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POPULATION STRUCTURE IN GRASSLAND BIRD COMMUNITIES DURING WINTER

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ABSTRACT.—Mid-winter populations of birds at 20 open-grassland sites of varied grazing pressure and cultivation practices in Oklahoma and Texas were examined to evaluate patterns of avian species' abundances and distributions. Most of the 23 non-raptorial bird species observed were winter residents. Of these, only 14 were present on more than 2 of 53 censuses. Except for meadowlarks and the Sprague's Pipit (*Anthus spragueii*), these species are granivores. Regional distinctions in species composition of 5°-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 the most abundant bird species. Sites with similar grazing pressures were generally placed into the same cluster. However, sites in Oklahoma classified as moderately grazed were grouped with either heavily or lightly grazed grasslands depending on the predominant avian species.

Estimates of bird biomass were highest on northern Oklahoma and southern Texas sites. Biomass was 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 sites (and also among species) in central Oklahoma. The year 1976 was a drought year and fewer birds were present during the winter of 1976–1977 than in other winters. However, Savannah Sparrows (*Passerculus sandwichensis*) were less numerous and Smith's Longspurs (*Calcarius pictus*) most abundant during the coldest winter (1978–1979) with unusually high snowfall. The highest winter bird population estimates in southern Texas occurred in a period with record rainfall (1976–1977).

Population dynamics and the role of birds as consumers in grassland ecosystems have been studied intensively during the breeding season (Mitchell 1961, Finzel 1964, Spiers and Orenstein 1967, Feist 1968, Owens and Myres 1973, Wiens 1973, 1974a, b, Raitt and Pimm 1976). Analyses of grassland bird populations at other seasons, however, are limited in scope (Quay 1947, Finzel 1964, Emlen 1972, Raitt and Pimm 1976), some being restricted to counts of birds from roadway routes (Wiens et al. 1972, 1974, Risser 1981). As indicated by Wiens (1974a) and Wiens and Dyer (1975), analysis of grassland bird communities is hampered by the paucity of quantitative population studies conducted during non-breeding periods. Yet, much of the structure of bird communities during the breeding season may be determined by winter resources (Pulliam and Enders 1971, Fretwell 1972, Wiens 1974a, Raitt and Pimm 1976) and by climatic factors influencing birds during the winter.

In temperate grasslands, the winter 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 use different foods. The food for many temperate passerine species during winter consists primarily of seeds, which can be abundant (Johnston and Odum 1956); seed abundances are established at the time of the first frost, and decrease as the season progresses. The days are shorter in winter and afford less time for all activities. Competition may be heightened by increased over-

TABLE 1. January population estimates (birds/100 ha), total and granivore biomass (kg/100 ha), and dominance for grassland bird communities in Oklahoma.

				Biomass				Most abundant species[c]			
								First		Second	
County	Site symbol	Treatment[a]	Year	Total	Granivore	D_s[b]	No. of species	Name	Density	Name	Density
McClain	1a	LG	1976	1.75	1.42	0.47	3	SAVAS	64	LECOS	43
		MG	1977	1.05	0.50	0.55	4	SAVAS	23	EMEAD, TREES	4
		MG	1978	3.85	2.00	0.31	5	SMITL	48	SAVAS	19
		HG	1979	11.50	6.41	0.39	6	SMITL	150	HORNL	49
Grady	1b	LG	1976	1.74	0	1.00	1	EMEAD	16	—	—
		LG	1977	1.16	0.29	0.61	2	LECOS	22	EMEAD	8
		MG	1978	1.07	0.20	0.51	2	EMEAD	8	HORNL	6
		MG	1979	6.96	5.65	0.67	3	SMITL	169	HORNL	29
Grady	2a	MG	1976	2.69	0.84	0.29	4	TREES	22	EMEAD	17
		MG	1977	1.82	0.29	0.30	5	EMEAD	14	HORNL, SAVAS, CHESL	5
		MG	1978	2.64	1.01	0.29	5	CHESL	37	TREES	25
		MG	1979	5.79	3.94	0.61	5	SMITL	120	HORNL	16
Cleveland	2b	MG	1977	11.14	8.41	0.86	2	SMITL	305	EMEAD	25
		HG	1978	10.54	8.90	0.69	4	SMITL	280	SAVAS	23
		HG	1979	11.07	9.44	0.83	3	SMITL	320	HORNL	18
Grady	2c	MG	1977	11.35	5.56	0.25	5	SMITL	103	CHESL	69
		MG	1978	8.71	2.30	0.28	6	SMITL	52	EMEAD	52[d]
		MG	1979	8.92	5.88	0.60	5	SMITL	181	EMEAD, HORNL	5
Noble	2d	MG	1976[e]	23.93	23.93	0.85	4	SMITL	803	CHESL	41
		MG	1978[f]	6.60	6.60	0.55	3	SMITL	174	CHESL	46
Cleveland	3a	HG	1976	26.25	20.80	0.70	4	SMITL	690	SAVAS	56
		HG	1977	7.12	2.98	0.25	4	SMITL	49	CHESL	46
Pawnee	3b	HG	1976[e]	89.48	89.48	0.95	2	SMITL	3,182	CHESL	83
Cleveland	4a	CU	1976	13.68	7.91	0.43	3	LAPLL	184	HORNL	79
		CU	1977	11.73	4.43	0.46	4	LAPLL	131	EMEAD	65
Cleveland	4b	CU	1977	8.83	3.60	0.60	2	LAPLL	127	EMEAD	48
		SG	1978	27.40	22.58	0.74	5	SAVAS	1,060	CHESL	166
Cleveland	4c	CU	1977	1.09	1.09	1.00	1	HORNL	32	—	—
		CU	1978	0.27	0.27	1.00	1	HORNL	8	—	—
Cleveland	4d	CU	1977	5.68	3.61	0.39	3	HORNL	62	LAPLL	53
		CU	1978	25.51	4.72	0.42	3	EMEAD	200	LAPLL	99

[a] LG = Lightly grazed grassland; MG = Moderately grazed grassland; HG = Heavily grazed grassland; CU = Cultivated field; SG = Successional grassland.
[b] Dominance index (see text).
[c] CHESL = Chestnut-collared Longspur; EMEAD = Eastern Meadowlark; HORNL = Horned Lark; LAPLL = Lapland Longspur; LECOS = LeConte's Sparrow; SAVAS = Savannah Sparrow; SMITL = Smith's Longspur; TREES = Tree Sparrow.
[d] Also present were an estimated 18 CHESL, 11 HORNL, 7 WMEAD and 6 SAVAS.
[e] Censused 20–21 December 1975.
[f] Censused 6 March 1978.

lap in ranges (of many species), and by the initial high postbreeding populations, which include many young birds.

Grasslands can undergo radical changes annually, as well as during 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 effectively magnify grazing pressure. Furthermore, many of the grasslands in the Great Plains are used to produce various crop monocultures. Farming practices can completely change the nature of a grassland site in a short period.

This paper is one of a series (Grzybowski 1976, 1980) dealing with resource utilization and population structure in grassland bird communities during the winter. My purposes 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 that may influence them.

STUDY AREAS

I estimated avian populations at 20 sites in Oklahoma and Texas from December 1975 through January 1979. These sites included two in northern Oklahoma (Noble and Pawnee counties), 10 in central Oklahoma (Cleveland, Grady and McClain counties; Table 1), four 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). I selected sites on the basis of their uniformity, absence of trees or shrubs, and large size (permitting adequate sampling and minimal edge effect). 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 covered less than 0.5%, being isolated individual plants less than 3 m in height.

Sites were classified into treatment categories on the basis of grazing pressure or cultivation. A site was considered a lightly grazed grassland (LG) where the dominant palatable grasses had uniformly grown to heights approaching their maximum potential height. Where these dominant grasses occurred in distinct clumps, the site was considered a moderately grazed grassland (MG). Where 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 classified as a heavily grazed grassland (HG). The only cultivated sites (CUs) 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 a prairie dog town and a lightly grazed grassland.

OKLAHOMA SITES

Oklahoma localities were in the region classified as bluestem-grama prairie (*Andropogon-Bouteloua*) by Kuchler (1964). Table 1 identifies sites by county location and treatment type. The dominant palatable grass on the Oklahoma sites was little bluestem (*Schizachyrium scoparium*). I used this species to gauge grazing pressure, as it occurs in decreasing abundance from LGs to HGs (P. G. Risser, pers. comm.). As grazing pressure increased,

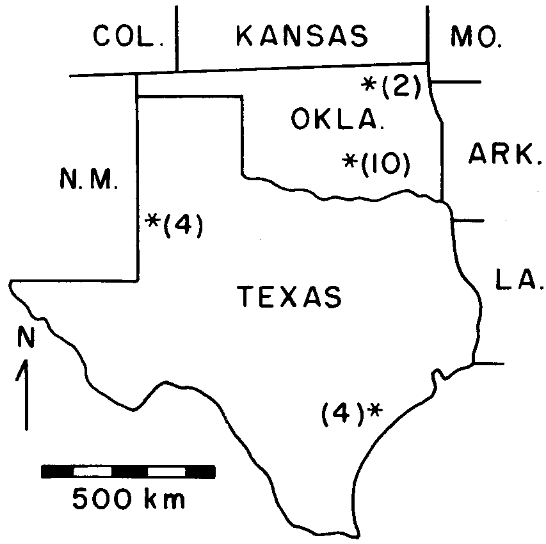

FIGURE 1. Census locations. Number of sites evaluated at each regional location is given in parentheses.

bluestem grasses decreased and became patchy, or disappeared; three-awn (*Aristida* spp.), silver beardgrass (*Andropogon saccharoides*), and forbs, primarily broom-snakeroot (*Gutierrezia sarothrae*) and common ragweed (*Ambrosia artemisiifolia*) appeared and became larger and more in evidence. The dominant grasses on site 1a (LG), which included big bluestem (*Andropogon gerardii*) and indiangrass (*Sorghastrum nutans*), attained heights of 1.5 to 2.0 m; on site 1b (also LG), little bluestem reached 1.0 to 1.5 m. Height of little bluestem on MGs was about 1 m. Vegetation heights on HGs were less than 0.5 m.

On cultivated sites studied, crops of sorghum (*Sorghum bicolor*) had generally preceded the fall plantings of winter wheat. Vegetation height (or litter depth) on cultivated sites was less than 5 cm.

Grazing, agricultural practices, and variation in rainfall changed the character of several sites (Table 1). 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. In February 1977, this site was plowed and planted in cotton (*Gossypium herbaceum*). In 1977, one-half of cultivated site 4b (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 were located in the grama-buffalo grass plains (*Bouteloua-Buchloe*) of Kuchler (1964). Dominant grass species on LGs (sites 5a, 5b and 5c) 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.). On one LG (site 5a; also referred to as MIX), 20% of the transect route passed through an active prairie dog (*Cynomys* sp.) town. In the prairie dog towns and on a HG (site 5d), false buffalo grass (*Munroa squarrosa*), three-awn, and tumbleweed (*Salsola* sp.) were dominant plant species. Vegetation was generally less than 5 cm tall. On more alkaline soil, sea-blite (*Sueda* sp.) was present.

SOUTHERN TEXAS SITES (WELDER WILDLIFE FOUNDATION)

Weaver and Clements (1938) characterized the grasslands of this region as belonging to *Andropogon saccharoides-Stipa leucotricha* associations, although 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. Vegetation on MGs (sites 6a and 6b) was generally between 0.5 and 2 m tall, but mowed fire breaks crossed the sites. Huisache (*Acacia farnesiana*) was an invading brush species on sites 6b (MG) and also 6c and 6d (both HG). Heights of the brush patches were generally less than 1 m during the 1976–1977 winter, but by January 1979, some patches exceeded 2 m in height. Grass on sites 6c and 6d was less than 0.5 m tall.

More specific site descriptions are given in Grzybowski (1980). Brunner (1931) and Buck and Kelting (1962) provide detailed floral accounts of Oklahoma grasslands.

METHODS

In most cases, population estimates were 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). I walked transect lines through the grasslands from 0.5 to 4 h after sunrise. The one-half hour period just after sunrise was avoided because it appeared to be a brief 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 (30 ha), up to eight replicates were used for each estimate.

The location of each bird seen was recorded in relation to its perpendicular distance from the transect line. When groups were encountered, I used the distance of the individual farthest from the transect line and recorded the group size (cf. Emlen 1977). I calculated coefficients of detectability for each species on each grassland type and region from the data collected in March 1975, and between 15 November and 12 March of 1975–1976 and 1976–1977. 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). Groups are more detectable than individuals, however, 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), I estimated the size of larger groups 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 grassland types, years, and regions, I performed a cluster analysis, based on standardized population estimates of species (i.e., $\bar{Y} = 0$ and SD = 1.0 for each species). Species occurring on only one census were deleted from this analysis. Using NT-SYS (Numerical Taxonomy System; a series of multivariate computer programs developed by F. J. Rohlf, J. Kishpaugh, and D. Kirk), 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 estimate the biomass for a species, I multiplied the average weights for up to 10 individuals (five males and five females) 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 avian biomass, I assigned each species to one of the following foraging guilds on the basis of species' size and the primary food consumed (unpubl. data): doves; granivores; insectivores (other than meadowlarks); and meadowlarks (see Appendix for guild assignments). Means of avian biomass for treatments within and among regions were subjected to Duncan's multiple-range test (Kramer 1956).

An index of numerical dominance (D) was calculated for each site (S) using the formula:

$$D_S = \sum_{i=1}^{m} (n_i/n_t)^2, \quad (1)$$

where n_i is the number of individuals of species i, n_t is the total number of individuals of all species, and m is total number of species (Pielou 1975). 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 sites. I randomly selected 20 to 30 locations on a site and brushed debris from the surface of areas 10 × 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:

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

where r_i is radius of mean seed size in the ith class, n is number of classes, Y_i is the number of seeds in the ith 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. I sampled 264 points spaced 15 m apart

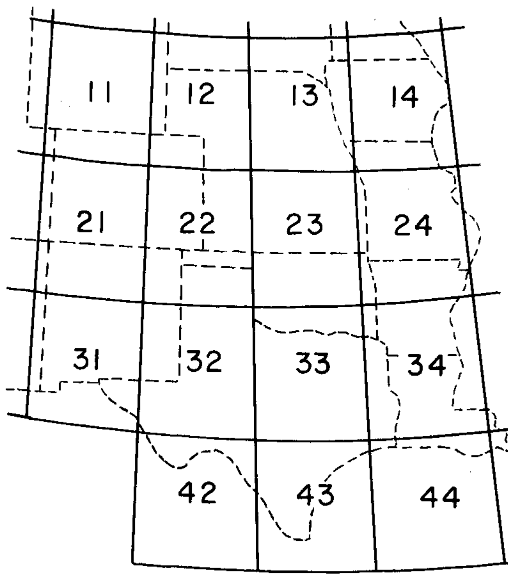

FIGURE 2. South-central United States showing 5°-latitude-longitude blocks used in summarizing results of Christmas Bird Count data.

in a strip 1,000 m long and 60 m wide at each site. At each point, I obtained four measurements of vegetation height and vegetation density. Vegetation density was the sum of the number of contacts made with the tip of a wire passed through the vegetation for 30 cm at 10-cm height intervals. Details of this sampling are described in Grzybowski (1980).

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 party-hour of observation time within a 5°-latitude-longitude block (Fig. 2). I averaged annual results from these censuses for a 10-year period (1962–1971) 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. Patterns of distribution among grassland bird species were assessed with a cluster analysis of grid-blocks, using proportion occurrence of species as variables.

RESULTS

The number of wintering grassland bird species was small in all areas studied (Tables 1, 2 and Appendix). A total of 23 species (excluding falconiforms 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 Rob-

TABLE 2. January population estimates (birds/100 ha), total and granivore biomass (kg/100 ha), and dominance for grassland bird communities in western and southern Texas.[a]

Site symbol	Treatment[b]	Year	Biomass Total	Biomass Granivore	D_s[c]	No. of species	Most abundant species[d] First Name	First Density	Second Name	Second Density
Western Texas sites (Muleshoe National Wildlife Refuge)										
5a	LG	1977	8.77	8.45	0.77	4	HORNL	231	CHESL	16
	LG	1978	9.67	3.53	0.30	5	HORNL	82	WMEAD	31
	LG	1979	11.97	10.90	0.58	5	HORNL	256	MCCOL	62
5b	LG	1977	9.63	6.85	0.58	5	HORNL	182	WMEAD	23
	LG	1978	1.50	1.29	0.91	2	HORNL	38	WMEAD	2
	LG	1979	0.59	0.16	0.34	3	WMEAD	4	HORNL, CHESL	3
5c	LG	1978	0.43	0	1.00	1	WMEAD	4	—	—
	LG	1979	0	0	—	—	—	—	—	—
5d	HG	1977	5.63	3.39	0.50	3	HORNL	86	CHESL	22
	HG	1978	5.13	4.49	0.50	4	HORNL	108	CHESL	35
	HG	1979	11.10	10.25	0.47	4	HORNL	213	CHESL	122
Southern Texas sites (Welder Wildlife Refuge)										
6a	LG	1977	38.46	30.86	0.53	11	SAVAS	1,228	LECOS	237
	MG	1978	45.91	20.84	0.33	7	SAVAS	685	VESPS	213
	MG	1979	27.94	15.64	0.51	7	SAVAS	665	GRASS	95
6b	MG	1977	78.46	54.70	0.44	4	LECOS	1,888	SAVAS	1,580
	MG	1978	28.93	20.76	0.55	4	SAVAS	876	GRASS	201
	MG	1979	52.30	20.63	0.57	6	SAVAS	919	LECOS	263
6c	HG	1977	21.55	1.01	0.27	4	EMEAD	102	SPRAP	90
	HG	1978	24.58	1.88	0.47	3	EMEAD	202	SAVAS	101[e]
	HG	1979	11.09	3.29	0.32	4	SAVAS	144	EMEAD	63[f]
6d	HG	1978	8.90	1.16	0.34	3	SPRAP	80	SAVAS	62
	HG	1979	20.16	1.78	0.31	4	EMEAD	145	SPRAP	64

[a] Censuses indicated for January 1977 in southern Texas were actually conducted 21–23 December 1976.
[b] Treatment symbols as in Table 1.
[c] Dominance (see text).
[d] GRASS = Grasshopper Sparrow; MCCOL = McCown's Longspur; SPRAP = Sprague's Pipit; VESPS = Vesper Sparrow; WMEAD = Western Meadowlark; other species symbols as in Table 1.
[e] Also present were an estimated 28 SPRAP.
[f] Also present were an estimated 42 SPRAP and 51 LECOS.

in, 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—Ground Dove and Lincoln's Sparrow in southern Texas, and Baird's Sparrow in western Texas. Ground Doves and Lincoln's Sparrows have previ-

TABLE 3. Proportion occurrence of grassland bird species by 5°-latitude-longitude grid-blocks. Data from 1962–1972 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	0.06	0.15	0	0.01	0.06	0.48	0	0.07	0.18
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	0.42	0.56	T	0	0	0	0	0	0	0	0	0	0

[a] T = trace (<0.005).

ously 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 left only 14 species that 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

Distributions of species at the regional level were evaluated from CBC data.Table 3 gives proportional occurrence of most passerine species that occurred on two or more censuses by grid-block. Tree and Lincoln's sparrows, more typical of non-grassland habitats (Bent 1968), are not tabulated; however, the Snow Bunting (*Plectrophenax nivalis*), a species of open habitats in the northern plains (Bent 1968), is included.

A cluster analysis of grid-blocks, using proportion occurrence of species as variables (Table 3), is shown in Figure 3. The cophenetic correlation is 0.888, indicating little distortion in representing the original correlation matrix. Several regional clusters can be discerned. One for the four northwestern grid-blocks identifies an area where the Horned Lark was a dominant species. Blocks 13 and 14 are the northernmost in the east; the Snow Bunting is typical of this area. The eastern blocks 24 and 34, where LeConte's Sparrows are more concentrated, are identified as being similar. Blocks 31 and 42 in the southwest show similarity in the occurrence of the Baird's Sparrow, while blocks 43 and 44 in the southeast are alike in the preponderence of Sprague's Pipits and Savannah Sparrows. However, the central grid-blocks (22, 23, 32 and 33) exhibit little similarity. Species composition changes across this zone. Grid-block 23 stands alone; Lapland and Smith's longspurs typify this block. McCown's and Chestnut-collared longspurs, and the Western Meadowlark are most abundant in block 32; block 33 is typified by the Eastern Meadowlark. This analysis shows that species composition changes dramatically along north-south (blocks 22 to 42, and 13 to 43) and east-west (blocks 22 to 24, and 31–34) axes in the southern Great Plains. Species distributions appear basically independent of each other.

SITE COMPARISONS

A cluster analysis (Fig. 4), using population estimates from the 52 censuses (Tables 1 and 2; 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. 4; cophenetic

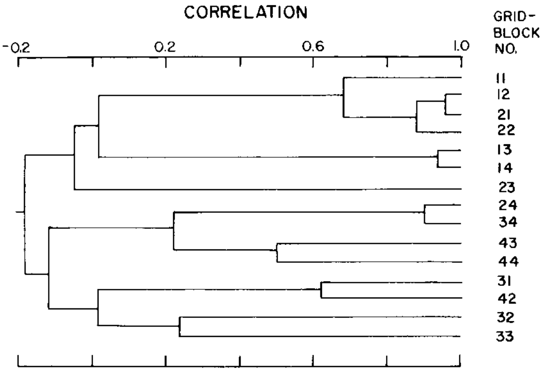

FIGURE 3. Correlation phenogram of Christmas Bird Count grid-blocks based on an unweighted pair-group method of cluster analysis using arithmetic averages (see text). Block numbers correspond to those in Figure 2.

correlation = 0.893), the Savannah Sparrow was a dominant bird species on sites in group 1. The LeConte's Sparrow was co-dominant on sites 1a in 1976 and 6b in 1977 of this group (see Fig. 4). All samples for sites 6a and 6b (group 1) were very similar, indicating a low annual turnover in species. In 1979, both of these sites were lightly to moderately grazed.

The second group in the cluster analysis includes four sites where meadowlarks were the dominant species 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 move locally to adjacent shrubby habitats, which affects estimates of their abundance in open grassland (unpubl. data); such movements may have contributed to my clustering results.

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 Savannah Sparrows had increased, this site for 1979 was placed with the first group. Group 4 is the largest group and includes heavily to moderately grazed sites in 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 1). Smith's Longspurs on these three sites were less common than on the other sites in this group.

Group 5 includes cultivated sites where Lapland Longspurs were dominant. This species occurred only sporadically and in low numbers on other sites. On localities included in the last group, Horned Larks were most common; this

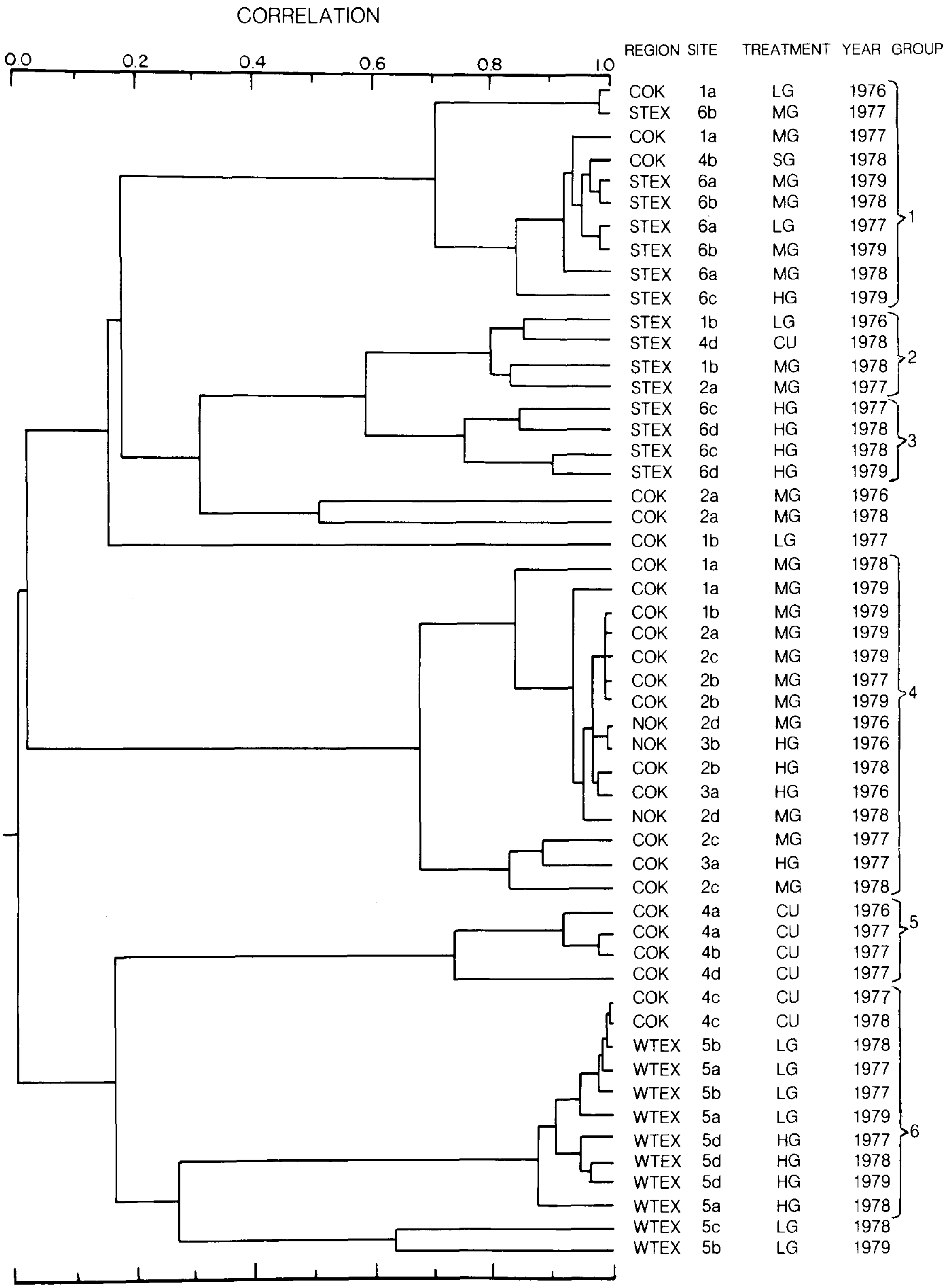

FIGURE 4. Correlation phenogram of censuses based on an unweighted pair-group method of cluster analysis using arithmetic averages. Region symbols are: COK, central Oklahoma; NOK, northern Oklahoma; STEX, southern Texas; WTEX, western Texas. Site and treatment symbols as in Tables 1 and 2; January date for year of winter season is used.

group includes site 4c, a cultivated field where 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. 4). Both had very low density estimates for all species present (see Table 2). On site 2a in 1976 and 1978 (Fig. 4; between groups 3 and 4), the Tree Sparrow was one of the most common species; densities were also low at this site. Site 1b in 1977 (Fig. 4) contained only low densities of meadowlarks and LeConte's Sparrows.

The cluster analysis shows that MGs overlapped the more extreme habitats with respect to bird species. On the more lightly grazed grasslands, the Savannah Sparrow (and sometimes also the LeConte's Sparrow) was the dominant bird species; on the more heavily grazed of the MGs, Smith's Longspurs predominated. The size of suitable habitat patches on a site influences a species' abundance. Regional differences in species composition are evidence for groups 1 and 3, which are primarily composed of southern Texas sites, and group 6, composed mainly of western Texas sites.

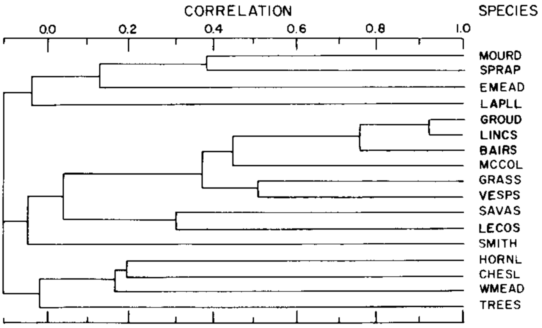

FIGURE 5. Correlation phenogram of species based on an unweighted pair-group method of cluster analysis using arithmetic averages. See Appendix for species symbols.

A cluster analysis of species (Fig. 5; cophenetic correlation = 0.759) further exemplifies the generally weak relations among most of the species. The most closely associated species were the Ground Dove, the Lincoln's Sparrow and the Baird's Sparrow. The first two were uncommon on MGs in southern Texas; the latter is a rare western Texas species. These associations are based on similarities in nonoccurrence for species found on only two cen-

TABLE 4. Mean biomass (kg/100 ha) and dominance estimates for various treatment censuses in different regions of Oklahoma and Texas. Standard deviations (SD) given in parentheses. Treatment symbols as in Table 1.

Treatment	n	Biomass					Dominance
		Total	Granivore	Meadowlark	Insectivore	Dove	
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[a]	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)

[a] Site 5a of Table 2 (see text).

TABLE 5. 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									
	A[b]	A		A			A		A
			B	B		B		B	B
					C				
Granivore biomass									
	A	A		A		A	A		A
			B					B	B
					C				
Meadowlark biomass									
	A	A	A	A			A	A	A
				B	B				
					C	C			

[a] Treatment symbols as in Tables 1 and 4.
[b] Treatments with same letters are not significantly different ($P > 0.05$).

suses each. Overall, none of the 17 species is similar in their response to particular site characteristics.

TREATMENT COMPARISONS

In central Oklahoma, avian biomass tended to increase from LGs to HGs (Table 4). However, few of the treatments were significantly different ($P < 0.05$; Table 5). The HGs had significantly higher granivore biomass than MGs or LGs ($P < 0.05$). Biomass estimates for cultivated sites were high, but extremely variable. The biomass estimate for the HG (site 3b) in northern Oklahoma was the highest of any estimate on any site. The Smith's Longspur (Table 1) was dominant on this site, comprising 97% of all individuals.

Population estimates for western Texas sites were highest on site 5a (MIX; Table 4), which was a lightly grazed area partially traversing a prairie dog town. MIX had significantly higher ($P < 0.05$) estimates of granivore and total avian biomass than LGs in western Texas. Granivore biomass was higher on MGs than HGs ($P < 0.05$) in southern Texas. Total biomass also was higher on MGs than on HGs ($P < 0.05$).

Insectivorous birds (other than meadowlarks) were inconsequential on the Oklahoma and western Texas sites (Table 4). 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). The Sprague's Pipit was the only obligate insectivore consistently appearing on some southern Texas sites (sites 6c and 6d; Table 2), although meadowlarks in southern Texas were entirely carnivorous in the winter (unpubl. data). I found no significant differences ($P > 0.05$) 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 4 and 5). Western Texas and central Oklahoma sites did not differ in biomass ($P > 0.05$). Biomass estimates for all groups were considerably greater on the LG in southern Texas than for LGs in central Oklahoma or western Texas (Table 4). While HGs in southern Texas, central Oklahoma, and western Texas (including MIX) did not differ in total avian biomass, HGs in southern Texas had significantly fewer granivores and significantly more meadowlarks than HGs in other regions ($P < 0.05$; Tables 4 and 5). 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 1 and 2). HGs in southern Texas had the lowest mean for any treatment (0.342, SD = 0.078), but were not significantly different ($P > 0.05$) from HGs in central Oklahoma and western Texas or 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 approached that of complete evenness; i.e., the expected dominance value if all species were equally common (in this case, 0.280).

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, 1976–1978; site 4d, 1977; see Table 1).

ANNUAL VARIATION

All Oklahoma sites censused showed decreases in total bird biomass and granivore biomass from the winter of 1975–1976 to that of 1976–1977 (Table 1). The year 1976 was dry with 45.9 cm of rainfall compared to a mean of 80.0 cm (N.O.A.A. 1978). Standing crop biomass (as measured by vegetation contacts) was lower on the sites in December 1976 than in December 1975.

Several MGs in Oklahoma showed increases in granivore biomass from 1977–1978 to 1978–1979 (Table 1), owing to the incursion of Smith's Longspurs. In fact, much of the annual variation in granivore biomass in MGs and HGs was attributable to this species (Table

1). Smith's Longspurs normally 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 1978–1979 was the coldest on record (mean January temperature −3.2°C; 30-year mean, 2.8°C; N.O.A.A. 1979), and these longspurs were abundant on many sites in central Oklahoma. However, Smith's Longspurs are habitat specialists (Grzybowski 1980) 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 1978–1979 on the grassland sites in central Oklahoma (unpubl. data); only a few scattered individuals could be found at some locations. Heavy mortality of these sparrows may have occurred in the severe winter of 1977–1978 (unpubl. data), when snow covered the ground for a record 38 days in central Oklahoma (N.O.A.A. 1978). Savannah Sparrows were very abundant on a first-year successional field in 1977–1978 and were present on most sites in 1975–1976 and 1976–1977 (Grzybowski 1980).

In western Texas, temperature and rainfall were similar in the different years of my study (unpubl. Muleshoe National Wildlife Refuge weather summary). On the HG (site 5d), biomass estimates were high in 1979 (Table 2) 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 (rainfall 305 cm; 87 cm considered normal at Welder Wildlife Foundation). Granivore biomass peaked in 1976–1977, being extremely high on site 6b (MG), because of the large numbers of Savannah and LeConte's sparrows (Table 2). 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 1976–1977 to January 1979, but increased slightly on the HGs over this period (Table 2). Savannah Sparrows were a consistently abundant element of the granivore biomass. Meadowlarks were generally more abundant on the HGs than on the MGs (Table 2). Bobwhites (*Colinus virginianus*) were occasionally noted on the MGs, but were not recorded on any of the

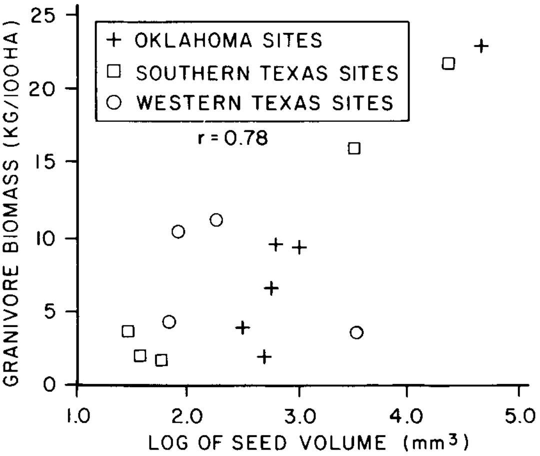

FIGURE 6. Relation of granivore biomass to seed abundance (of seeds 1–4 mm in length).

morning transects. Turkeys (*Meleagris gallopavo*) were also observed traversing site 6a.

Seed abundance was measured on several sites in January of 1978 and 1979. Plotting granivore biomass against the log of seed volume (Fig. 6), I obtained a correlation of 0.78, 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 sizes of populations on sites of intermediate to low food abundance. The sites where seeds were most abundant had the highest granivore biomass, and those with very low seed abundance supported very low granivore biomass (Fig. 6). Site 4b was left fallow in the winter of 1977–1978, and the abundant seed crops of invading grasses and weeds attracted large numbers of Savannah Sparrows (Table 1).

The 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 nine 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 farther north (Sutton 1967). However, solitary meadowlarks could be heard 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 the Mourning Dove, Ground Dove, Eastern Meadowlark and Cardinal 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) found 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 that indicate high species turnovers from fall to winter and winter to spring (72–95%) for three "true prairie" sites. One of their localities (Osage) is near my northern Oklahoma sites.

Many grassland birds are habitat specialists in winter (Grzybowski 1976, 1980). 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 1980). 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.

Climatic tolerances also influence distribution of birds. The CBC data show north-south gradients in distribution for eastern plains regions (Fig. 7) similar to distribution patterns during the breeding season. Thus, the passerine species breeding farthest north—the Snow Bunting—has the most northerly wintering range (Godfrey 1966). The Smith's and Lapland longspurs are tundra species (Godfrey 1966) whose winter distributions typify the central-northeastern grid-blocks (Fig. 7A). Many sparrow species breeding in northern plains grasslands (Bent 1968) winter along the southern border of the United States (Fig. 7B).

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 1968). The Smith's Longspur is typically abundant in north-central and northeastern Oklahoma. In 1978–1979, an unusually cold winter in Oklahoma (N.O.A.A. 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 they dominated grasslands in western Texas. Colorado studies (Wiens 1974a) during the breeding season showed that they were more common in dry years. The preference of Horned Larks for arid conditions may be manifest in their east-west distribution patterns (Fig. 7C). 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. 7). 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 noted 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 opportunistically use concentrated food sources. Abundance of individuals was related to food abundance. Savannah Sparrows were very common on a successional field in central Oklahoma where seed density was very high. High densities were present at MGs in southern Texas in 1976–1977 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 1980) 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

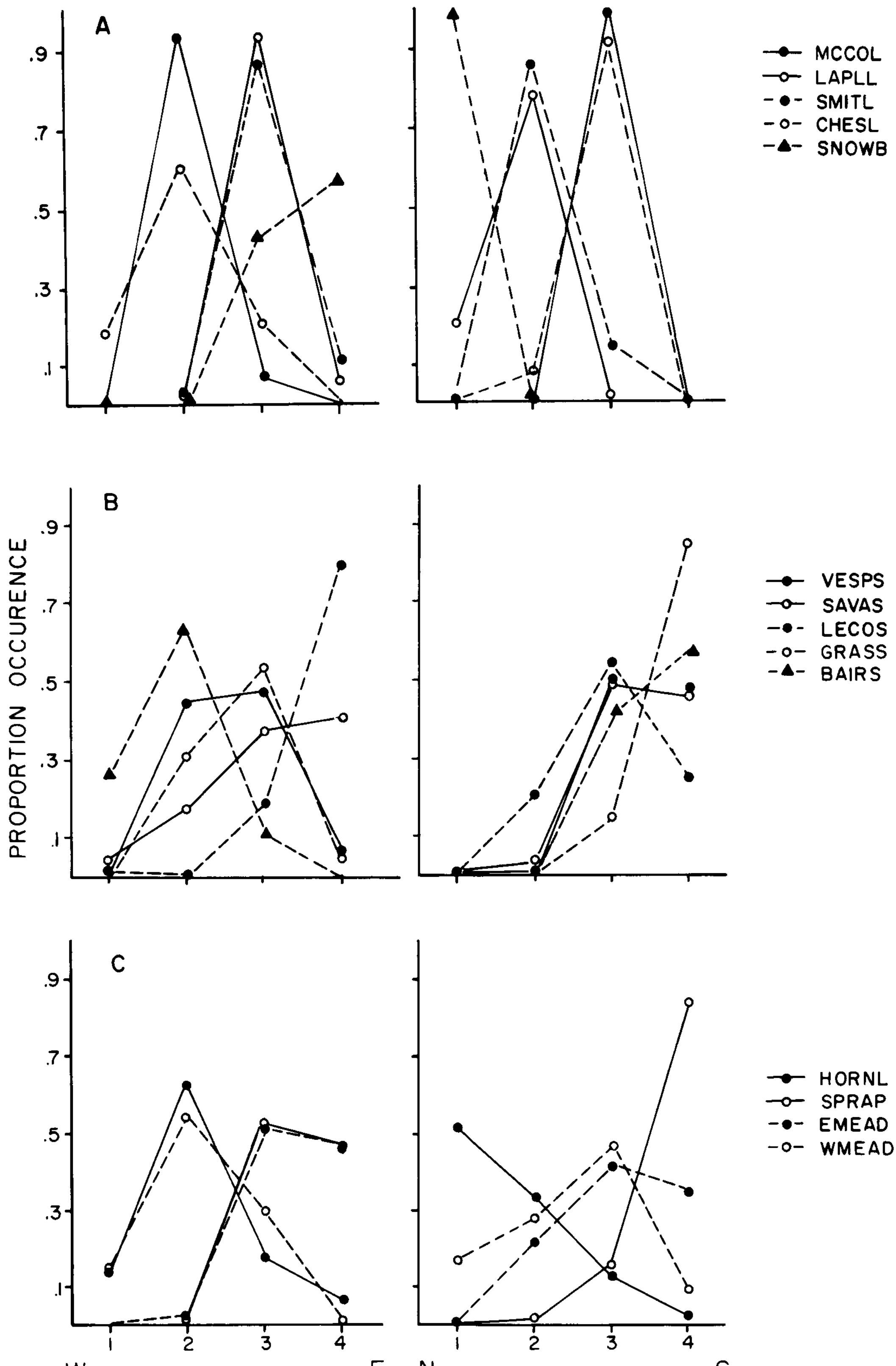

FIGURE 7. Proportion occurrence of species (see text) along west-east and north-south axes for Christmas Bird Count data in south-central United States: (A) longspurs and Snow Bunting; (B) sparrows; and (C) Horned Lark, Sprague's Pipits and meadowlarks.

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 increase in avian biomass from LGs to HGs may be a trend influenced by the reproductive habits of dominant plant species.

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

Since 1850, grasslands have changed dramatically. The large herds of bison (*Bison 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 with single crops. Many ungrazed areas are mowed regularly for hay. 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. 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 drastically reduced its range (Bent 1968). Others, such as the Horned Lark, have expanded their range in response to open agricultural conditions (Hurley and Franks 1976). During winter in central Oklahoma, Lapland Longspurs are abundant on cultivated plots, particularly those on which sorghum was the fall crop.

Wiens (1973) indicated that grassland bird communities in summer may not be "as closely controlled or integrated as, for example, forests (Whittaker and Woodwell 1972), because of their more direct interfacing with, and greater sensitivity to seasonal and long-term abiotic variation." In winter, patterns in regional distribution and annual variation of bird populations reflect climatic influences. Little similarity is found among species in site occupancy (Fig. 5) or regional distribution (Table 3); yet most grassland birds appear to respond somewhat to sets of factors such as climate and habitat (Grzybowski 1976, 1980). Mobility of grassland birds allows opportunism, as seen in the relation of granivore biomass to seed abundance (Fig. 6), and the invasion of sites by new species as grazing pressure or cultivation practices change.

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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.

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. Found. Contrib. No. 5, Ser. B.

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. Popul. Biol. 2:142–158.

EMLEN, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley Publ. Co., Reading, MA.

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 sage-brush-grassland habitat in central Montana. Audubon Field Notes 22:691–695.

FINZEL, J. E. 1964. Avian populations of four herbaceous communities in southeastern Wyoming. Condor 66:496–510.

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

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Canada, Bull. 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. 1980. Ecological relationships among grassland birds during winter. Ph.D. diss., Univ. Oklahoma, Norman.

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.

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, Asheville, NC.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1979. Local climatological data: Oklahoma City, Oklahoma. National Climatic Center, Asheville, NC.

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.

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.]. 1981. The true prairie ecosystem. Dowden, Hutchinson and Ross, Stroudsburg, PA.

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, NB.

WEAVER, J. E., AND F. E. CLEMENTS. 1938. Plant ecology. McGraw-Hill, New York.

WHITTAKER, R. H., AND G. M. WOODWELL. 1972. Evolution of natural communities, p. 137–159. *In* J. A. Wiens [ed.], Ecosystem structure and function. Oregon State Univ. Press, Corvallis.

WIENS, J. A. 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. U.S. For. 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. U.S./I.B.P. 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. U.S./I.B.P. Grassland Biome Tech. Rep. No. 267.

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

Name	Species symbol	Category[a]	Mean wt. (g)
Common Snipe (*Capella gallinago*)	COMMS	I	104.0
Mourning Dove (*Zenaida macroura*)	MOURD	D	120.0
Ground Dove (*Columbina passerina*)	GROUD	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 lincolnii*)	LINCS	G	17.5
McCown's Longspur (*Calcarius mccownii*)	MCCOL	G	27.6
Lapland Longspur (*Calcarius lapponicus*)	LAPLL	G	28.4
Smith's Longspur (*Calcarius pictus*)	SMITL	G	27.6
Chestnut-collared Longspur (*Calcarius ornatus*)	CHESL	G	20.7

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