat (Triticum aestivum). A sorghum (Sorghum bicolor) crop had been harvested prior to this planting. Detailed site descriptions are provided in Grzybowski (1980a).

Strips approximately 1,000 X 60 m were established on each site, and divided into 15-meter-square blocks, each representing a unit in the vegetation analysis. A total of 1,052 blocks (about 264 at each site) were evaluated during December 1975 in central Oklahoma. An equivalent number of blocks per site were sampled on the western and southern Texas sites during late November and late December 1976, respectively. The lightly grazed and heavily grazed sites in central Oklahoma were resampled in December 1976.

Measures of vegetation were made in the center of each block. Four point samples of vegetation height and litter depth, as well as forb and grass cover were taken. In addition, the density of the vegetation was assessed from each point sample for each 10-cm height interval by counting the number of vegetation contacts made with the tip of a wire passed through the vegetation for 30 cm. Litter depth was considered as the depth of the non-living vegetation broken, or otherwise detached from vegetation maintaining its normal living structure. Since most above ground vegetation is dead during winter, this definition was employed to avoid using vegetation height as litter depth. A summary of the variables, measured and derived, and their abbreviations are provided in Table 1.

Frequency of occurrence of bird species in the blocks was recorded during each visit to each study site from 7 November 1975 to 12 March 1976, and from 15 November 1976 to 4 March 1977. The entire strip was searched during each visit so that the amount of time spent searching each block was approximately the same. From 14 to 20 visits were made to each site during each season. Each observation of an individual in a block was assigned the values of the measured and derived vegetation variables for that block to characterize the species' habitat preferences and utilization patterns.

These data were subjected to principal component (PCA) and discriminant function (DFA) analyses. DFA was used to identify those habitat variables important in species separation across all sites combined, and for each region.

The data were analyzed using a computer program (BMDP-PROG7M) developed by Dixon and Brown (1977). In the discriminant model, variables are entered in a step-wise fashion based on their ability to discriminate among species. At each step, the variable which adds the most to the separation of groups is entered. In the first step, the *F*-value to enter for a variable corresponds to the the *F*-statistic computed from a one-way analysis of variance on the variable for the groups used in the analysis. The variable with the highest *F*-value is entered first. At each subsequent step, the *F*-value to enter for each remaining variable is computed from a one-way analysis of covariance where covariates are the previously entered variables. In addition, the program performs a multivariate analysis of variance (MANOVA) on the species once all variables contributing to the discrimination of these species have been entered. The program also plots the distribution of observations, and means for the species, along the first two discriminant axes.

To assess relations among species by site and by region, PCA was used (Morrison 1967). This analysis was used in assessing regional and site specific relations, both within species occurring in more than one site or region, and among species.

Niche width was estimated in the following manner. The values of the measured and derived vegetation variables were averaged for each site (each year for two of the Oklahoma sites), and standardized (mean=0, SD=1); the sites were then entered into a PCA. Component loadings for the variables were determined along axes which explained the greatest amount of variation encompassed by all grid-blocks. Then component scores for each block were calculated according to the formula:

$$Y_m = \sum_{i=1}^{n} a_i X_i \qquad (1)$$

where Y_m is the component score for block m, a_i is the component loading for variable i, and X_i is the standardized value for variable i.

The component scores were assigned to each observation of a species in a block. Frequency distributions of the values for each species were generated in class increments along the first two PCA axes. These class values were then entered as resource states into Clark's (1977) monotonic transformation of Colwell and Futuyma's (1971) niche width equation. Thus niche width could be determined for each species using all sites combined, for any region, or for an individual site along standard and comparable axes. Distances from niche centers were determined for each analysis as the Euclidian distance from the origin to the standardized species' means. Abundance was assessed as the frequency occurrence of species in the grids. The values for niche width, frequency occurrence, and distances from niche centers of species were then compared using a diagramatic scheme generated by Shugart and Patten (1974) to evaluate patterns in community structure for grassland bird communities.

RESULTS

Table 2 gives the *F*-values for entering the habitat variables in a step-wise manner of several analyses. In the first case, for all observations combined across all regions, GRASS was the best discriminator among species' habitats. VEGHT and FORB also had high *F*-values for entering, and added to the discriminating power. In combination, GRASS and FORB were also the best discriminators for the Oklahoma grasslands, but VEGHT was replaced by a correlated counterpart--MAXHT. GRASS and VEGHT were also important in southern Texas sites, but HALFHT, in combination with GRASS and VEGHT, was the next best discriminator. While the low discriminatory power of HALFHT in the combined and Oklahoma analysis may appear paradoxical, the *F*-value for entering HALFHT at the first step was 351.1 and 416.2, respectively (Table 2). HALFHT was correlated with other variables, which once entered, reduced the ability of HALFHT to discriminate further among groups. For species habitats in western Texas grasslands, DENS25, LITDEP and LITCOV, in combination, were the most important variables.

Figure 2 illustrates an ordination for all species observations based on the first two discriminant axes. A gradient of increasing grass cover occurs from low to high values along the first axis. High values on this axis represent taller, lightly grazed grasslands, while low values indicate low vegetation density at the 15-cm height interval. The point shown for a species is the mean for all observations of that species. Observations of LeConte's Sparrows and, to a lesser extent, Grasshopper Sparrows, are spread along the second axis, less so on the first (Fig. 3). Observations of Horned Larks, Lapland Longspurs and Smith's Longspurs exhibit restrictive dispersion on the habitat axes (Fig. 3). However, Savannah Sparrows and Eastern Meadowlarks exhibit considerable dispersion across the entire spectrum of habitats sampled. None of the species overlapped significantly (MANOVA, $\underline{P}>0.05$).

Figure 4 shows results of a PCA analysis using the same data. Table 3 gives component loadings of the vegetation variables. The first axis accounts for 70% of the total variation; the second for an additional 17%. The first axis of the PCA is one of increasing vegetation height and density; the second is one one of increasing litter depth and decreasing forb cover. Horned Larks and Lapland Longspurs, similar in the low amount of GRASS in their habitat (Fig. 2, axis I), differ notably in the amount of forb cover (Fig. 4, component II).

Figure 5 shows the results of a PCA for each species by site, and also shows the positions of the sites relative to the species. In this way we can compare and evaluate species use patterns relative to each other and the site means. Observations for the two seasons on two Oklahoma sites are separated (1a and b, and 2a and b). The first axis is similar to that in Fig. 5; the second is one of increasing litter depth and cover.

Savannah Sparrows and Easterm Meadowlarks are scatterred across the diagram. They occur on eight and seven of the sites, respectively, in a variety of habitat conditions. Vesper Sparrows on the lightly grazed grassland in southern Texas (LG-STEX) are quite deviant from the the site mean and other species at that site. LeConte's Sparrow occurs in the taller grasslands; the three points for the species are very close to each other (Fig. 5). The two points for Horned Lark are close to each other, as are those of Smith's Longspur. The three points for Chestnut-collared Longspur are also very similar. Thus, these latter four species show restrictive habitat use even though they occur on several sites.

The differences that occurred between seasons can be seen in Fig. 5. On one site, a dramatic change in habitat occurred between the winters of 1975-76 and 1976-77, from a lightly grazed grassland (LG-OK[1a]) to a moderately grazed grassland (MG-OK[1b]). Only Savannah Sparrows and Easterm Meadowlarks were present on this site the second season. In the case of a heavily grazed grassland, the change in the vegetation for the site means and species means between the 1975-76 season (HG-OK[2a]) and the 1976-77 season (HG-OK[2b]) is represented by changes along the first principal component axis.

Species appear to avoid the higher vegetation heights and densities. Except for LeConte's Sparrow, species occupying LG-OK(1a), MG-OK, and HG-OK(2a and 2b) occur at vegetation heights, densities, and litter depths lower than the site mean.

Niche width estimates of grassland birds based on the first two PCA axis (accounting for the greatest amount of site variation) are given in Table 4. Since component I accounts for 70% of the total variation at all sites, niche widths can be compared using this single axis. For all sites combined, Eastern Meadowlarks and Savannah Sparrows show the broadest niche widths. The niche widths of other species are intermediate to low by comparison. The Western Meadowlark has a relatively low niche width. This species was not common in the open grassland habitats sampled. Vesper Sparrows occurred on only a very restrictive portion of the lightly to moderately grazed grassland sampled, namely cut fire breaks. Its niche width is also low. Sprague's Pipits and Grasshopper Sparrows were present in southern Texas, but uncommon. Their niche widths are relatively lower than other species.

In Oklahoma, Eastern Meadowlarks and Savannah Sparrows show much broader niche widths than other species. The LeConte's Sparrow had slightly lower niche width than the rest of the species in Oklahoma, occupying dense and tall lightly grazed grasslands. The Lapland Longspur also had a very narrow niche width, being restricted to cultivated fields.

In southern Texas, Savannah Sparrows and Eastern Meadowlarks also had the highest niche widths; Vesper Sparrow has the lowest. Grasshopper and LeConte's sparrows had very similar niche widths. LeConte's Sparrow's value was higher than in Oklahoma.

In western Texas, Horned Larks show the broadest niche width. It was the most abundant species. The Eastern

Meadowlark was rare in western Texas. It has a very low niche width value. Western Meadowlark also has a low niche width value, an unexpected result considering the distributional range of this species. But Western Meadowlarks were uncommon in open grassland compared to adjacent areas with shrubs, or along roadsides. Sprague's Pipit and Leconte's Sparrow both had very low niche values in western Texas. Both were rare. LeConte's Sparrow is at the very edge of its distributional range.

Table 5 shows the distances from the niche center calculated from the first two principal components for each group of data. Figure 6A gives the distribution of species along axes of niche width, distance from the regional niche center, and abundance. The points for two species having broad niches--Eastern Meadowlark and Savannah Sparrow--are located close to the niche center; these species are common. Most other species have intermediate or low niche widths. One species, the Lapland Longspur, stands out. Even though this longspur's niche width is relatively narrow compared to other species, and it is located far from the regional niche center, it is very abundant. Lapland Longspur occurs almost exclusively on cultivated sites in central Oklahoma. Equally distant from the niche center, but with a relatively broader niche than the Lapland Longspur, is the Horned Lark. It too occupies open habitat in high numbers. Two other species, Grasshopper and LeConte's sparrows, also occur relatively far from the niche center (Fig. 6A). Both these sparrows occupy the tallest and densest habitats. In contrast to Horned Lark and Lapland Longspur, however, they occur in low numbers.

Two species with intermediate niche widths were generally similar in this analysis--Smith's and Chestnut-collared longspurs. Smith's Longspurs occupied a slightly broader niche and was generally more abundant, but the two are similar in their positions in niche attributes.

The Western Meadowlark occurs fairly close to the niche center and has an intermediate niche width, but was rare. The Sprague's Pipit occurred primarily in southern Texas, was uncommon and was somewhat specialized in its habitat preference. Vesper Sparrows had the narrowest niche breadth and was uncommon. It was recorded on only one site and then only along cut firebreaks.

Shugart and Patten's (1974) graphic representation can be used to compare patterns among regions. In Oklahoma, Horned Larks were not as abundant (Fig. 6B). Otherwise, species show similar attributes as in Fig. 6A. For the southern Texas region (Fig. 6C), several shifts among species occur. LeConte's and Grasshopper sparrows show broader niches. Eastern Meadowlarks and Savannah Sparrows are located further away from the niche center than in other regions. The patterns in western Texas (Fig. 6D) indicate the numerical dominance of Horned Larks, and the general lack of other species. This reflects the low utilization of much available habitat in this region. The species present have narrow niche widths.

DISCUSSION

Cody (1968) showed several patterns of habitat separation for species in summer. In lightly grazed tall grass prairie, species showed separation on the basis of vegetation height, but on short-grass plains, there was considerable habitat overlap among the species. Unlike Cody's study, my results indicate that few species occupy short-grass habitats in western Texas. The species that occurred were rare, and some were more abundant in adjacent habitats (i.e., Western Meadowlarks). McCown's Longspurs were expected to co-occupy habitats in western Texas with Horned Larks, but the former were rare at my study site (Grzybowski 1980a), occurring in heavily grazed areas. Baird's Sparrows were present in low numbers. They were observed in only one of three winters at the western Texas sites (Grzybowski 1980a), and occurred on the lightly grazed areas. Chestnut-collared Longspurs were present in western Texas, yet were encountered primarily when they came to roost in the lightly grazed portions of the site (unpubl. data). Only a few scattered individuals were located during the day in lightly grazed grasslands.

Pulliam and Mills (1977) found Chestnut-collared Longspurs and several other species, which were not present on the western Texas sites, on short grass prairies in southeastern Arizona. Horned Larks were not mentioned by Pulliam and Mills. Thus, some intrinsic differences between these regions in species composition are evident. The study sites in western Texas may be subjected to more severe weather conditions than in southeastern Arizona. They may also be different from Arizona localities in other ways. The low number of individuals is best explained by the low seed avaiability in lightly grazed areas (Grzybowski 1980b). The dominant grasses were species of Sporobolus. This group has very small seeds which may be too small for grassland birds to exploit effectively.

Western Meadowlarks were rare and usually solitary in open grasslands in western Texas during winter. They were encountered in adjacent areas (often in groups) where some shrub cover was present (unpubl. data). It appears that open grasslands are not preferred habitats of this species in the winter.

Eastern Meadowlarks were more often encountered than Western Meadowlarks in open grassland in Oklahoma and southern Texas. However, Eastern Meadowlarks were also more common in adjacent shrubby areas (unpubl. data). They may have been encountered more often in open grassland in Oklahoma and southern Texas than in western Texas because of intrinsic differences in the regions. Any point in an open grassland in Oklahoma and southern Texas was generally nearer to some shrub cover because of the increased interspersion of woody habitats in these regions as opposed to western Texas.

The Vesper Sparrow showed a very restricted niche. Its habitat in southern Texas appears consistent with that noted by Pulliam and Mills (1977) in southeastern Arizona. These authors found Vesper Sparrows in grasslands close to cover.

This habitat is structuraly similar to fire breaks cut through tall grass areas in southern Texas. This combination of cut areas and tall grass cover may localize this species' dispersion pattern. Wiens (1969) found that Vesper Sparrows preferred sparsely vegetated areas in summer. The large territory sizes of this species during the breeding season (Bent 1968) may reflect the patchy use of specific elements in the habitat. This sparrow was unusual among the species encountered in my study in being relatively close to the niche center, yet having a narrow niche and being uncommon.

Shugart and Patten's (1974) interpretations of niche patterns are not always consistent with results in my study. They indicated that a species occupying a position similar to Vesper Sparrows would have a narrow niche, would be well adapted to the region, and should be highly mobile. Vesper Sparrows do not possess this latter attribute. Species occupying a position similar to Lapland Longspur were predicted to occupy stable habitats that persist over long periods of time. Yet, the cultivated sites are of recent origin. Abundance of longpsurs on these sites is dependent on the previous crop. In central Oklahoma, Lapland Longspurs were most readily found in areas previously planted in sorghum. Longspurs are highly mobile. Abundance did change considerably over the course of the season (unpubl. data).

Shugart and Patten (1974) also indicated that species occupying positions similar to Horned Larks in western Texas should be poorly adapted to the region and be highly mobile.

Horned Larks dominated the region.

Another consideration in the use of Shugart and Patten's niche diagram is the relative abundance of habitats. The objective in my study was to represent the spectrum of habitats available. A species' distance from the regional niche center is thus dependent on the habitat types in the region. Horned Larks in western Texas and Lapland Longspurs in central Oklahoma occupied very abundant habitat types. If consideration was given to abundance of habitat types, Horned Larks and Lapland Longpsurs would be represented as closer to the niche centers, while LeConte's and Grasshopper sparrows would move farther from the niche center.

The paucity in use of taller and denser grassland habitats in Oklahoma and western Texas may be related to seed abundance. It was lower on lightly grazed grasslands than on heavily grazed grasslands (Grzybowski 1980b); estimates of bird biomass were also lower in lightly grazed grasslands. These taller habitats appear to be seed-sparse with few bird species, which are rare or uncommon.

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LITERATURE CITED

Anderson, S.H., & H.H. Shugart. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828-837.

Beals, E. 1960. Forest bird communities in the Apostle Islands. Wilson Bull. 72:156-181.

Bent, A.C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monogr. 27:351-384.

Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. Marine Biology 40:277-289.

Cody, M.L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102:107-147.

________, & J.M. Diamond. 1975. Ecology and evolution of communities. Cambridge, Massachusetts, Belknap Press. Massachusetts.

Colwell, R.K., & D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Dixon, W.J., & M.B. Brown (Eds.). 1977. Biomedical computer programs, P-series. Berkeley, Univ. California Press.

Fretwell, S. 1972. Populations in a seasonal environment. Princeton, Princeton Univ. Press.

Grzybowski, J.A. 1976. Habitat selection among some grassland birds wintering in Oklahoma. Ann. Okla. Acad. Sci. 6:176-182.

________. 1980a. Population structure in grassland bird communiuties during winter. Condor (MS).

________. 1980b. Sociality and space use among grassland birds during winter. Ecology (MS).

James, F.C. 1971 Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215-236.

Pulliam, H.R., & G.S. Mills. 1977. The use of space by wintering sparrows. Ecology 58:1393-1399.

Shugart, H.H., Jr., & B.C. Patten. 1974. Niche quantification and the concept of niche pattern. Contributions in Systems Ecology No. 10., Univ. Georgia, Athens.

Whitmore, R.C. 1975. Habitat ordination of the passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

________. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253-265.

Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1-93.

________. 1974. Habitat heterogeneity and avian community structure in North American graslands. Am. Midl. Nat. 91:195-213.

Fig. 1. Locations of the study sites in Oklahoma and Texas.

Fig. 2. Two-dimensional ordination of species using the first and second discriminant function axes. The first axis represents a gradient of increasing grass cover. High values on the second axis represent taller, lightly grazed grasslands. CL=Chestnut-collared Longspur; EM=Eastern Meadowlark; GS=Grasshopper Sparrow; HL=Horned Lark; LL=Lapland Longspur; LS=LeConte's Sparrow; SS=Savannah Sparrow; SL=Smith's Longspur; SP=Sprague's Pipit; VS=Vesper Sparrow; WM=Western Meadowlark.

Fig. 3. Ordination showing dispersion of species observations along the first and second discriminant function axes. Axes and species symbols as in Fig. 2.

Fig. 4. Ordination of species using the first and second principal component axes. The first is an axis of increasing vegetation density and vegetation height. The second axis is one of increasing litter depth and decreasing forb cover. Species symbols as in Fig. 2.

Fig. 5. Principal component analysis of species by site. The first axis is one of increasing vegetation density and vegetation height; the second is one of increasing litter depth and cover. Each site mean is represented by a closed circle. Species mean preferences for a site are enclosed by dashed lines. Species symbols as in Fig. 2. LG=lightly grazed grassland; MG=moderately grazed grassland; HG=heavily grazed grassland; CUL=Cultivated; OK=Oklahoma; STEX=southern Texas; WTEX=western Texas.

Fig. 6. Niche diagrams for grassland bird species along axis of niche width (W), distance from niche center (D), and abundance (A); species observations for all sites (A) combined, (B) in Oklahoma, (C) in western Texas, and (D) in southern Texas.

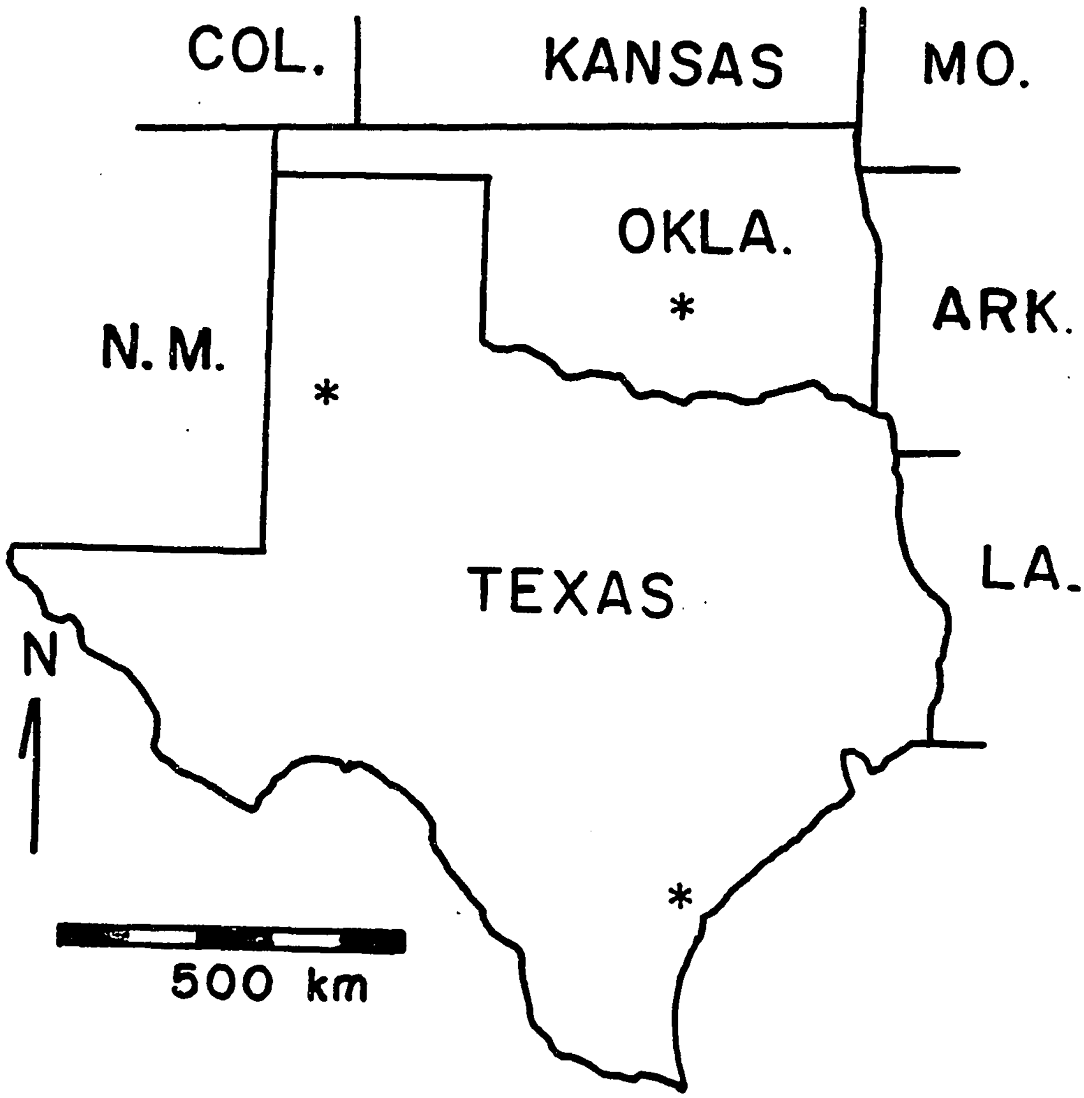

Figure 1

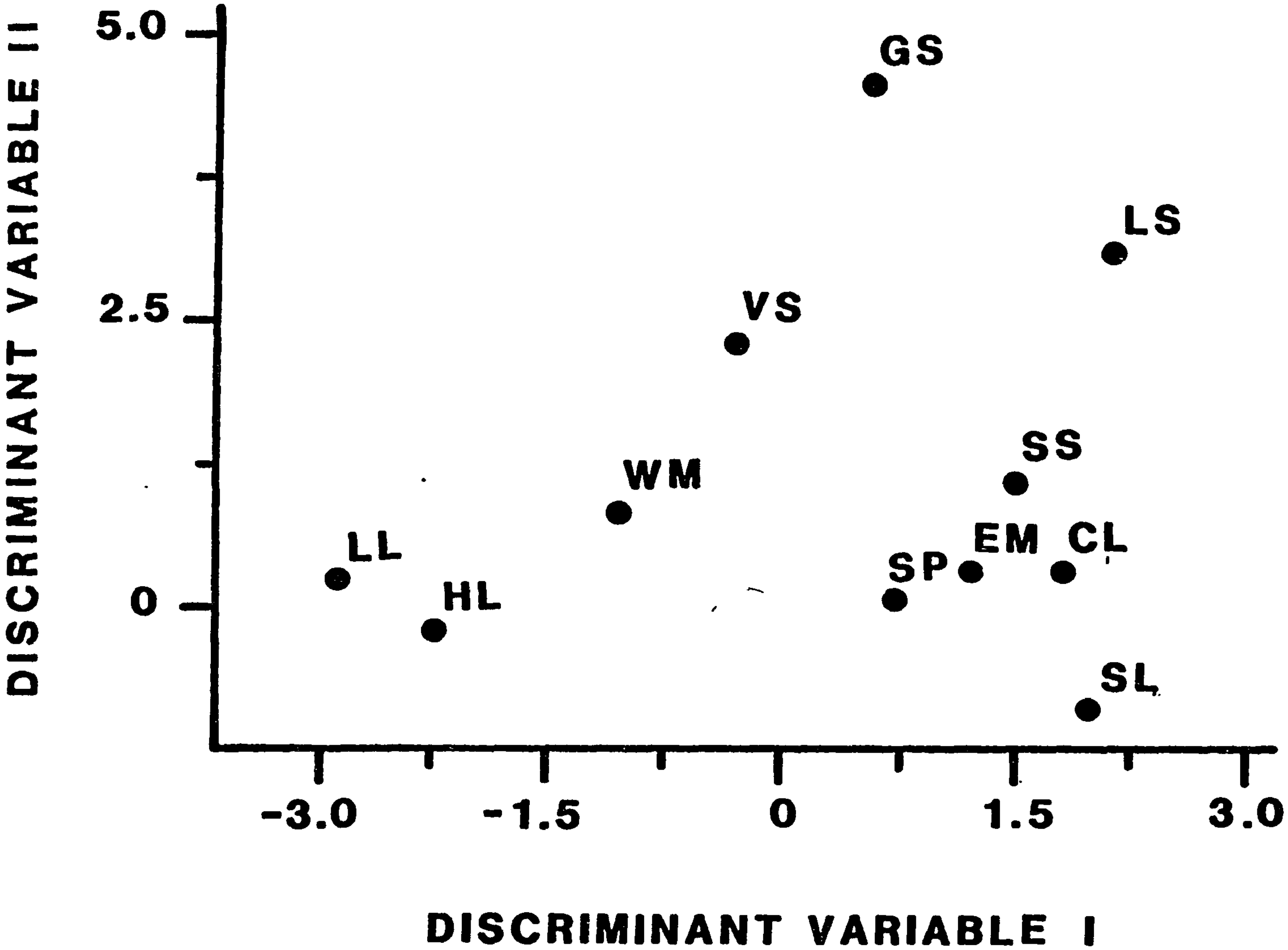
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Figure 2

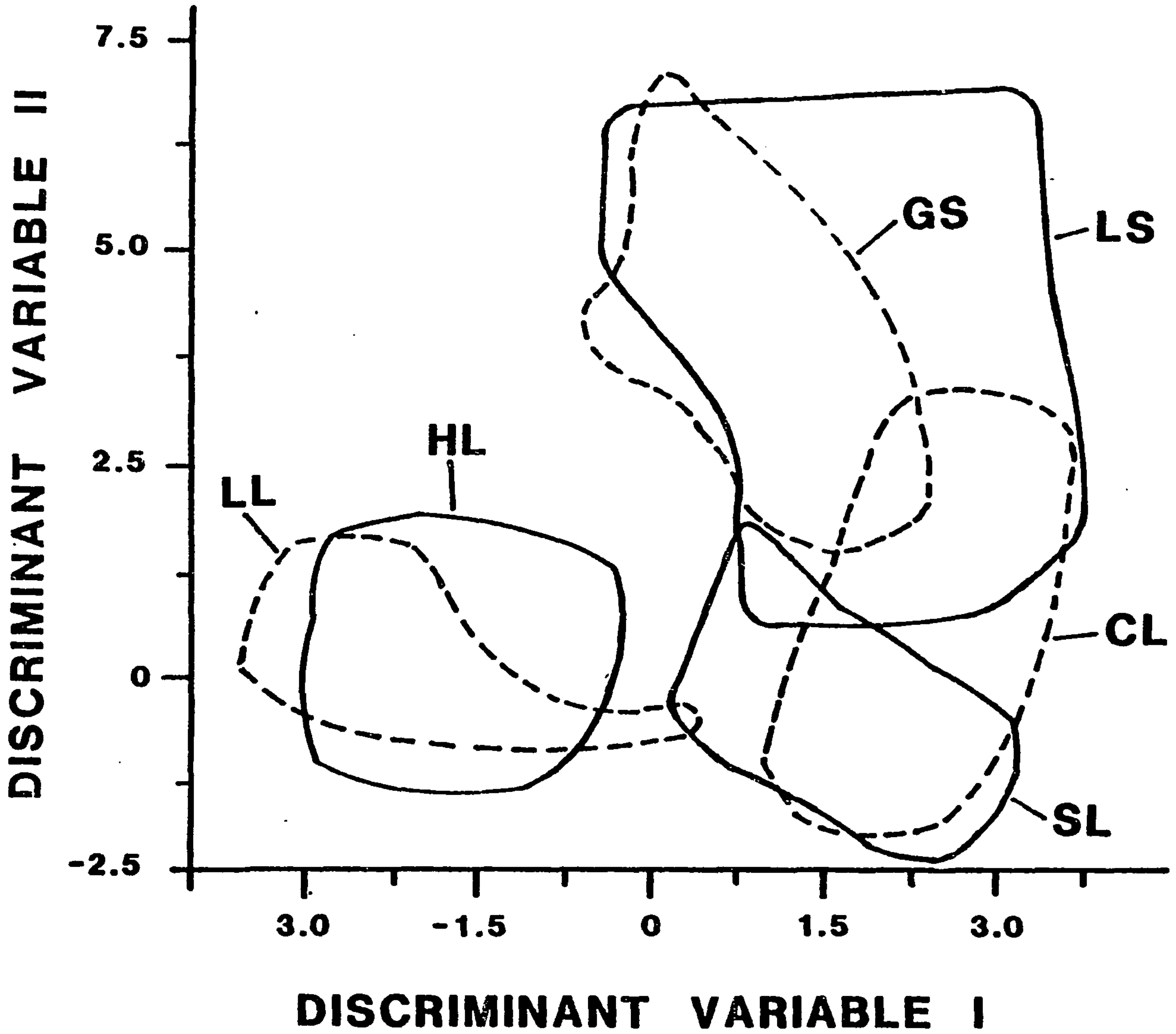
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Figure 3

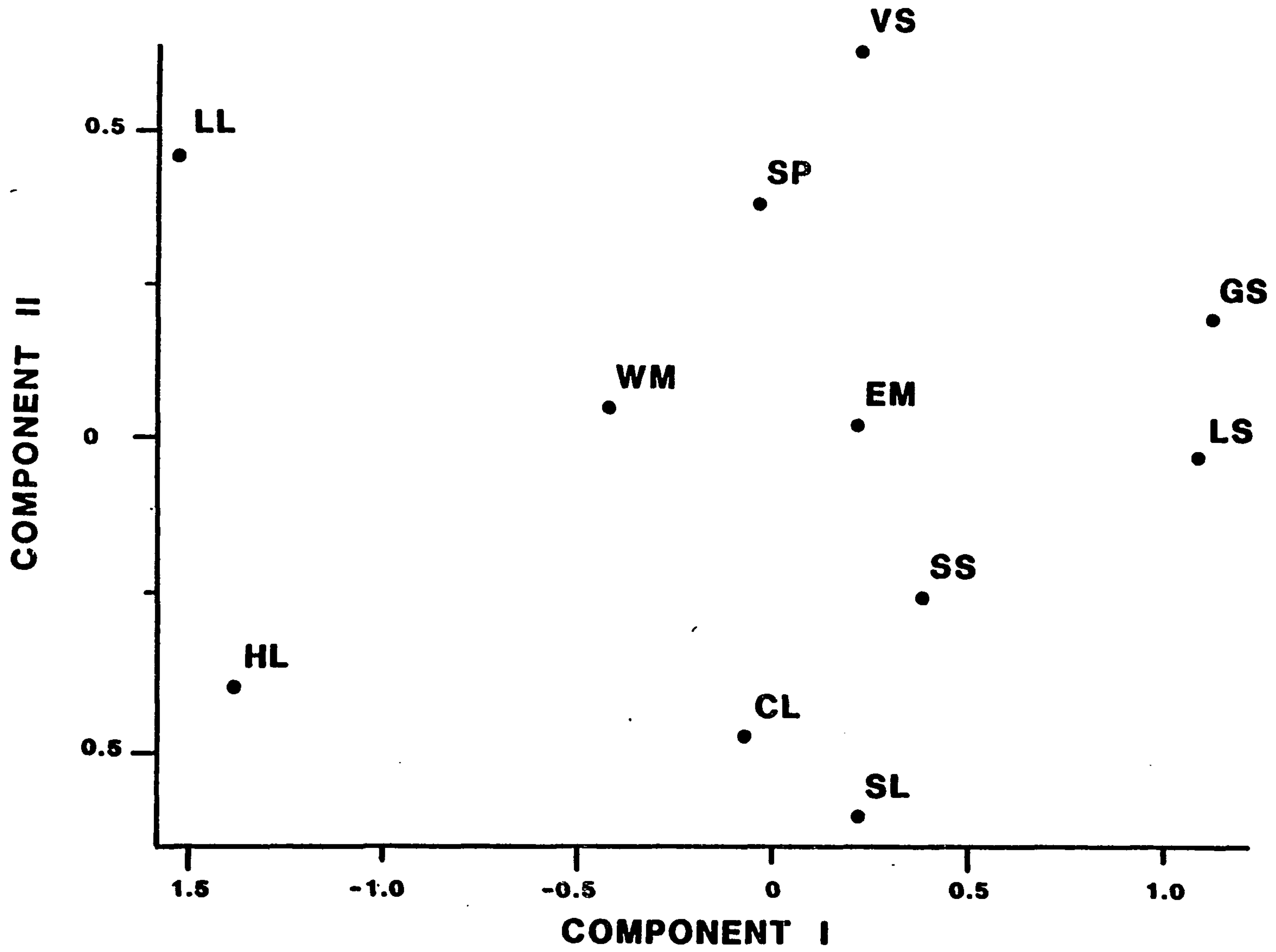
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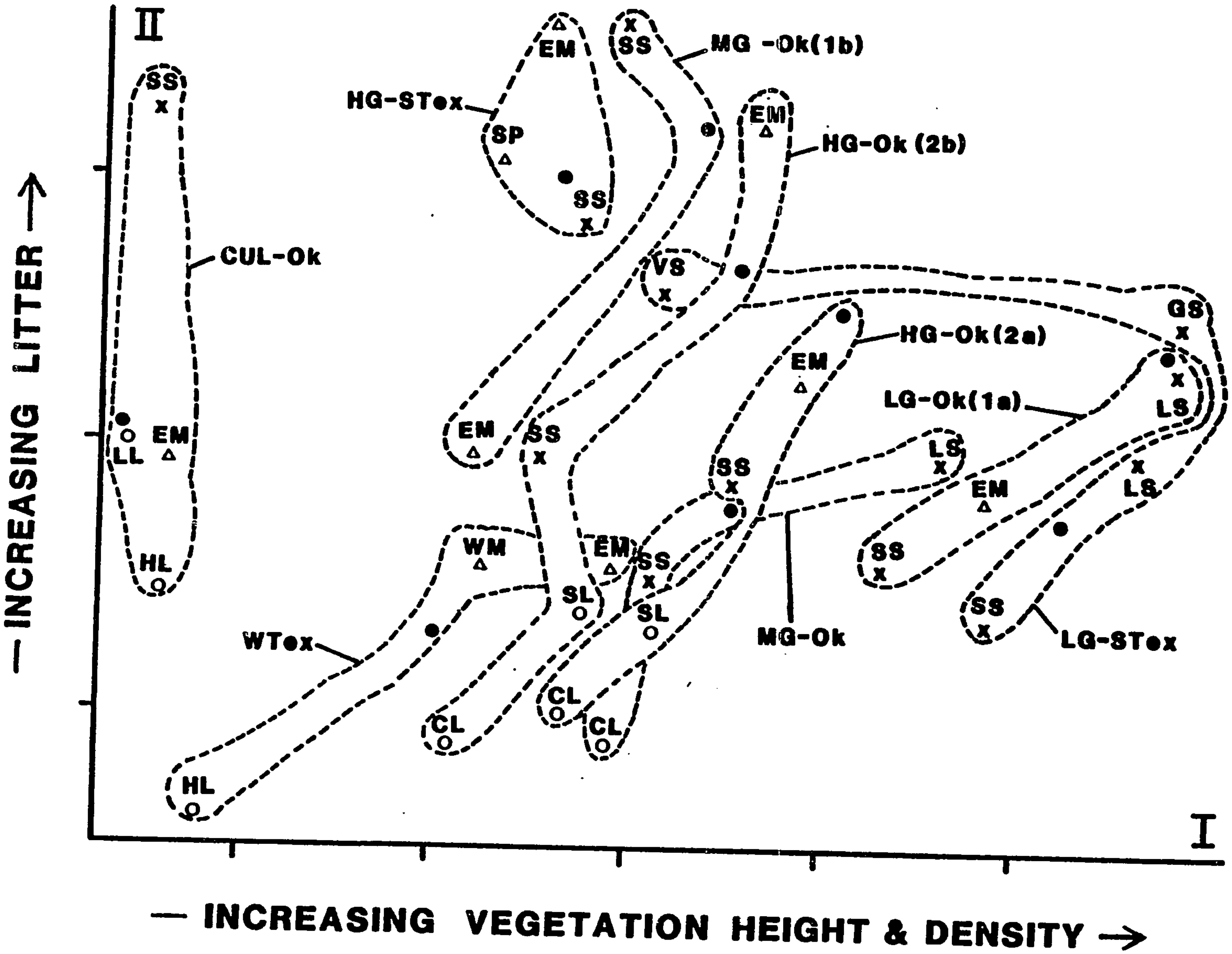
Figure 4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MG -Ok(1b)
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HG-Ok(2a)
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Figure 5

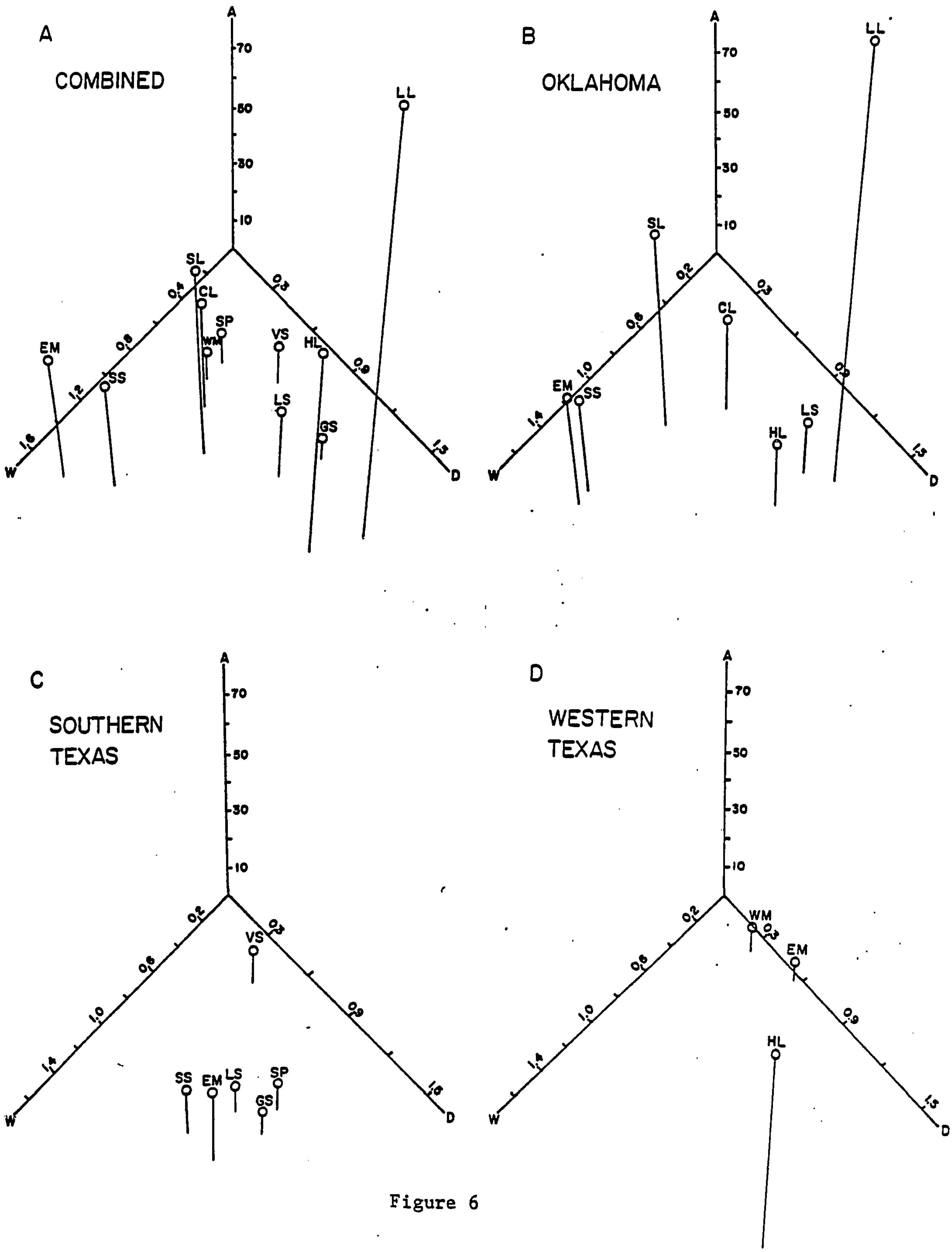

Figure 6

TABLE 1. Summary of vegetation variables, measured or derived, for each block.

Variable abbreviation	Description
VEGHT	Average vegetation height from four point samples.
MAXHT	Maximum of four point samples.
MINHT	Minimum of four point samples.
HETIN	Heterogeneity of vegetation height within a grid (from Wiens 1974).
DENS5	Sum of number of vegetation contacts made by passing a wire through vegetation for 30 cm for four point samples at 5 cm (for 0-10 cm height interval).
DENS15	Same as DENS5 at 15 cm.
DENS25	Same as DENS5 at 25 cm.
CONSM	Sum of densities for all height intervals.
HALFHT	Height interval at which the (CONSM/2)th vegetation contact was recorded.
EFHT	Tallest height interval at which vegetation density was equal to or greater than 8 (i.e., an average of two vegetation contacts per point sample).
LITDEP	Litter depth in centimeters.
LITCOV	Percent litter cover as 25 times number of point samples with litter.
GRASS	Percent grass cover as 25 times number of point samples with grass cover.
FORB	Percent forb cover as 25 times number of point samples with forb cover.

TABLE 2. F-values of vegetation variables for the combined, Oklahoma, southern Texas, and western Texas analyses.

	Combined		Oklahoma		Southern Texas		Western Texas	
Variable	Stepwise	ANOVA	Stepwise	ANOVA	Stepwise	ANOVA	Stepwise	ANOVA
VEGHT	290.4	874.3	12.8	938.3	89.9	89.8	--	26.6
MAXHT	25.9	754.3	224.2	819.6	--	58.4	--	20.8
MINHT	10.5	537.7	13.5	559.1	--	29.1	--	14.2
HETIN	8.7	33.1	17.3	54.8	--	7.9	--	0.0
DENS5	55.2	804.1	54.7	817.5	--	3.7	--	34.1
DENS15	16.6	539.4	9.0	450.1	--	31.5	12.3	48.7
DENS25	11.9	329.8	8.0	239.8	--	40.7	59.5	59.5
CONSM	36.8	827.2	44.8	754.5	--	32.1	--	42.7
HALFHT	7.5	351.1	26.7	416.2	17.4	70.8	--	13.6
EFHT	8.6	621.9	5.3	529.8	5.2	34.6	--	50.1
LITDEP	76.4	106.0	67.6	33.5	--	4.6	22.3	32.3
LITCOV	30.0	109.3	9.3	44.1	--	7.7	33.6	32.3
GRASS	1,235.7	1,235.7	1,261.9	1,261.9	30.1	47.8	5.5	11.7
FORB	108.1	89.5	91.1	143.6	12.4	28.1	--	5.8

TABLE 3. Loadings for vegetation variables on the first two principal component axes.

	Component	
Variable	I	II
VEGHT	0.967	-0.108
MAXHT	0.964	-0.062
MINHT	0.933	-0.253
HETIN	-0.525	0.758
DENS5	0.935	-0.049
DENS15	0.978	0.105
DENS25	0.928	0.183
CONSM	0.986	0.060
HALFHT	0.940	0.175
EFHT	0.966	0.175
LITDEP	0.601	0.698
LITCOV	0.738	0.404
GRASS	0.535	-0.486
FORB	0.337	-0.817
Percent total variation explained	70.0	16.6

TABLE 4. Niche width estimates for grassland birds based on the first principal component axis.

	Niche width			
Species	Combined	Oklahoma	Southern Texas	Western Texas
Horned Lark	0.087	0.075	--	0.114
Sprague's Pipit	0.049	--	0.068	(0.009)[a]
Eastern Meadowlark	0.159	0.155	0.112	0.002
Western Meadowlark	0.062	--	--	0.012
Savannah Sparrow	0.142	0.145	0.112	--
Grasshopper Sparrow	0.048	--	0.082	--
LeConte's Sparrow	0.070	0.050	0.084	(0.007)[a]
Vesper Sparrow	0.035	--	0.026	--
Lapland Longspur	0.063	0.041	--	--
Smith's Longspur	0.091	0.089	--	--
Chestnut-collared Longspur	0.074	0.057	--	--

[a] Present in low numbers in November.

TABLE 5. Distance from regional niche centers of grassland birds for the combined, Oklahoma, southern Texas, and western Texas analyses.

Species	Distance from niche center			
	Combined	Oklahoma	Southern Texas	Western Texas
Horned Lark	1.397	1.183	--	1.475
Sprague's Pipit	0.392	--	0.979	(0.624)[a]
Eastern Meadowlark	0.235	0.458	0.922	0.561
Western Meadowlark	0.392	--	--	0.325
Savannah Sparrow	0.455	0.441	0.745	--
Grasshopper Sparrow	1.116	--	1.003	--
LeConte's Sparrow	1.076	1.171	0.828	(0.898)[a]
Vesper Sparrow	0.675	--	0.421	--
Lapland Longspur	1.574	1.294	--	--
Smith's Longspur	0.665	0.481	--	--
Chestnut-collared Longspur	0.486	0.617	--	--

[a] present in low numbers in November.