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Ecology

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DISSERTATION

HABITAT EXPLOITATION BY AN AVIAN GROUND-FORAGING GUILD

Submitted by

Phillip D. Creighton

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

March, 1974

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COLORADO STATE UNIVERSITY

March, 1974

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY PHILLIP DAVID CREIGHTON ENTITLED HABITAT EXPLOITATION BY AN AVIAN GROUND-FORAGING GUILD BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

HABITAT EXPLOITATION BY AN AVIAN GROUND-FORAGING GUILD

Mechanisms employed by sympatric species to effectively partition a habitat have offered a rich avenue for ecological investigations. The majority of community comparisons have been concerned with competitive interactions of closely related species, however ecological similarity need not reflect close taxonomic relationships. The guild concept was used in this study as a technique for comparative community studies. The guild is a functional category combining species that overlap significantly in their ecological requirements, but differ slightly in methods of extracting their requisites. This study's objectives were to determine habitat exploitation patterns of Horned Larks (Eremophila alpestris), Lark Buntings (Calamospiza melanocorys), McCown's Longspurs (Calcarius mccownii), and Chestnut-collared Longspurs (Calcarius ornatus); and to isolate methods used to minimize competitive interactions between these species. Because the four species do exploit the same habitat in similar ways, they qualify for guild membership--the ground-foraging guild.

Parameters of habitat exploitation of this guild were investigated on the Pawnee National Grassland in northcentral Colorado from 1970

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through 1972. The habitat was viewed as potentially being partitioned in space, time and diet. Time budget analysis, catalogs of how and where individuals spend their time, was used to quantify adaptive relationships found in the guild.

Measures of habitat features and vegetation structure associated with guild members were made at 20 randomly-selected, 10.2 ha plots. Areas occupied by guild members differed significantly in the coverage of shortgrass, midgrass, sedges and exposed soil. In part, these habitat differences resulted from nest-site requirements of the four species. Lark Buntings and Chestnut-collared Longspurs nested in close association with midgrasses and shrubs. Interspecific association analysis indicated that McCown's Longspurs and Horned Larks, and Chestnut-collared Longspurs and Lark Buntings were significantly ($P < .01$) associated with each other, while the two longspurs were significantly ($P < .01$) disassociated.

Temporal segregation was accomplished by guild members concentrating nesting at slightly different times of the breeding season. In 1971, Horned Larks initiated most (78%) of their nests in April and May with a nesting peak during the week of 2 May. The nesting peak of McCown's Longspurs was 2 weeks behind that of Horned Larks. Lark Bunting nesting peaks occurred during late May and early June. No recognizable nesting peak was found in Chestnut-collared Longspurs. Temporal overlap for the entire breeding season was lowest between Horned Larks and McCown's Longspurs, species highly

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associated spatially; and between Horned Larks and Lark Buntings, the two most abundant species during the breeding season. Species not spatially associated had high degrees of temporal overlap.

Foods fed to nestlings were used as an index of food specialization occurring within the guild. Orthopterans formed the buld of nestling diet for Lark Buntings, Chestnut-collared and McCown's Longspurs. Coleopteran were of major importance in nestling Horned Lark diet. Mean prey item length of nestling Lark Buntings was significantly ($P < .05$) larger than average items of other guild members. An average diurnal diet returned to nestlings by males, and dietary overlap within the guild are also described. Differences in the frequency that various food items were procured also contributed to efficient habitat utilization.

The use of the guild concept in analysis of community structuring in the shortgrass prairie indicates that habitat partitioning is achieved through combinations of adjustments and divergences in use of time, space and food; and species coexistence results from a complex of compromises serving to reduce the intensity of competition between species exploiting the same habitat.

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This work is dedicated to the memory of my father, Daniel K. Creighton who first introduced me to biology and to birds. I still remember his talk to me when I was five concerning camouflage of killdeer eggs and the importance of distraction displays. I only wish he could have seen this finished work.

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INTRODUCTION

The ecological niche concept contains within its framework mechanisms for comparisons of species' attributes and interactions. Regardless of the potential usefulness of this theory, the niche concept remains one of the least understood in ecology. In part the confusion results from the term's conflicting introduction into ecological usage. Grinnell (1917), viewing a "niche" as a subdivision of the environment, first defined the concept spatially in terms of a species' habitat. Elton (1927) defined "niche" as more of a functional concept, embodying the role of a species in its environment. Elton's definition included, somewhat vaguely, the position of a species in the food web as well as other specific properties.

The dichotomy of usage remained until Hutchinson in 1957 incorporated elements of both Grinnell's spatial niche and Elton's trophic niche definitions into his "multidimensional hypervolume" niche model. Hutchinson redefined the niche, to involve an infinite number of species' attributes, by suggesting one look simultaneously at all possible environmental factors which delimit the existence of a species. By plotting the species' exploitation and existence curves for each factor, an n-dimensional space or hypervolume is encompassed. This hypervolume is defined by Hutchinson as the fundamental niche.

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If the fundamental niche is viewed as a composite of species' attributes, an environmental "space" occupied by a species through its behavioral, physiological and morphological characteristics (Wiens, 1969), the niche can be equated to a temporally isolated gene pool or species, or what Silvestri, et al. (1962) called the taxonomic space. If the fundamental niche serves in this way as a functional definition of a species, then to speak of niche exploitation (Root, 1967), in light of Hutchinson's definition, is ambiguous. What is being exploited is the habitat.

How then can the niche concept be useful for collating attributes of various species? MacArthur (1968) suggested niches of species can be compared with precision by restricting measurements to one or two operationally significant components at a time, thus avoiding the abyss of the fundamental niche. One can then address differences in feeding behaviors or spatial utilization of species, and isolate concrete niche differences.

These considerations lead to the purposes of this study which were: 1) comparison of the habitat exploitation patterns of four species of grassland songbirds; viz. Lark Bunting (Calamospiza melanocorys), Horned Lark (Eremophila alpestris), McCown's Longspur (Calcarius mccownii) and Chestnut-collared Longspur (Calcarius ornatus); 2) determination of and how these patterns limit or offset interspecific competition; and 3) recognition of how a habitat is

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partitioned among these four species. The specific questions asked were:

1. Are there spatial segregations and differential vegetational utilization shown by these birds?

2. Is there temporal segregation of ecological demands by these four species?

3. Are there differences in prey capture techniques and food items utilized?

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LITERATURE REVIEW

Ornithological literature is replete with observations of species' feeding ecologies and methods of habitat partitioning. The competitive exclusion principle (Hardin, 1960) states that no two species can occupy the same niche at the same time or place; thus it is not unusual that particular interest has been generated by ornithologists, and ecologists in general, for comparative studies of the variations demonstrated by species in their habitat exploitation patterns. To relieve competitive pressures, closely related, sympatric species would be expected to reflect differences in choice of microhabitat or food, and it is this competition which may play an important part in structuring the relationships between species in a particular habitat.

Cody (1968) compared methods of habitat partitioning and patterns of distribution of bird species in grassland communities, and found constant ecological differences between species in this type of habitat. His results demonstrated that grassland communities are predictable, and similar grasslands support bird species of similar ecology. Cody recognized three possible methods of resource division in which coexistence (which was defined as "the occurrence of two or more species in a habitat type") was achieved and competitive elimination avoided:

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1. Spatial segregation (both vertical and horizontal habitat partitioning).

2. Temporal segregation (both daily and seasonal)

3. Food specialization.

Although he did not consider temporal segregation, vertical habitat partitioning or actual prey items of the species involved, Cody's study determined the shortgrass prairie permits development of species-specific patterns of food procurement, and each shortgrass prairie contains usually one species of prober (e.g., meadowlarks), launchers (e.g., horned larks), and foliage gleaners (e.g., most sparrows). He reasoned that members of avian communities are able to coexist by developing differences in habitat preferences and feeding behavior, and the persistence of species groups in a particular habitat will be determined by the ecological differences between them. Cody's main contribution to this current study is organizational--patterns of habitat partitioning will be divided into the realms of spatial segregation, temporal segregation and food specialization.

These specializations enhancing habitat partitioning may be viewed at various levels of resolution or refinement. Habitats partitioned by broad spatial or temporal adjustments through specific ecological requirements or preferences may be viewed as "coarse-grained"; while behavioral differences, such as prey-capture technique or prey-size selection, within the same spatial or temporal framework may be comparatively viewed as "fine-grained" adjustments.

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Spatial Segregation

Hartley (1953) presented one of the earliest studies of spatial separation of species' demands. He performed an ecological study of the feeding habits of five species of English titmice, and found that each species exploited discrete feeding levels and concentrated on different tree species. Within the same tree, finer grain adaptations to various microsite areas were demonstrated. Hartley concluded that interspecific competition was avoided and coexistence maintained by combinations of these interspecific differences of exploitation.

In a similar study, Gibb (1954) found niche separation of feeding stations of tits in England. The five species investigated--the Great (Parus major), Marsh (P. palustris), Longtailed (Aegithalos caudatus), Blue (P. caeruleus), and Coal Tit (P. ater), segregated feeding activities at different heights, on different plant species, and on different foods at the same place on the same plant. The species always exhibited partial segregation, no matter how plentiful the supply of food, but utilized more distinctive vertical strata and specific plant species when food was scarce. Gibb concluded that coexistence for these species was achieved by this segregation of feeding sites.

MacArthur (1958), in his study of five parulid warblers breeding in the coniferous forests of northeastern United States, reported discrete stratal segregation of all five species. Although each species fed in different positions, captured prey in slightly different fashions

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and moved in characteristic directions through the trees, difference in habitat preferences resulting from the species' segregation of feeding zones was probably the most important factor permitting the species to coexist. In addition to these microsite preferences within the same conifer, MacArthur determined populations of each species were roughly proportional to the volume of foliage in the macrohabitats of the type in which they normally fed.

Sturman (1967) analyzed the coexistence of the Black-capped Chickadee (Parus atricapillus) and Chestnut-backed Chickadee (P. rufescens), and found foraging sites of the two species very different. He recognized that rufescens foraged higher in trees, nearer the ends of branches and more often in hardwoods than did atricapillus. When foraging on the same branches, rufescens foraged on the upper branch surfaces while atricapillus foraged on the lower surfaces. These tree-utilization differences contrasted markedly the foraging areas of the two species: in conifers the region of the tree in which they foraged was different while in hardwoods they segregated by the surface of branch from which they fed.

Studies of habitat partitioning between members of divergent taxonomic groups have been limited. Competition between closely related species has usually been assumed to be more intense than between distantly related ones, although Gilbert, Reynoldson and Hobart (1952) have stressed that a close taxonomic relationship is not

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necessarily involved in a concept of ecological similarity. Johnston (1971) investigated those strategies which enable sympatric flycatchers to partition environmental resources of the eastern deciduous forest. His work concerned four different genera (Myiarchus, Sayornis, Contopus and Empidonax) which employ flycatching--aerial sorties from perches to procure flying insects--as the principal prey capture tactic. He found stratal preferences both for nest sites and feeding zones. Myiarchus tended to feed in the canopy, from 15-21 m or more; Contopus showed a distinct preference for subcanopy at a mean height of 10.6 m; and Empidonax, although overlapping with the zone of Contopus, had a mean feeding height of 7.6 m. However, Sayornis, which usually required a man-made structure for its nest site, showed no apparent preference for specific feeding zones. Johnston concluded that "selection has favored interspecific differences in body and bill size, feeding and nest heights, choice of vegetation densities, and choice of food size; all of which are sufficient in various combinations to reduce competition and thereby permit effective partitioning of resources."

Austin and Smith (1972) quantified the interspecific relationships of winter foraging flocks, and found difference in vegetation utilized for foraging was the major factor by which species in the flocks achieved spatial separation. The seven species most commonly comprising these flocks segregated as to perch size, perch surface

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character, foraging surface character, vegetation usage and foraging height. The investigators concluded that because of these patterns of segregation, an optimal flock size and species composition was demonstrated, and these optima led to maximum efficiency in resource utilization.

Morse (1967) investigated the foraging relationships of the Brown-headed Nuthatch (Sitta pusilla) and Pine Warbler (Dendroica pinus). In flocks composed of both warblers and nuthatches, Sitta foraged mainly on distal parts of limbs and twigs while Dendroica foraged on proximal parts of limbs and regularly ventured onto the trunk. However, in single-species flocks, foraging areas of each species were significantly different. In pure nuthatch flocks, Sitta foraged substantially longer on large limbs and trunks, while in pure warbler flocks, Dendroica spent proportionally more time on the distal parts of limbs. Morse concluded that the demonstrated displacement in areas when the species foraged together suggested that Brown-headed Nuthatches and Pine Warblers share many ecological similarities, and the spatial segregation was a result of competition for food between the two species. Division of the foraging areas in this manner promoted efficient harvesting of resources, and minimized the time and energy lost in hostile encounters between the two species.

There are relatively few studies of avian habitat segregation in forested communities of lower relief or in grassland situations where

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vertical vegetational stratification is much less apparent. However, in areas of reduced stratification, the mosaic pattern of habitat characteristics is still readily visible, and some attention has been given to horizontal habitat partitioning.

Lanyon (1956) examined various aspects of the sympatric distribution of the Eastern Meadowlark (Sturnella magna) and Western Meadowlark (Sturnella neglecta), and determined environmental moisture was responsible for the mosaic pattern of distribution of the two species in areas of overlap. S. magna exhibited a preference for more moist areas while neglecta selected more xeric environments. A correlation between the overlapping breeding ranges and average spring precipitation was further evidence that environmental moisture was a major proximate factor in determining species presence. Marginal magna habitats were drier upland sites or drained and cultivated areas, and it was at these sites where neglecta was found.

Cody (1968) explored horizontal habitat segregation as one method grassland birds may employ to achieve coexistence. On the shortgrass prairie of northeastern Colorado, he noted that several bird species are intimately associated with a single plant species, and the mosaic of bird distribution reflected patchiness of the plant species. For example, Sage Thrashers (Oreoscoptes montanus), Brewer's (Spizella brewerii) and Cassin's Sparrows (Aimophila cassinii) were found confined to patches of Atriplex. However, Cody concluded that

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most birds, even with fairly specialized food and habitat preferences, are unable to discriminate between similar plant species for possible exploitation. Interspecific habitat preferences of species in grasslands of Colorado, Kansas and Minnesota were also compared. By associating specific birds censused with grass height and vertical vegetation density at each site, Cody recognized that interspecific habitat separation increased as complexity (patchiness) of the grassland increased. He found little horizontal habitat segregation in short grass areas, although in middle and tall grass areas the habitats were divisible horizontally.

Giezentanner (1970) determined distributional patterns of birds on the shortgrass prairie of Colorado in relation to varied cattle grazing intensities and seasonal use. Because grazing schedules were rigorously maintained over time, structurally distinct plots were censused, and height of vegetation or grass type could be roughly correlated to grazing pressure. He was able to confirm associations of meadowlarks (S. neglecta), Lark Bunting, Chestnut-collared Longspur and Brewer's Sparrow with increasing plant biomass, while usage by Horned Lark, McCown's Longspur, and Mountain Plover was negatively correlated with increasing plant biomass. More specifically, Giezentanner found the Horned Lark, McCown's Longspur and Mountain Plover showed definite preference for heavily-grazed, semibare areas. McCown's Longspur preferred hilltops while Mountain

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Plovers nested and foraged in low areas. Western Meadowlarks and Lark Buntings preferred plots which were lightly-grazed and had denser vegetation. Chestnut-collared Longspurs were found in tall, bunch-grass areas, while Brewer's Sparrows were again found restricted to patches of Atriplex.

Tramontano (1971) also recognized horizontal segregation in foraging microsites of six species of grassland sparrows in Arizona. He found that Grasshopper Sparrows (Ammodramus savannarum) foraged in patches of low to medium grasses, Botteri's Sparrow (Aimophila botterii) in tallgrass patches and Cassin's Sparrow in intermediate patch-types. Lark Sparrows (Chondestes grammacus) utilized open ground and patches of litter; Black-throated Sparrows (Amphispiza bilineata) exploited bare ground and the periphery of shrubs; and Rufous-crowned Sparrows (A. ruficeps) were much more general in habitat utilization and frequented all microsites except shrubs. He determined that the selection of prey items by all six species was similar even though their foraging microhabitats differed, therefore, coexistence was possible because of horizontal patch preferences.

Temporal Segregation

Habitat partitioning by birds is achieved usually by combinations of adaptations and not by one method of segregation alone. If competitive pressures are of consequence during only portions of species' life

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cycles, temporal segregation of demands during those times can promote coexistence.

Skutch (1966, 1967) found closely related species of tropical birds staggered their breeding seasons through time, promoting an increased species diversity. He concluded that the breeding seasons of potential competitors were precisely staggered to "divide the resources more evenly through time."

Recher (1971) investigated methods of habitat partitioning by Australian honeyeaters, viz., Phylidonyris nigra and P. novaehollandiae. These species are similar in size, appearance and behavior, and occupy the same general habitat for nesting and foraging. One important difference he isolated between these species was temporal segregation of reproductive cycles. Nesting peaks recorded for nigra over 3 years occurred in August, contrasted with a peak nesting period in October for novaehollandiae. This segregation of reproductive demands permitted both species to apply heavy utilization pressure on the same habitat by extracting requisites at different times. As Recher concluded: "though both species use very similar resources, seasonal changes in these resources that favor one species and then the other allow both to use the same habitat, but at different times."

Kroodsma (1973) determined intense competition between Bewick's Wrens (Thryomanes bewickii) and House Wrens (Troglodytes aedon) was diminished, in part, by differences in timing of the species'

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breeding seasons. The majority of Bewick's broods was initiated and fledged before those of sympatric House Wrens. He assumed the greatest strain on the food supply of the two species occurred during the nestling-fledgling periods, therefore temporal segregation of demands during those periods was important for diminished competition.

Shorter term temporal segregation may be as important in negating effects of competition as seasonal partitioning. For example, Marti (1969) discussed circadian segregation of foraging times of four sympatric owl species: Bubo virginianus, Asio otus, Speotyto cunicularia and Tyto alba. From field observations and evaluation of the development of the facial disc of these owls, he concluded each species employed characteristic foraging periods--Speotyto is an active diurnal forager, Bubo crepuscular, and Tyto and Asio strictly nocturnal. These discrete activity periods functioned to reduce the level of competition.

Food Specialization

It has been adequately reported, beginning with Huxley (1942) and Lack (1944), that size differences in the bills of birds permitted exploitation of different food items thus helping to reduce interspecific competition. Other surveys of additional morphological variations among sympatric species have also provided insight as to ways species partition resources. Much less emphasis has been placed on the

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different prey capture techniques or behavioral variations species may employ. Differences of these latter tactics permit particular species to exploit prey items exposed by virtue of their unique way of seeking those items. The importance of species being exposed to prey in slightly different ways, and capturing food by different techniques was recognized by MacArthur (1958). He found important food item differences of five species of warblers resulted partially from behavioral differences in feeding. He quantified feeding techniques by resolving all motions into three directions the species commonly moved in the tree canopy: vertical, radial and tangential; and capture tactic employed, i.e., long flight, hawking and hovering. The foraging beat of each species varied in respect to amount of time spent hovering and hawking, and in foraging direction. Those species employing similar prey capture tactics moved through the canopy in different directions. Likewise, those species which progressed through the trees in similar fashion, captured prey by less similar tactics.

Root (1967) determined members of the foliage-gleaning guild he investigated exhibited characteristic mixtures of feeding maneuvers and foraging beats which improved the efficiency of habitat exploitation. He defined the basic feeding maneuvers as:

Maneuver	Position of Prey	Position of Bird
glean	on substrate	on perch
hover	on substrate	in the air
hawk	in the air	in the air

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Each guild member used these tactics in varying proportions in their foraging beat. Root concluded niche segregation within the guild, initially achieved by a combination of adaptations, is maintained by variations in efficiency of exploitation of common resources.

Ashmole (1968) also concluded that differences in feeding maneuvers are evidently of greater importance in maintaining ecological segregation among less closely related species. He investigated techniques of habitat segregation of five tern species in the tropical Pacific Ocean, and found coexistence promoted by species extracting available prey items by different feeding modes. These differences of feeding methods, reflecting differences in size and morphology of the species studied, demonstrated a way selection could operate to adjust feeding techniques, by segregation of size and morphology, to exploit a common range of available foods.

The Guild Concept

In 1967, Richard Root introduced the concept of the "ecological guild", defined as "a group of species which exploit the same class of environmental resources in similar ways", as an effective new technique for comparative community studies. As has been pointed out above, the majority of community comparisons is concerned with competitive interactions within particular taxonomic groups, often obscuring functional or ecological relationships because species

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exploiting the habitat in fundamentally different ways are considered together. The guild concept is a functional category combining species, without regard to taxonomic position, that overlap significantly in their requirements, and exploit the habitat with generally similar patterns. Thus a particular guild is defined by the basic habitat which the species are exploiting, and not by their taxonomic relationships. If specific requirements of species do overlap, natural selection would tend to favor some minimal divergence in the exploitation patterns of guild members. This divergence has been shown to occur by temporal and spatial segregation of species' demands and food specializations, and in any particular guild, a spectrum of divergences may be expected.

On the shortgrass prairie of Colorado, there are four species of ground-nesting songbirds which exploit the same habitat in similar ways, and therefore qualify for guild membership. I have named this association, the ground-foraging guild, and in this study, I have attempted to quantify divergences of habitat exploitation patterns of guild members.

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DESCRIPTION OF THE STUDY AREA

The Pawnee Site

This study was done as part of the International Biological Program's (IBP) Grassland Biome Study at the Pawnee Site, on the Central Plains Experimental Range (CPER) (Figure 1). The Pawnee Site, designated as the intensive site for the Grassland Biome Project, is located 13 km north and 1.6 km east of Nunn, Colorado in Weld County within Township 10N, Range 66W at 104° 45' west longitude and 40° 50' north latitude. The CPER, managed by the Agriculture Research Service of the U.S. Department of Agriculture, is in turn located within the northwestern division of the Pawnee National Grassland; the latter is administered by the U.S. Forest Service.

The Pawnee Site, chosen as representative of the shortgrass association, is dominated by blue grama (Bouteloua gracilis) and buffalograss (Buchloe dactyloides). Midgrasses such as western wheatgrass (Agropyron smithii), crested wheatgrass (A. desertorum), little bluestem, (A. scoparius), needle and thread grass (Stipa comata), green needlegrass (S. viridula), and red threeawn (Aristida longiseta) are found with the dominant shortgrasses. Annual forbs include Russian thistle (Salsola kali), pale evening primrose (Oenothera pallida), cryptantha (Cryptantha crassisepala), and

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Figure 1. Map of the Pawnee Site, U.S. I.B.P. Grassland Biome, showing location of bird studies and other research locations.

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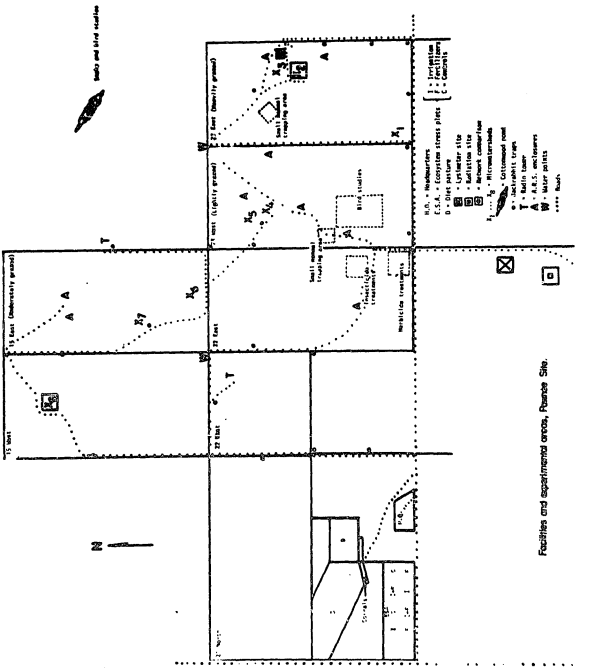

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lambsquarter (Chenopodium album). Scarlet globemallow (Sphaeralcea coccinea), surfpea (Psoralea tenuiflora), tansyleaf aster (Aster tanacetifolius), scarlet gaura (Gaura coccinea), and starlily (Leucocrinum montanum) are among the more common perennial forbs. Shrubs include saltbush (Atriplex canescens), rabbitbrush (Chrysothamnus nauseosus), broom snakeweed (Gutierrezia sarothrae), fringed sage (Artemesia frigida) and winterfat (Eurotica lanata). The principal cactus is the plains prickly pear (Opuntia polyacantha). A detailed vegetation map of the Pawnee Site based on areas delineated by observable differences in aerial photographs is shown in Figure 2.

Elevation at the site ranges from 1,640 to 1,684 m (5,378 to 5,526 ft). The topography consists of gentle slopes and flat areas accentuated by small rises and low swales (Figure 3). The soils of the area are representative of the dark brown and brown soils of the semiarid grassland where about 85% are loams ranging from clay to sandy loam (Klipple and Costello, 1960). The soils at the Pawnee Site have been described by Jameson (1969) as belonging to the Ascalon, Vona, Renohill, and Shingle series.

Precipitation is one of the most important factors affecting the area. Average annual precipitation ranges from 25.4 to 38.1 cm (10-15 in), and 72% of the moisture is received in the period May through September restricting the growing season to about 127 days (U.S. Department of Agriculture, 1941). Winds are predominantly

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Figure 2. Map of vegetation types of the Central Basin Watershed and the Pawnee Site Headquarters. See U.S. I.B.P. Grassland Biome technical Report No. 150 for vegetational type codes.

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Figure 3. Topography of the Pawnee Site, Colorado I.B.P. Grassland Biome.

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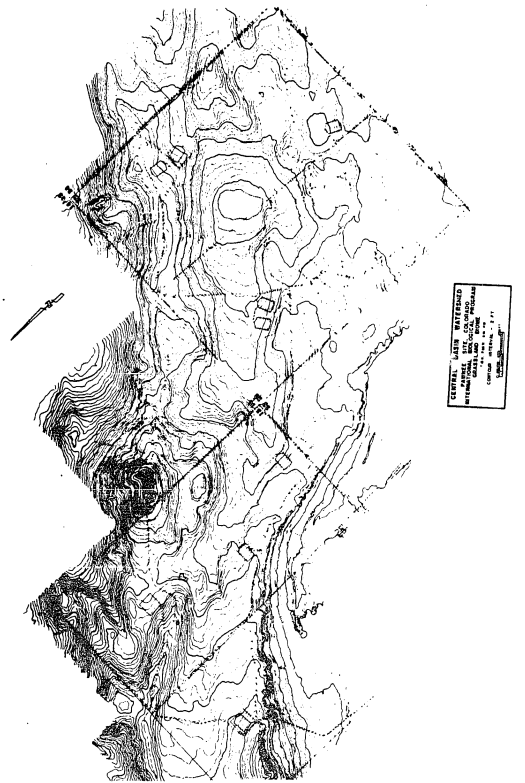

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from the north or northwest, and velocities may exceed 35 mph during the summer (Costello, 1944).

Temperatures are variable and often extreme. Daily air temperatures averaged 26.7° C., with a high of 38° C and a low of -20° C occurring during this study. Average yearly extremes varied from 36.1° C in August to -24.4° C in January (Bement et al., 1970). Giezentanner (1970) summarized temperature fluctuations during the early phases of this current work. Jameson (1969) and Klipple and Costello (1960) provided detailed descriptions of the biotic and abiotic characteristics of the Pawnee Site.

Primary Site

A 9.7 ha area in a short and midgrass pasture located 3.2 km east of the Pawnee Site Headquarters (T10N, R66W, Sec 23W) was chosen as the primary site for this investigation (Figure 4). It was selected as the principal study area because it was one of the few fields, of the sections selected for IBP use, where all four guild species were nesting in reasonably close proximity to each other. It is designated a light summer-grazed pasture for CPER grazing studies, i.e., 13 head of yearling cattle are maintained on the field from 15 May to 15 October annually. Vegetation in the study area, mapped by Shaver and Fisser (1972), is quite uniform in plant species composition (Figure 5). Blue grama is the dominant shortgrass with

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Figure 4. Map of the soil types in Section 23W of the Pawnee Site showing the location of the Primary Study Site.

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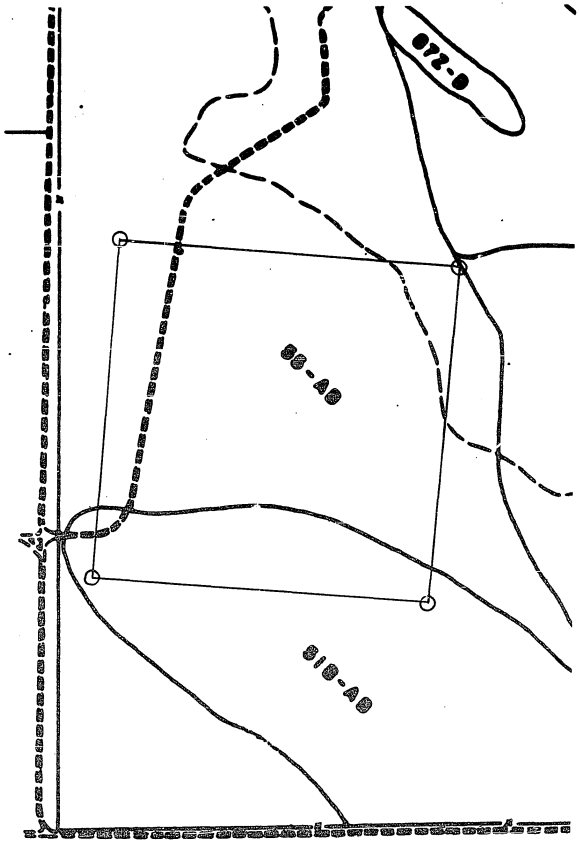

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Figure 5. Map of vegetation types in Section 23W of the Pawnee Site. See U.S. I.B.P. Grassland Biome Technical Report No. 150 for vegetational type codes.

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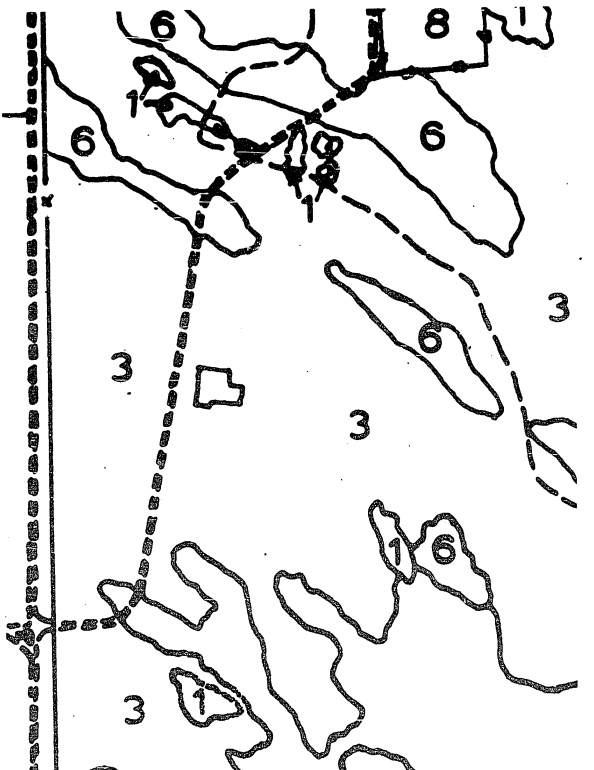

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midgrass, red threeawn, interspersed. Associated with these two major grasses are needleleaf sedge (Carex eleocharis), needle and thread, broom snakeweed, rabbitbrush, saltbush, plains pricklypear, and fringed sage. When comparing the vegetation map with the soils map (Figure 4) and the topographical map (Figure 6), it can be noted that vegetation is closely associated with soil type as well as relief.

The field is bounded on the west by a barbed wire fence, and bisected by an unpaved road which occasionally received light traffic by other researchers. A fenced-in, 0.5 acre exclosure is also located in the study area.

In the spring of 1972, color-coded, 0.6 meter-high stakes (Figure 7) were placed in a 10x10 grid system at 30.5 m intervals in the study area. These stakes added a valuable spatial reference which permitted me to accurately locate foraging areas, territorial boundaries, nests, and activity sites. Although all four species used the stakes as song perches and resting places, it is unlikely the stakes increased attractiveness or "desirability" of the field, for densities of the species remained at the same levels as before the grid was established.

Other species breeding in the field were three to five pairs of Western Meadowlarks, two pairs of Common Nighthawks (Chordeiles minor), and two or three pairs of Mourning Doves (Zenaidura macroura). Brewer's Sparrows and Sage Thrashers nested in

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Figure 6. Topography of the primary study area in Section 23W of the Pawnee Site.

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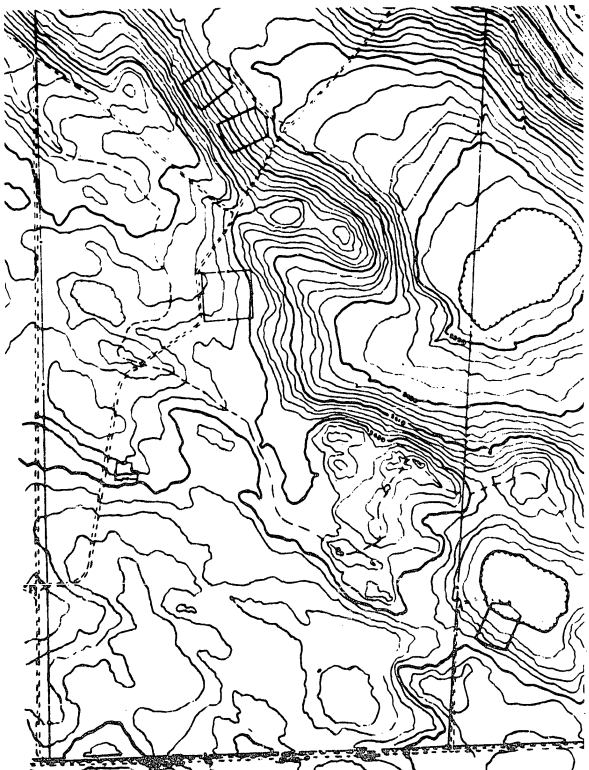

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Figure 7. Example of color-coded wooden stakes used to reference locations within the grid system of the primary study area.

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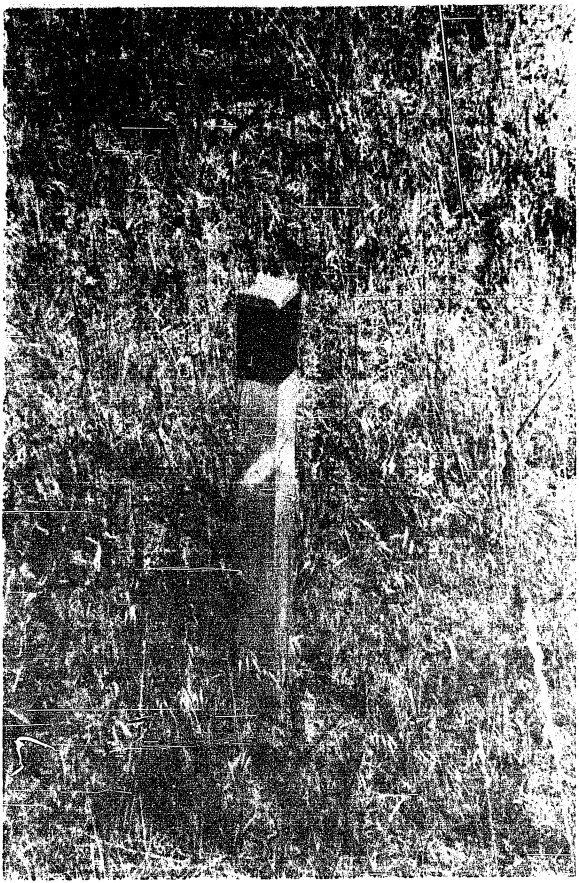

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adjacent field to the west and often foraged in the study area. Killdeer (Charadrius vociferus) and Mountain Plovers (Eupoda montana) foraged in the field, but I found no nests of those species in that area. Numerous other species, best summarized by Giezentanner (1970), Strong and Ryder (1970), and Ryder (1971), occasionally foraged in or over the pasture.

Secondary Site

Because numbers of Chestnut-collared Longspurs were low (two nesting pairs) at the primary site, a secondary area (T10N, R66W, Sec. 28W) was selected where density of this longspur was sufficient for adequate and randomized observations. This area is 6.4 km west of the primary site. The vegetational structure and composition of this pasture differed markedly from the primary field. Rather than uniformity in plant composition, distinct spatial heterogeneity or patchiness was apparent in this field, with a mosaic formed of mid-grasses and shortgrasses (Figure 8). The dominant midgrasses were crested and western wheatgrass; with red threeawn, Indian ricegrass (Oryzopsis hymenoides), and needle and thread present in lesser amounts. Patches of shorter grass were composed of buffalograss, woolly Indianwheat (Plantago purshii), six weeks fescue (Festuca octoflora) and needleleaf sedge. Also common were Canada thistle (Cirsium arvense), prairie pepperweed (Lepedium densiflorum) and yellow sweetclover (Melilotus officinalis).

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Figure 8. Secondary study area, demonstrating the mosiac pattern of mid and short grasses.

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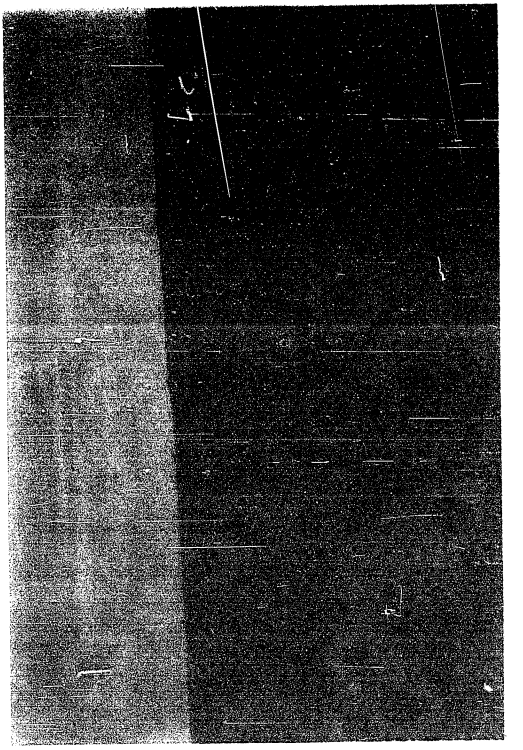

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Behavioral observations of Chestnut-collared Longspurs were mainly obtained from this area. Lark Buntings and Horned Larks were also nesting in the field, although in lesser numbers, while McCown's Longspurs were not found there. Although about one-quarter of my time was spent in this pasture, I did not place a reference grid system there. The presence of fairly large numbers (13 to 15 nesting pairs) of Chestnut-collared Longspurs and the absence of McCown's Longspurs in this field, initially suggested to me that distinct bird and plant species associations may exist for guild members, and these associations may serve to reduce interactions between potential competitors.

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MATERIALS AND METHODS

This field study encompassed a total of 329 days spent at the Pawnee National Grassland observing species of the ground-foraging guild on their breeding territories during the following periods: 1 May-15 September 1970; 27 April-31 August 1971; and 15 March-31 August 1972. Because unseasonable weather in 1972 prevented complete observations of the early breeding behavior of Horned Larks, an additional period, totalling 19 days, was spent in the field in Spring 1973 to supplement those earlier incomplete observations. Qualitative information was gathered on the breeding biology of Horned Larks, McCown's Longspurs, and Chestnut-collared Longspurs in 1970 while quantitative results were being gathered on the Lark Bunting (Creighton, 1971). Full attention was placed on the four species as a unit--an ecological guild--in 1971 and 72, and it is from these two research seasons that quantitative accounts presented here are based.

Location of Nests

Assessment of exploitation patterns and categorization of behaviors depended on accurate knowledge of the reproductive status of birds in the guild. Considerable effort was therefore directed at locating all nests in the study area, and recording nesting progression

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each day. Many nests were found during their construction or early in egg desposition although success of finding nests varied among species. A majority of nests was found by carefully watching females until they returned to nest sites. Behavioral characteristics of each species also aided location of nests. Male Chestnut-collared Longspurs often utilized preferred song perches adjacent to nest sites, and by searching near the perch the nest could usually be found. The descent of the flight song or moth flight (Creighton, 1971) of male McCown's Longspurs frequently ended near its incubating female and again nests could be discovered. Both Lark Bunting sexes would give a "chitter call" (nest relief call) (Baldwin, et al., 1969) on returning to nests, and by following the birds nests could be easily located. When female Horned Larks returned to nest sites, they did so with a very direct, low-to-the-ground flight which eventually became recognizable. Once a nest was found, a nest number was assigned, surveyor flags were placed 2.5 m north and south of the nest, the nest associated vegetation was identified, and an accurate count of nest contents was made. In 1972, for photographic referencing of nestling foods, a 0.6 m stake was also placed beside the nest so adults would become accustomed to utilizing the perch before entering the nest.

Nest Treatment

Territory sizes were determined by use of Wiens' (1969) multiflush techniques, and by recording associated stake locations as birds

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moved about in the reference grid. With the multi-flush technique, territorial males were repeatedly flushed 20 times and their point of landing marked with a flag outlining the perimeter of their territory. Territories were mapped during stages of territorial establishment and incubation to determine permanency of boundaries. As Giezentanner (1970) indicated, success of this technique varied considerably between species.

In 1971, I inspected nest contents daily between the hours 0700 and 0830 (MST). Eggs were marked by felt-tipped pens in the order they were laid, and young were also distinctively marked to reflect hatching sequence. Later banding was also done in numerical order of hatching. Nestlings were weighed on an Ohaus Cent-o-Gram balance to the nearest 0.1 gm. Before weighing, nestlings were handled to encourage venting of fecal sacs. The length of the first primary feather was also measured as an additional growth parameter. A standardized growth curve from the increase in length of this primary feather was used to approximate the age of flightless, unmarked fledglings found away from nests.

Daily records of egg and nestling mortality, and nestling growth were kept on IBP Field Data Sheets (Figure 9) for eventual submission to the data bank and computor analysis. Much of this growth information was presented by Strong (1971).

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Figure 9. U.S. I.B.P. field data sheet used for recording daily observations at nests of guild members.

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IBP

GRASSLAND BIOME

U.S. INTERNATIONAL BIOLOGICAL PROGRAM

FIELD DATA SHEET--AVIAN NESTING AZU209

Data Type	Site	Gen/Spp	Nest No.	TWP	Range	Sec	Ht (cm)	Habitat	Code
I-2	3-4	5-8	9-12	13-15	16-18	19-20	21-24	25-69	70

Data Type	Site	Initials	Date			Time	Eggs	Young	Age	Adult	Height	Length	Primary	Number	Height	Length	Primary	Number	Height	Length	Primary	Number	Height	Length	Primary	Code
			Day	Month	Year																					
I-2	3-4	5-7	8-9	10-11	12-13	14-17	18-19	20-21	22-23	24-25	26	27-30	31-33	34-36	37	38-41	42-44	45-47	48	49-52	53-55	56-58	59	60-63	64-66	67-69	70
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Site
01 NLE
02 Bison
03 Bridger
04 Cottonwood
05 Dickinson
06 Hays
07 Hoagland
08 Jornada
09 Osage
10 Pantex
11 Pawnee

Number
E EGG
1,2, ... N
Bird No.

Code
C Comment follows
S Nest summary card follows

Adult
01 Building
02 Incubating
03 Brooding
04 Near nest, alarmed
05 Not seen
06 Other

Outcome
01 Fledged, young seen leaving nest
02 Fledged, adults excited near
03 Fledged, adults with young near
04 Fledged, nest empty, in tact
05 Failure, nest deserted
06 Failure, weather
07 Failure, predator
08 Failure, other
09 Unknown

Data Type	Site	Initials	Date			Time	Outcome	Eggs Laid	Incubation Period	Eggs Hatched	Fledgling Period	Young Fledged	Comments	Code
			Day	Month	Year									
I-2	3-4	5-7	8-9	10-11	12-13	14-17	18-19	20-21	22-23	24-25	26-27	28-29	30-69	70
26														

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At sites visited daily, a hardware cloth fence, measuring 20 cm high and 1.2 m in diameter, was placed around the nests. These fences effectively excluded potential predators, primarily the Thirteen-lined Ground Squirrel (Spermophilus tridecemlineatus), from taking nest contents; while keeping young birds in the general nest area beyond normal fledging times, for additional growth measurements. Nests protected by fences were not included in totals when overall nesting success was calculated. During 1972, direct approach to nests was avoided, and assessment of nest contents was made from a distance through binoculars.

Banding and Color-Marking

A variety of techniques was employed to capture adults for banding and color-marking. Use of baited traps was fairly successful in capturing birds as they foraged. Traps used were a four-chambered cloverleaf trap; a four-cell Potter trap; and 20, 6 1/2 in. Sherman traps. All were baited with oats and could be deployed while other research activities were underway. Many flies and other insects were attracted to the bait, and it is not known whether the birds were enticed to the traps by the oats or associated insects.

By far the most successful capture method used, once incubation was initiated, was a technique modified from Martin (1969). A 12 m mist net was placed on 3 aluminum poles in a "V" arrangement

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around the nest. Once the adult returned to the nest, the bird was flushed toward the vortex of the net where it would become entangled or trapped against the net. This arrangement was successful even when only the female incubated or brooded, for when she became entrapped she often attracted the male, by her distress calls, into the net also. Only one bird escaped from this net arrangement in over 125 times of use, and no associated nest abandonment occurred. The capture results for each species is shown in Table 1.

Because this research relied heavily on continual observations of resident adults, individual recognition of guild members was essential. Therefore, extensive efforts were concentrated on capturing and marking the birds. Most adults in the study area were banded with a Fish and Wildlife Service aluminum band as well as combinations of colored celluloid leg bands. To avoid confusion with other researchers' concurrent color-marking efforts, birds banded in the primary study area and secondary area were recognized by specific band colors. Placed on the bird's leg with the aluminum band was an orange band for birds resident in Section 23W, and a red band for birds in Section 28W. The color-band sequence for the bird's other leg was developed by a modification of a computer programmed banding progression by Buckley and Hancock (1968). The latter color-band sequence would signify a year and nest number; therefore both adults from the same nest would have identical color-bands (Creighton, 1971).

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Table 1. Summary of banding results of guild members, 1970-72.

Species	1970			1971			1972		
	Males	Females	Young	Males	Females	Young	Males	Females	Young
Lark Bunting	10	16	47	14	19	58	9	11	41
Horned Lark	2	3	9	4	7	18	9	10	24
Chestnut-collared Longspur	3	6	12	3	4	17	7	8	27
McCown's Longspur	2	5	15	5	5	21	15	16	25

The color-bands were cemented closed with plastic glue, effectively preventing early loss of bands. Bands of several birds remained on, although faded, for all 3 years of the study.

To facilitate long distance recognition of individuals, various color dyes were applied to specific feather tracts of each species. These tracts were for the Lark Bunting, the humeral; Horned Lark, the spinal and alar; Chestnut-collared and McCown's Longspurs, the caudal particularly the outer rectices. Dyes used were picric acid (yellow), rhodamine B (red), picric acid-rhodamine B (orange) and methyl green (blue). Dyes significantly increased individual recognition while having no apparent affect on the bird's behavior or survival.

Time Budgeting

Following MacArthur's (1968) suggestion for comparing species by looking only at one or two niche components at a time, one must ascertain how differences in guild members' habitat exploitation patterns can be quantified. Schartz and Zimmerman (1971) effectively argued that involvement of a species with various habitat attributes can be quantified by recording the amount of time apportioned to various activities in which birds are engaged, or in other words constructing a time budget of that species. By carefully recording the behaviors of guild members, I was able to develop time budgets for each

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of the four species, and compare behavioral elements among guild members.

A prerequisite for time budget studies is a detailed familiarity with species' behavioral patterns, and in 1970 I devoted much of the summer acquainting myself with the behavioral repertoire of species in the guild. This orientation also permitted development of relevant behavioral codes and recognition of temporally pertinent elements of the species' breeding biology. Observations were made from either a pickup truck or from the ground level with the aid of 7x35 binoculars and a 15-60X spotting scope.

Time budgeting procedures require selected birds to be highly visible during the entire observation period. However, as a bird moves through its environment it commonly becomes obscured from view by vegetation or microtopographical irregularities even in a relatively unstratified habitat as a shortgrass prairie. Therefore, some type of observation tower is extremely beneficial for detailed behavioral-ecology studies. In 1971, two wooden towers (6.3 m and 4.5 m) were built in Section 23W, and a portable tower was purchased for use with a pickup truck (Figure 10). This portable structure consists of a heavy-grade fiberboard and aluminum swivel "highchair" on a 4.5 m steel stand. The swivel seat can be revolved 360°, and a spotting scope attached for an effective observational vantage. The setup, secured to the pickup truck bed by 4-inch bolts, formed an

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Figure 10. The mobile observation tower secured to the bed of a pickup truck.

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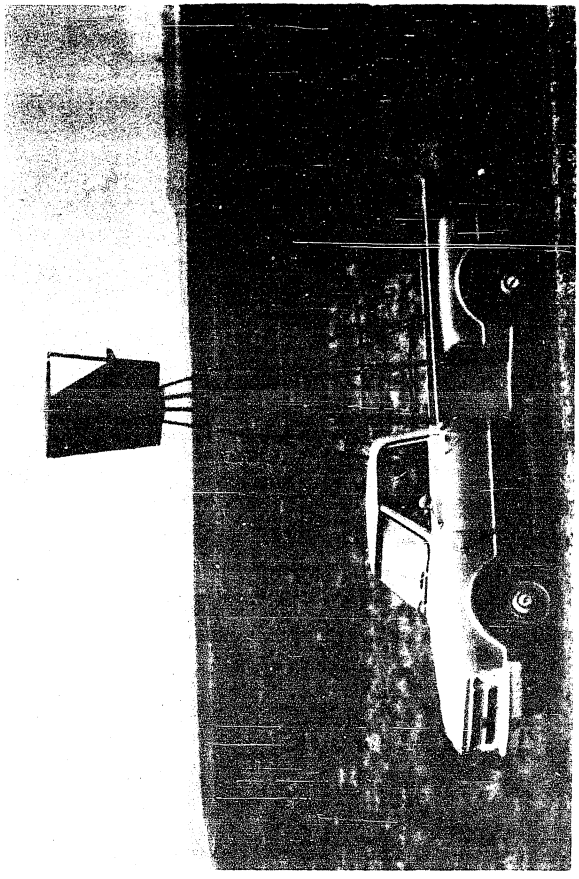

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extremely mobile unit able to supplement the fixed towers nicely. It was from these towers 160 hours (40 hours per each species) of time budgets of male guild members were obtained. Time budgets were also taken of females, but the bulk of these data are not yet analysed and attention in this report will be restricted to males.

Suggestions made by Wiens et al. (1970) for conducting field studies of behavioral ecology served as a framework for my time budget methods. The procedure I followed consisted of randomly selecting an individual involved in a known nesting stage; for instance, the third day of incubation, and recording sequentially, by shorthand or coded notations, the bird's behaviors and activity sites for a standarized period of 20 minutes. This period was punctuated at 10 second intervals by audible pulses from a small, battery operated, variable frequency metronome. The use of coded behavioral notations (Table 2) permitted transcription of birds' activities as rapidly as they occurred, with insertion of a standard mark for each 10 second pulse, and required me to glance only occasionally at my written record.

The period of each day from 0.5 hour before sunrise to 0.5 hour after sunset was divided into five equal time periods of approximately 3 hours each, and efforts were made to obtain at least one complete behavior schedule of all four species during each of the five diurnal periods. The order species were observed was rotated daily if

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Table 2. Coded notations used in recording time budgets of guild members.

F	FLIGHT, DIRECT
Fa	FLIGHT TO ELEVATED POST
Fgd	FLIGHT TO GROUND
CF	CIRCLE FLIGHT
HF	HIGH FLIGHT
FS	FLIGHT SONG
S	STATIONARY SONG
Sa	ABBREVIATED SONG
...n	NUMBER OF NOTES IN Sa
P	PREEN
APC	AERIAL PREY CAPTURE
GPC	GROUND PREY CAPTURE
VPC	VEGETATION PREY CAPTURE
PCa	ATTEMPTED (MISSED) PREY CAPTURE
ev	EAT VEGETATION
BW	BILL WIPE
TF	TAIL FLICK
Ma	ATTEMPTED MOUNT
FO	FACE OFF
WF	WING FLICK
Cp	COPULATION
Cpu	UNSUCCESSFUL COPULATION
Cpd	POST-COPULATORY DISPLAY
MF	MOTH FLIGHT
MFn	MOTH FLIGHT, JOINED BY (n) MALES
NA	INACTIVE
I	INCUBATION
B	BROODING
FY	FEED YOUNG
E n	ENTER NEST
W	WALK
h	HOP
f	FORAGE
sat	STATIONARY
stl	STATIONARY LOOK
rw	RAPID WALK
rf	RAPID FORAGE
j	JOIN
ws	WING SPREAD
sk	SHAKE
sF	SHORT FLIGHT
ff	FEATHER FLUFF
sup	SUPPLANT

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Table 2. (continued)

sc	SCRATCH
cc	CHITTER CALL
sh	SHRUB
gd	GROUND
p	POLE
fn	FENCE
SB	SALTBUSH
RB	RABBITBRUSH
st	STAKE
n	NEST AREA
/	METRONOME PULSE
lll	CONTINUING BEHAVIOR
bu	BILL UP DISPLAY
cr	CROUCH
hb	HEAD BOB

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possible, although the temporal differences in breeding stages of guild members often prevented equal daily coverage. For example, time budgets of only Horned Larks could be obtained in late March and early April when other guild species were not present on the grasslands. From the behavioral observations of 1970, five reproductive stages were recognized in the overall activity budget format: territorial establishment, pair formation and courtship, copulation and nest-building; egg laying and incubation; and brooding and feeding nestlings. Current records were kept on the number of activity schedules completed for each reproductive stage, and daily adjustments were made in selecting birds for scheduling to equalize coverage of all stages. Nest numbers were classified according to their current stage of reproductive involvement. Once a stage was selected for coverage, the actual nest number was drawn from a hat, and behavioral scheduling would be done on the male associated with that nest number. This procedure effectively equalized coverage of reproductive stages while recognizing Wiens' (1969) caution of pitfalls involved by not randomly selecting individuals for behavioral observations. By preselecting an individual for observation and recording its activities for the specified time period, regardless of the relative interest of its behavior, the danger of sampling only conspicuous behaviors was avoided.

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Nestling Foods

Referencing of foods fed to nestlings can be used as an index of differential exploitation of available habitats (Orians and Horn, 1969), and nestling foods were used in this study to help illuminate food specialization of guild members. Basic to the assumption that foods fed to nestlings reflect actual food specialization is the hypothesis that guild members forage in a manner to maximize energy gain per time and energy expenditure (MacArthur, 1961; Emlen, 1966). With this consideration it is unlikely that adults would discriminate against certain prey items for their own food intake or as food for nestlings unless the items were otherwise unsuitable by being unpalatable or difficult to procure when encountered (Orians and Horn, 1969). An important advantage of using nestlings' foods as an index of food specialization, rather than adult stomach samples, is that it is not necessary to shoot birds within a population where identifiable individuals are returning behavioral information, to find out what items are being exploited.

Foods samples from nestlings were initially obtained by tying a #3 white thread around the young bird's throat preventing the nestling from swallowing prey items. These thread collars could be tied and removed without wrenching or pinching the nestlings' necks as sometimes occurred with the use of pipe cleaners when used in the same manner (Orians 1966; Willson 1966). Thread collars could also be

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tightened on necks of very young birds when pipe cleaners could not be used. Twenty minutes after tying the thread or after each visit of an adult to the nest, nestlings were inspected for food. If present, items were removed by forceps, placed in vials containing 75% alcohol, and the thread collars removed. Collars were removed after 40 minutes if no sample was recovered in that period. In 1970, 1971, and 1972 - 127, 73 and 47 samples respectively were obtained by the throat collar technique.

The pipe cleaner or thread collar technique has inherent disadvantages in that it requires human interference at the nest which disrupted observations and behavioral scheduling, and regular routines of the adults. Besides, only a few samples per hour can be obtained.

In 1972, a photographic technique (S. G. Martin, pers. comm.) was initiated to sample nestling foods. The camera setup, shown in Figure 11, consists of a motor-driven, battery operated 35mm camera, mounted with a 300mm, f/4.5 lens, 2X tele-converter and 4-ring extension tubes. The camera was positioned on a tripod 3 m from the nest, and speaker wire, with a micro-switch attached, was extended from the motor drive unit to a nearby tower. Adults returning with food for nestlings generally perched on a stake placed near the nest. By prefocusing the camera on the plane of the stake, and remotely discharging the camera, a color exposure of foods returned

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Figure 11. The camera unit, used for recording foods fed to nestlings, consisting of a motor-driven, battery operated 35mm camera, mounted with a 300 mm, f/4.5 lens, 2X tele-converter and 4 ring extension tubes.

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to nestlings was obtained. Because prey items were occasionally visible on only one side of the adult's bill, to record all bill contents, a second exposure was taken as the bird turned its head from side to side. This photographic technique resulted in a head and shoulders portrait of adults with insect materials clearly visible in the bird's bill. Foods were identified by examining the slides under a binocular microscope, and items were keyed to family and often to genus.

All species did not perch on nest stakes with the same consistency, therefore modifications in the setup were occasionally necessary to compensate for individual variations. Samples could also be obtained by prefocusing the camera on other preferred perches or on favored approach paths to nests. The camera technique was most successful for Lark Buntings and least successful for Horned Larks. At nests where photographic referencing of food items was not successful, items were sampled by the throat collar technique. In 1972, 1,490 transparencies were obtained, and this procedure allowed me to record as many as 23 feeding trips to a nest in an hour period. Interference with birds' activities was also minimized by this method, and behavioral scheduling could be done concurrently. By this simultaneous recording of behaviors and nestling foods, it was possible to document the area where an individual captured a prey item, the specific prey capture technique employed, what items were captured by the various tactics, the exact amount of food fed per specific

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amount of time, and whether sexual or temporal variations existed in both kinds and amounts of food items returned to the nest.

Approximation of individual food item length was made by comparing the width of each species' bill with amounts of exposed prey item shown in the transparency, or items were measured directly from throat collar samples. Mean bill widths for each species were found by averaging bill measurements of birds collected at the Pawnee Site by P. H. Baldwin (Baldwin, et al., 1969, Creighton, 1971, Baldwin and Creighton, 1972). Birds were collected at the same general area as this study was being conducted, thus geographic variations of bill characteristics were minimized when average characteristics were used. From a reference collection made at the Pawnee Site, individuals of selected lengths from major invertebrate orders and families were oven dried and carefully weighed (Baldwin, et al., 1969, Baldwin and Creighton, 1972). A regression curve was developed from these weights and lengths, and derivation of nestling prey item dry weights were made by fitting their length to curves for their most definitive taxa level. Selected checks using various taxa and body lengths demonstrated each regression was a sensitive estimation of body length-dry weight relationships.

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Avian Census

MacArthur et al. (1961, 1962) demonstrated that spatial heterogeneity, principally vertical height diversity, of plant communities has profound influences on avian diversity and abundances in various forests habitats. In grassland situations, the relative simplicity of habitat structure and absence of well-defined vertical layering should act to confine heterogeneity to a single horizontal plane. I set out to determine if spatial distribution of the four species of the ground-foraging guild was correlated to specific plant characteristics (vegetation height and plant density) by censusing random areas of the Central Plains Experimental Range.

Various census techniques for grassland birds proposed by investigators can be summarized as either: a) strip-census techniques (Dice, 1930; Breckenridge, 1935; Merikallio, 1958; and Logan, 1961) or b) plot-count techniques (Kendeigh, 1944; Finzel, 1962; and Emlen, 1971). I used a plot-count technique to census 26 plots of 40 acres (10.2 hectares); in 1972, one plot was sampled weekly from 15 March to 31 August.

A random numbers table was used to serially select a particular township, range, section, and quarter section for sampling. The day before a census was to be taken, I would reference the 40 acre plot within the selected quarter section by placing surveyor flags, marked

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by a column letter (A-H) and row number (1-22), at 30.5 m intervals in an 8x22 location grid. A directional compass and range finder were used to position the flags in the grid. Censuses were conducted by walking back and forth on odd-numbered rows through the plot. When a bird was sighted or flushed, I recorded the species and its location (distance and direction from the nearest flag) on a field form. To correct for possible temporal influences on birds' activities, I divided the observational period into 30-min intervals, consisting of six, 5-min tallies, and conducted all censuses between 0700 and 1200 hrs (MST). I made four replications of this 30-min interval for each plot.

Because the objective of these counts was to elucidate bird and plant species associations, after the 4 replicates had been completed, I sampled the plants at about the same location at which birds had been seen or flushed. A 0.5 m^2 quadrat was placed at that approximate location, and the dominant plant species in the quadrat were identified or collected for later identification. The density and height of the vegetation was sampled by a procedure similar to that of Wiens (1969). The distance from each corner of the quadrat to the base of the nearest plant was measured as was the height of the plant. Plant densities were calculated from the formula (modified from Wiens, 1969):

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$$\text{Plant density/0.01 acre} = \frac{404710.7}{\left(\frac{\Sigma d}{N}\right)^2}$$

where, d = distance from quadrat corner to nearest plant
N = number of corner distances measured
404710.7 = cm^2 per 0.01 acre

The mean distance values for "plant density" were used for comparing associations of particular guild members with general vegetational characteristics, and not for determining actual density values of plants in various grassland situations. The restriction of this method to this comparison negated the criticism of Grieg-Smith (1964) and Risser and Zedler (1968) for application of this technique to grasslands. The affiliation of guild members with characteristic plant species and vegetation height and density are intended to demonstrate bird-plant associations and should not be interpreted as demonstrating bird preferences.

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RESULTS AND DISCUSSION

Habitat Characteristics and Spatial Segregation

Because of micro-responses to moisture, soil-type, topography and agriculture, a grassland offers a spectrum of habitat situations, displayed horizontally, for potential exploitation by various bird species. In spite of the relative simplicity of grasslands, there have been few attempts to characterize the community structure of their avifaunas (Finzel, 1964; Cody, 1968; Wiens, 1969 and 1973). Among the principal objectives of this study were the delineation of spatial relationships of guild members--what portion of the habitat spectrum does each species characteristically occupy, and are there differences and similarities in habitat features associated with the presence of particular species? This question was posed because of the observation that occupancy by guild members was not continuous throughout the range of habitat types, but associated with various vegetational features. Qualitative conclusions by other observers parallel this impression. Finzel (1964) deduced that Lark Buntings, on the Cheyenne Plains of Wyoming, preferred either a more moist situation or taller vegetation than did Horned Larks and McCown's Longspurs. Dubois (1935), Mickey (1943), Cody (1968) and Felske (1971) referred to preference for dry, sparsely vegetated habitat sites

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in McCown's Longspurs. Bigelow (1902), Pickwell (1942), Behle (1942) and Beason (1970) characterized habitats occupied by Horned Larks in much the same way as those of McCown's Longspurs--exposed sites lacking dense vegetation. Dubois (1937) and Smith and Smith (1966) identified the habitat occupied by Chestnut-collared Longspurs as mid grass and short grass associations.

Although references to habitat "preferences" have been made by these and other authors, preference is a difficult quality to measure. Occupancy of a particular habitat, rather than a matter of preference, could have resulted from ecological or behavioral interactions with other species; or because population size was so reduced, occupation of other sites was unlikely. Habitats that are occupied can be characterized for each species found there, and bird-plant associations can be recognized. However, tenancy of habitats can be viewed as occurring on two levels: ultimate and proximate. The ultimate factors influencing choice of habitat for suitable occupancy are those factors that influence the survival and reproductive success of individuals. The proximate factors are those environmental features which induce settling behavior (Orians, 1971). What are generally being inferred when correlations between habitat features and bird presences are made, are the proximate factors.

Measurements of habitat features and vegetation structure associated with guild members from 20, 10.2 hectare plots are

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summarized in Tables 3 and 4. Differences in areas characteristically occupied by each species in the ground-foraging guild are apparent, and generally support the subjective observations gathered from earlier work on these same species.

McCown's Longspurs occupy areas of very sparse short grass, possessing large amounts of exposed soil. Giezentanner's (1970) observation that McCown's Longspurs were most commonly associated with semi-bare hilltops and rises was repeatedly confirmed. These areas were dominated by buffalo grass and blue grama with diversity of other plants relatively low compared to habitats occupied by the other species. The composition in Figure 12 is representative of an average habitat that McCown's Longspurs would occupy. Felske (1971) proposed two reasons why McCown's Longspurs would occupy this habitat. He felt exposed slopes and hilltops, and the absence of higher vegetation would permit those areas to become snow-free sooner in the year, offering an early warm nest site. Thus the exposure would effectively advance the season microclimatically and facilitate early breeding. Alternatively, the warm dry soil conditions may present favorable conditions for insect food supplies early in the breeding season.

As demonstrated in Tables 3 and 4, the habitat characteristics associated with Horned Larks were similar to those of McCown's Longspurs. Although Horned Larks were more abundant and more

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Figure 12a. Representative habitat associated with McCown's Longspurs at the Pawnee Site.

Figure 12b. Closeup of the amount of ground cover found in habitats associated with McCown's Longspurs at the Pawnee Site.

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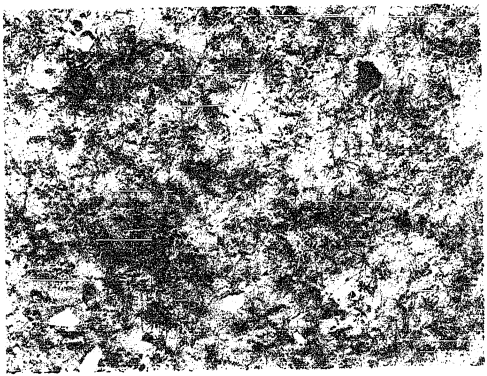

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Table 3. Habitat-structure characteristics of areas occupied by members of the ground-foraging guild on the Central Plains Experimental Range.

Species	Percent Cover							
	Short Grass	Mid Grass	Sedge	Forb	Cactus	Shrub	Bare Ground	Rock
Chestnut-collared Longspur	45.04	22.13	11.07	5.84	1.85	0.16	12.37	0.54
Horned Lark	64.72	1.58	5.83	6.57	2.34	0.82	16.90	1.24
Lark Bunting	65.61	4.70	7.82	7.22	2.11	2.10	9.73	0.71
McCown's Longspur	66.06	1.17	3.14	1.61	2.15	0.89	23.45	1.53

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Table 4. Habitat characteristics associated with species of the ground-foraging guild and census results of guild members on the Central Plains Experimental Range. Standard deviations are included in parentheses.

Character	Lark Bunting	Horned Lark	Chestnut-collared Longspur	McCown's Longspur
Vegetation Height (cm)	13.4 (7.1)	7.2 (5.7)	15.2 (5.4)	5.2 (3.7)
Density*	32.17	24.25	29.85	18.50
% Bare Ground**	10.44	18.14	12.91	24.98
Number of Sites Censused***	477	513	27	162
Average Number Seen per Census (n=30)	15.9 (6.22)	17.1 (12.47)	0.9 (0.75)	5.4 (8.39)

*Expressed as plants/0.1m^2 but should be considered a relative index and not a measure of actual plant density (See text).

**Including exposed soil and rocks.

***Number of birds referenced during the 30 censuses.

widely distributed than McCown's Longspurs (Giezentanner, 1970; Ryder, 1971), the occupied habitat of both species was characterized by shortgrass, although the coverage of forbs is greater and the amount of exposed soil is less in Horned Larks' habitat.

The areas occupied by Chestnut-collared Longspurs and Lark Buntings, typified by more mid grasses and sedges with reduced amounts of bare ground, are less extreme than those of the two species in the shortgrass areas. Lark Buntings are also abundant and widely dispersed over the CPER although they seldom occurred in very short grass habitats. The midgrass commonly associated with the bunting was red threeawn and the shrub was saltbush. The attributes of habitats utilized by Lark Buntings are represented in Figure 13.

Figure 14 exemplifies the habitat occupied by Chestnut-collared Longspurs. A comparison of this figure with Tables 3 and 4 indicates this longspur utilized areas characterized by patchy regions of shortgrass sedge and taller bunch grass. Two bunch grasses invariably associated with Chestnut-collared Longspurs are crested and western wheatgrasses. Fields with quantities of these wheatgrasses were limited (only four plots of 30 areas sampled) on the CPER, and distribution of the longspurs was also restricted. Another plant associated with Chestnut-collared Longspurs was Canada thistle, which males commonly used as song posts. Although other habitat features

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Figure 13a. Representative habitat associated with Lark Buntings at the Pawnee Site.

Figure 13b. Closeup of the amount of ground cover found in habitats associated with Lark Buntings at the Pawnee Site.

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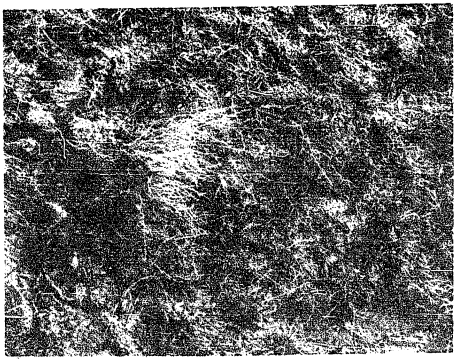

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Figure 14a. Representative habitat associated with Chestnut-collared Longspurs at the Pawnee Site.

Figure 14b. Closeup of the amount of ground cover associated with Chestnut-collared Longspurs at the Pawnee Site.

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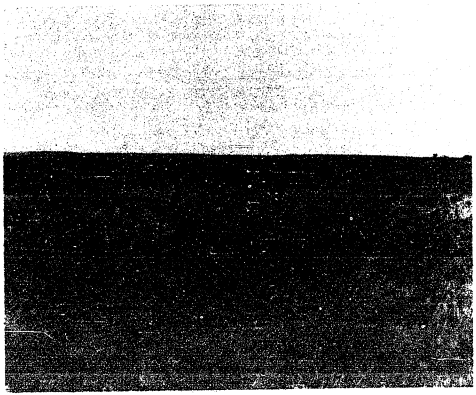

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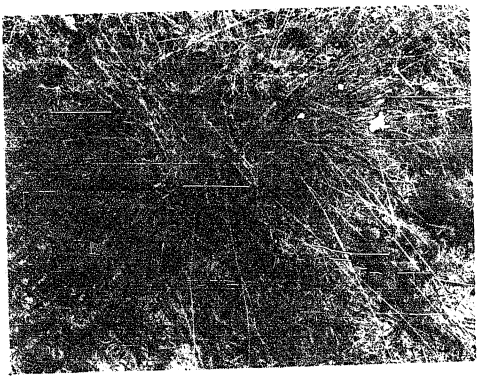

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may influence the occupancy of a particular area by species, response to height of vegetation and plant density seem particularly important for guild members (Figure 15 and 16).

The observations that Horned Larks commonly occurred in areas with McCown's Longspurs, and Lark Buntings with Chestnut-collared Longspurs can be tested by association analysis, using Cole's (1949) index of interspecific association (Figure 17). In this analysis, guild members' mutual occupancy or absence from a habitat were measured from data resulting from the 30 bird censuses on random areas of the CPER. As indicated, McCown's Longspurs were associated with Horned Larks, and Chestnut-collared Longspurs with Lark Buntings at a highly significant ($P < .01$) frequency during the censuses. Horned Larks and Lark Buntings, both abundant and widespread, were also significantly ($P < 0.05$) associated with each other. However, habitats occupied by the two longspurs were most different and there is a highly significant disassociation ($P < .01$) between these two species. Pielou (1969, 1972) pointed out that positive associations may occur because of a common response to proximate factors, a social cohesiveness between species, or a behavioral or ecological exclusion from other areas forcing mutual occupation of the habitat. Negative associations may result from responses to different proximate factors, competitive behavioral and ecological interactions, or effects of past population histories.

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Figure 15. Characterization of habitats by % coverage of short and mid-grass associated with the occurrence of guild members.

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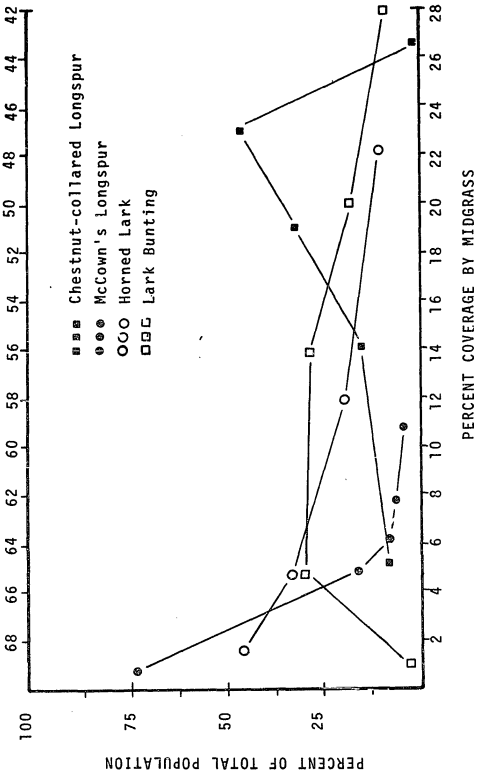

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Figure 16. Mean values for plant density and vegetation height in areas occupied by guild members.

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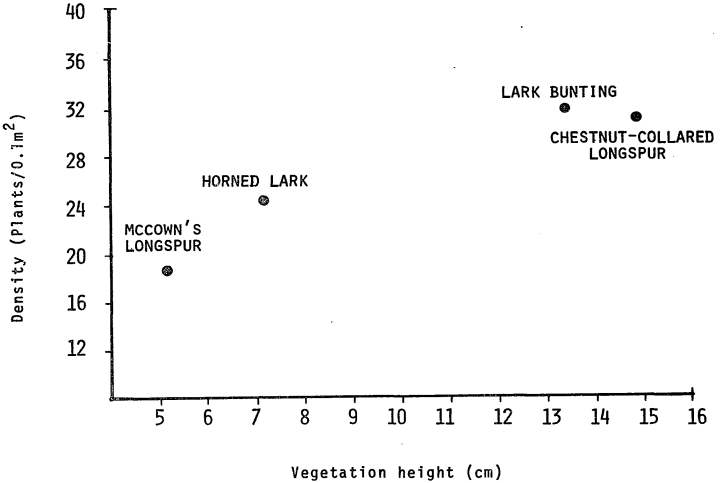

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Figure 17. Interspecific association matrix for guild members. Associations were based on mutual occurrence or absence in plot censuses at the Pawnee Site, using Coles' (1949) index of interspecific association.

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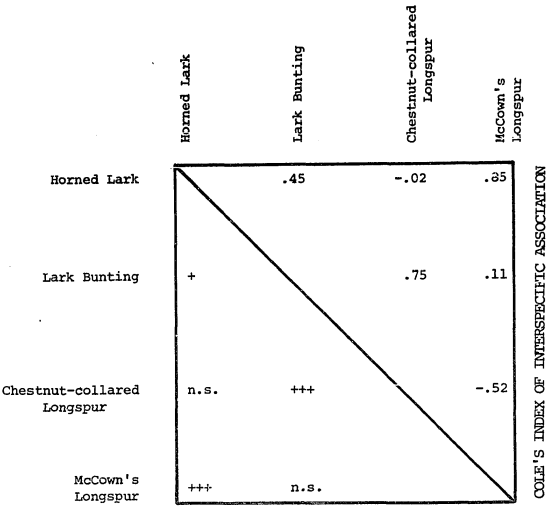

CHI-SQUARE SIGNIFICANCE LEVEL
(after Wiens, 1973)

CHI-SQUARE SIGNIFICANCE LEVELS

Association		Disassociation	
+	P<.10	-	P<.10
++	P<.05	--	P<.05
+++	P<.01	---	P<.01

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One such proximate factor influencing habitat occupation and particular guild member tenancy may be the availability of vegetation adequate for nest protection and concealment. Table 5 summarizes the vegetation directly associated with guild members' nests. Lark Buntings' and Chestnut-collared Longspurs' nests are invariably constructed under a canopy of vegetation. Nests of McCown's Longspurs and Horned Larks are usually not domed over and appear casually, if at all, associated with plants at the nest site. Nests of the former two species are predominately arched over by red threeawn, midgrass, or by a shrub, rabbitbrush or saltbush. Therefore, greatest breeding densities of the Lark Bunting and Chestnut-collared Longspur would be expected in habitats of midgrass or shrubs. Similarly, one reason these two species would not be expected to occur in short grass areas is the absence of adequate protective nest-cover.

Temporal Segregation

If the same habitat is being occupied by several guild members, these species can partition the resources of the area by extracting their necessary requisites at different times. Temporal segregation could be achieved by each member of the guild having a specific time of day in which feeding would be concentrated, or there could be separation of dates when each species initiated egg laying.

The most important activity of any individual would be the procurement of sufficient energy for existence. If maintenance requisites

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Table 5. Association of guild members' nests with plant species on the Pawnee National Grassland.

Associated Plant	Percent of Nests			
	Lark Bunting	Horned Lark	McCown's Longspur	Chestnut-collared Longspur
Aristida longiseta	49	7	--	83
Bouteloua gracilis	--	19	20	--
Chrysothamus nauseosus	26	7	5	--
Opuntia polyacantha	--	15	35	--
Atriplex canescens	13	4	--	--
Gutierrezia sarothrae	5	11	10	--
Others	7	15	10	17
None	--	22	20	--
Total Nests, n	90	51	34	26

could be accumulated more readily at one time of the day because of relaxation of interspecific competitive pressures, or specific behavioral or morphological adaptations of a particular species, food gathering activities would be concentrated in that time period. Diurnal concentrations in amounts of time spent foraging can be illuminated by time budget analysis. Verner (1965), in his work with polygynous male Marsh Wrens (Telmatodytes palustris) determined the most efficient period for food gathering would be during the afternoon, and the amounts of time spent foraging by the wrens peaked at that time period. However, Schartz and Zimmerman (1971), working on another polygynous species, found no diurnal changes in feeding activities of male Dickcissels (Spiza americana). Baldwin and Kendeigh (1938) described a bimodal daily feeding pattern in several species of birds which was associated with energy depletion during the nocturnal fast.

In situations where males are kept busy returning food continually to nestlings or fledglings, it would seem unlikely that foraging times could be profitably concentrated during only specific time periods. Table 6 shows the average amount of time spent gathering food by males of the ground-foraging guild. These percentages were obtained by averaging the amount of time spent foraging by males of each species during each diurnal period. Although slight variations in patterns do exist, no significant pulse of feeding activity is readily

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Table 6. Percent of total time spent foraging by males of the ground-foraging guild in an average diurnal period.

Time Period*	Species**			
	Lark Bunting	Horned Lark	McCown's Longspur	Chestnut-collared Longspur
1	32.60	31.75	28.01	26.61
2	31.14	29.29	29.17	27.33
3	36.09	34.15	31.42	28.00
4	35.37	33.07	29.22	28.67
5	38.36	36.41	32.04	28.85

*Each period is approximately 3 hours, starting 1/2 hr before sunrise to 1/2 hr after sunset.

**No statistical difference was found by analysis of variance between times spent foraging by guild members at the 95% confidence interval.

detected - foraging required about one-third of the total activity budget of all males each period.

Lack (1950) made the observation that birds apply maximum demands on their environment during the breeding season. These demands are associated with increased energy needs for male territorial establishment and defense, for female egg production, and for feeding nestlings and fledglings. Immelmann (1971) stressed that selection would favor an efficient timing program that adjusts nesting seasons to periods most appropriate for food availability and predator avoidance - time periods when species can raise young most efficiently.

There is good evidence that there are differences in timing of initiation of egg-laying in the ground-foraging guild. Figure 18 compares average dates when the first eggs were laid (nest initiation) of the four species in the guild during 1971 and 1972. It is clear that discrete nesting peaks are recognizable in Horned Larks, McCown's Longspurs and Lark Buntings; moreover, a progression of nest initiation occurred through the breeding season. Other behavior patterns for each species, i.e., territorial establishment, courtship, of course followed a similar progression.

In 1971, there was a period of 13 weeks from the first nest initiated (April 18) to the last (July 11), and this interval is called the total nesting period for the ground-foraging guild. Determination of how evenly the nesting period for each species is distributed through

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Figure 18. Temporal distribution of nest initiation (when first egg was laid) of guild members during the breeding seasons 1971-72.

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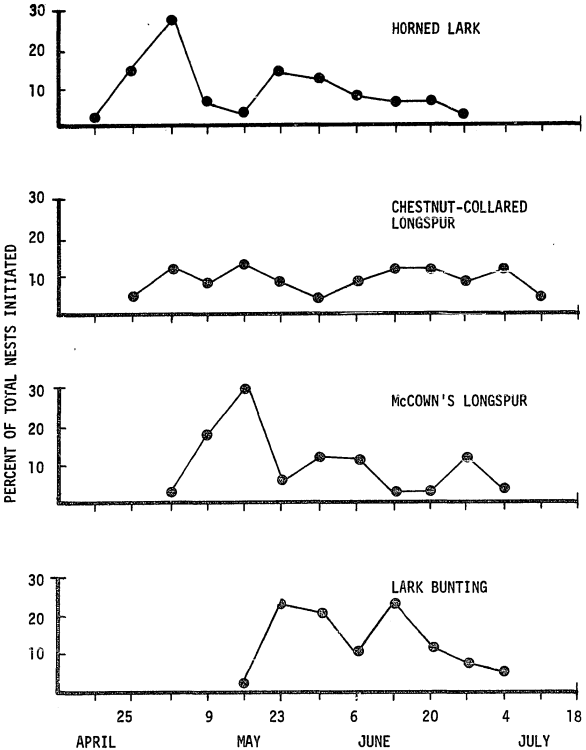

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its individual nesting period (and likewise the intensity of nesting peaks), is made by using the expression (Ricklefs, 1966):

$$e^{-\Sigma p_i \log_e p_i}$$

where p_i is the proportion of nests found during the i^{th} week. If nests are evenly distributed over n weeks, this formula reduces to n; and if nests are unequally distributed, it reduces to less than n. Guild member's nesting periods are compared with their respective temporal diversities in Table 7, and the degree of clustering and distribution of nest-initiations can be seen. In the same table, the "index of seasonal utilization" was developed to rank the species according to how their nesting was distributed throughout the total nesting period.

Because of the spatial relationships isolated in the last chapter, those guild members occupying the same general habitat might be expected to demonstrate the greatest degree of temporal segregation. Figure 19 compares nest initiation of those guild members found to be highly associated. During this study, Horned Larks initiated most of their nests in April and May with a nesting peak during the week of 2 May, and their median nesting date occurring by 12 May. A smaller peak, due largely to renesting, occurred on 23 May. The nesting peak of McCown's Longspurs was 2 weeks behind that of Horned Larks, with 29% of their nests initiated during the week of 16 May and their median date completed by 19 May. Lark Buntings did not disperse to

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Table 7. Breeding season characteristics of the ground-foraging guild.

Species	Total Nests	Month Initiated				Nesting Period (weeks)	Temporal Diversity (weeks)*	Index of Seasonal Utilization**
		April	May	June	July			
Horned Lark	50	21	18	11	0	11	8.42	7.12
Lark Bunting	90	0	40	46	4	8	6.62	4.07
Chestnut-collared Longspur	26	4	8	10	4	12	11.24	10.38
McCown's Longspur	34	1	22	10	1	10	7.48	5.75

* Temporal diversity = $e^{-\Sigma p_i \log_e p_i}$, where p_i is the proportion of nests found during the i^{th} week.

** Index of seasonal utilization = $(-\Sigma p_i \log_e p_i)\left(\frac{n_i}{N}\right)$, where n_i is the total number of weeks in which nests are initiated for species i and N is total number of weeks in which at least one nest is initiated by a guild member.

Figure 19. Comparison of nest initiation by those guild members which utilize similar habitats. Each data point represents an average number of nests initiated during the breeding seasons 1971-72.

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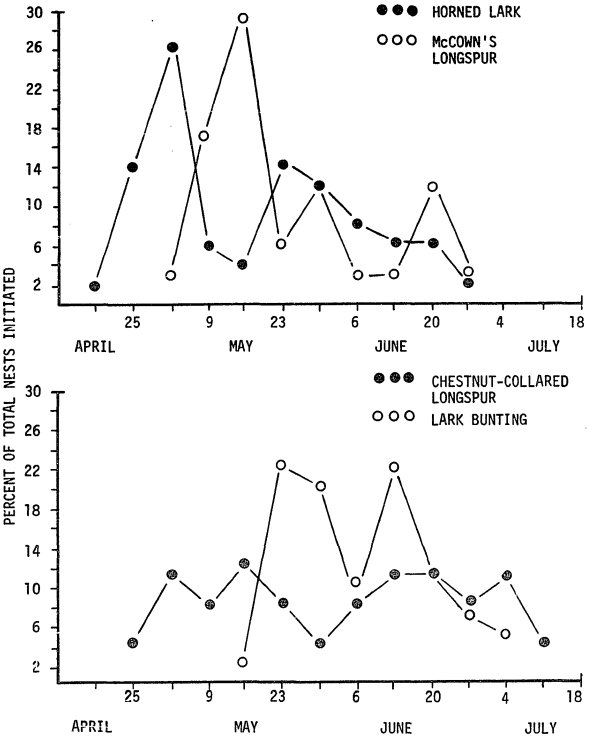

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territories on the primary site until 5 May, and did not initiate nesting until mid-May. Nesting peaks occurred during the weeks of 23 May and 13 June, and the median date for nest initiation for Lark Buntings was on 4 June. Chestnut-collared Longspurs did not have a recognizable nesting peak but maintained a fairly constant level through the total nesting season. This sustained breeding plateau can also be recognized from Table 7 with Chestnut-collared Longspurs having the highest temporal diversity (nesting distributed through their individual breeding season) and index of season utilization (breeding distributed through the total nesting season).

Quantitative analysis of the actual amount of overlap in nesting of guild members can be measured by using Horn's (1966) index of overlap, R_o where

$$R_o = \frac{\Sigma(x_i+y_i)\log(x_i+y_i) - \Sigma x_i \log x_i - \Sigma y_i \log y_i}{(X+Y)\log(X+Y) - X\log X - Y\log Y}$$

and x_i and y_i are the proportions of nests initiated in week i for species X and Y respectively. R_o can vary from 0 (no overlap) to 1 (complete overlap). Temporal overlap for guild members is summarized in Figure 20. Horned Larks and Lark Buntings (the two most abundant guild members at the Pawnee Site) have the smallest degree of temporal overlap. Horned Larks and McCown's Longspurs, species highly associated spatially, also have a relatively low value of overlap. Chestnut-collared Longspurs and Lark Buntings, spatially

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Figure 20. Matrix indicating degree of temporal overlap of nest initiation in the ground-foraging guild. Overlap values were based on mutual usage of weeks during the breeding season using Horn's (1966) index, R_o.

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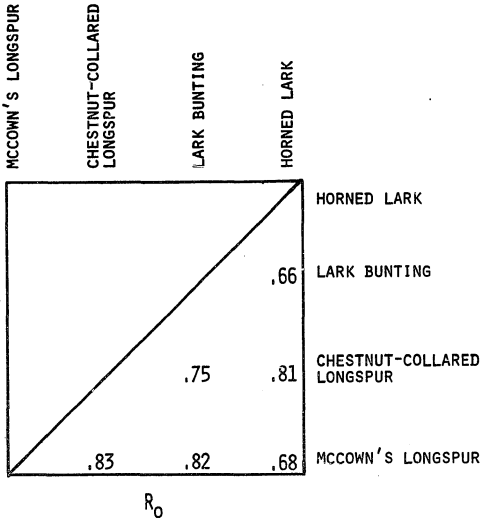

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associated in midgrass areas, have a somewhat higher value of overlap. Those species not spatially associated, i.e., Chestnut-collared Longspurs with Horned Larks and McCown's Longspurs, and Lark Buntings and McCown's Longspurs; have high values of temporal overlap. Other attributes of the nesting season for guild members are summarized in Table 8.

Food Specialization

Composition and quantity of food resources also may be expected to reflect spatial and temporal patterns; thus guild members exploiting those variable supplies are faced with the problem of procuring enough of the appropriate kind of food at the right time. Lack (1970) suggested birds select quantities and types of food items according to their metabolic and nutritional requirements. It would also be expected that birds, if capable of discriminating between prey items, would select those items which yield the greatest energy gain per energy expenditure. Of the total resources required annually for each species, only those items exploited as foods for nestlings are considered in this current study. Invertebrates comprise practically the complete diet of nestling guild members; because nestling diets are more restrictive than those of adults, which also utilize plant foods (P. H. Baldwin, personal communication), nestling foods may be more indicative of food specialization occurring within the guild.

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Table 8. Nesting summary of the ground-foraging guild, 1971 and 1972 combined.

Species	Total Nests	Clutch Size	Incubation Period (days)	Nestling Period (days)	Hatching Success (%)	Fledging Success (%)
Horned Lark	50	3.15	11.9	11.3	73.5	43.2
Lark Bunting	90	3.60	11.7	8.5	82.0	63.4
Chestnut-collared Longspur	26	3.53	11.9	9.6	76.0	47.3
McCown's Longspur	34	3.20	12.0	10.5	70.9	42.0

Food items were grouped by ordinal representation, although such grouping may have obscured fine differences in food selectivity. It was possible to group items at more definitive levels; however as Orians and Horn (1969) stressed, fine taxonomic categorization would be cumbersome and often misleading.

The total diet obtained from nestling food samples for each species in the guild, in terms of percent composition by number of individuals and total dry weight, is given in Tables 9-12. The actual number of prey items may obscure the energetic importance, as related to percent representation by dry weight, of various taxa in the diets. For example, although dipterans are of numerically minor importance in the diet of nestling Lark Buntings, they contribute about one-quarter of the total dry weight consumed. Similarly, in diets of nestling Horned Larks, hymenopterans are numerically important; but, because of their small size, their energetic contribution is small.

While all guild members exploited the same orders for prey items, they did so at greater or lesser extents. Orthopterans (primarily acridid grasshoppers) formed the bulk of nestling diets for Lark Buntings, McCown's and Chestnut-collared Longspurs, while coleopterans comprised about 50% of the total dry weight of nestling Horned Lark diets. Of the four species in the guild, nestling Lark Buntings received a diet highest in relative diversity while the diet of nestling Chestnut-collared Longspurs was the most restrictive. The

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Table 9. Dietary composition of nestling Lark Buntings at the Pawnee Site.

Order	No. Items	% Total Items	Dry Weight (g)	% Total Dry Wt.
Araneida	16	2.31	0.338	1.71
Coleoptera	114	16.57	2.693	13.62
Diptera	28	4.07	4.809	24.32
Hemiptera	10	1.45	0.036	0.18
Homoptera	8	1.16	0.024	0.12
Hymenoptera	64	9.30	0.503	2.54
Lepidoptera	86	12.51	1.528	7.68
Orthoptera	334	48.55	9.057	45.81
Unident.	28	4.06	0.792	4.01
Totals	688	100.00%	19.770	100.00%

Mean Prey Item Length = 14.77 cm.
Mean Prey Item Dry Weight = 0.031 g.
Diet Diversity Index ($-\Sigma p_i \log p_i$) = 1.4816.

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Table 10. Dietary composition of nestling Horned Larks at the Pawnee Site.

Order	No. Items	% Total Items	Dry Weight (g)	% Total Dry Wt.
Araneida	12	3.63	0.136	3.76
Coleoptera	82	24.85	1.738	47.86
Diptera	9	3.03	0.008	0.23
Hemiptera	11	3.63	0.015	0.42
Homoptera	4	1.21	0.008	0.21
Hymenoptera	100	30.31	0.355	9.77
Lepidoptera	72	21.82	0.592	16.29
Orthoptera	38	11.52	0.778	21.42
Unident.	--	--	--	--
Totals	328	100.00%	3.631	100.00%

Mean Prey Item Length = 11.94 cm.
Mean Prey Item Dry Weight = 0.011 g.
Diet Diversity Index = 1.3787

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Table 11. Dietary composition of nestling Chestnut-collared Longspurs at the Pawnee Site.

Order	No. Items	% Total Items	Dry Weight (g)	% Total Dry Wt.
Araneida	8	2.73	0.136	3.20
Coleoptera	92	31.40	1.398	32.91
Diptera	5	1.71	0.009	0.20
Hemiptera	1	0.34	0.004	0.10
Homoptera	2	0.69	0.002	0.04
Hymenoptera	24	8.19	0.131	3.08
Lepidoptera	22	7.50	0.147	3.46
Orthoptera	138	47.10	2.416	56.85
Unident.	1	0.34	0.006	0.14
Totals	293	100.00%	4.249	100.00%

Mean Prey Item Length = 11.4 cm.
Mean Prey Item Dry Weight = 0.015 g.
Diet Diversity Index = 1.0737.

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Table 12. Dietary composition of nestling McCown's Longspurs at the Pawnee Site.

Order	No. Items	% Total Items	Dry Weight (g)	% Total Dry Wt.
Araneida	8	2.23	0.058	0.88
Coleoptera	105	29.61	2.424	37.26
Diptera	11	2.80	0.415	6.37
Hemiptera	12	3.35	0.026	0.40
Homoptera	2	0.55	0.003	0.05
Hymenoptera	46	12.85	0.227	3.49
Lepidoptera	48	13.41	0.298	4.58
Orthoptera	126	35.20	3.056	46.97
Unident.	--	--	--	--
Totals	358	100.00%	6.507	100.00%

Mean Prey Item Length = 11.06 cm.
Mean Prey Item Dry Weight = 0.018 g.
Diet Diversity Index = 1.2243.

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mean prey item lengths for nestling Horned Larks, McCown's and Chestnut-collared Longspurs were very similar, although the mean prey item length fed to nestling Lark Buntings was significantly greater at the 95% confidence level than the mean prey item length of other guild members. Major food items for guild members are combined in Table 13, and a clearer view of diet specialization is seen. The overlap of nestling food composition and average prey length was calculated using Horn's (1966) index (Figure 21). The overlap in diet and prey length of Horned Larks and Lark Buntings were again the smallest of any guild-member pairing. Dietary and prey length overlaps were greatest for McCown's and Chestnut-collared Longspurs. Horned Larks and McCown's Longspurs, as well as Chestnut-collared Longspurs and Lark Buntings (species-pairs associated with very similar habitats) exploit similar food supplies, and this is demonstrated by the high overlap values for both prey composition and lengths on a seasonal basis.

In addition to a seasonal characterization of nestling foods, a diurnal pattern in diets also existed. The average daily diets fed to nestlings by males of the guild are shown in Tables 14-17. A pattern is indicated for all species in the amounts and composition of foods returned. The greatest amounts of prey items were fed to nestlings by males between the hours of 0700-1600 (MST), with reduced amounts in the first and last time periods. Diurnal dietary compositions may reflect greater visibility and activity of prey items during

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Table 13. Comparison of food types in the diet of nestlings of the ground-foraging guild at the Pawnee Site, in % total dry weight.

Order	Guild Member			
	Lark Bunting	Horned Lark	Chestnut-collared Longspur	McCown's Longspur
Araneida	1.71	3.76	3.20	0.88
Coleoptera	13.62	47.86	32.91	37.26
Diptera	24.32	0.23	0.20	6.37
Hemiptera	0.18	0.42	0.10	0.40
Homoptera	0.12	0.21	0.04	0.05
Hymenoptera	2.54	9.77	3.08	3.49
Lepidoptera	7.68	16.29	3.46	4.58
Orthoptera	45.81	21.42	56.85	46.97
Unident.	4.01	--	0.14	--
Total No. Items	668	328	293	358
Total Dry Weight(g)	19.770	3.631	4.249	6.507

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Figure 21. Matrix of overlap values, using Horn's (1966) index, R_o; by items of each order and average prey length of foods fed to nestlings of the ground-foraging guild.

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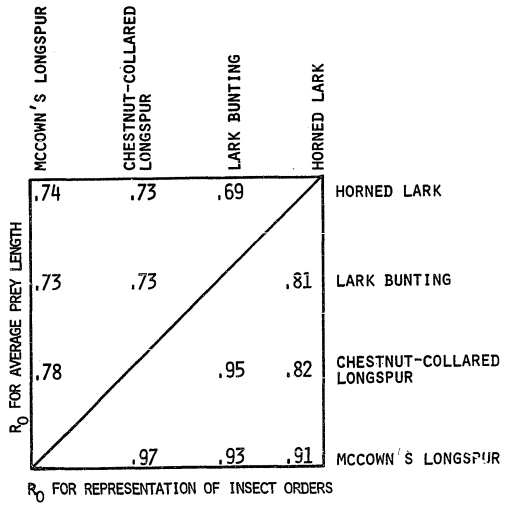

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Table 14. Average diurnal diet returned to nestlings by male Lark Buntings at the Pawnee Site.

	Diurnal Period*									
	1		2		3		4		5	
Order	No.	Dry Wt.**	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.
Araneida			1	.0714					1	.0175
Coleoptera	15	.1249	9	.1208	11	.0930	4	.0542	7	.1327
Diptera			1	.0159			1	.0159		
Hemiptera			1	.0083						
Homoptera									1	.0027
Hymenoptera	7	.0287	6	.0730	3	.0098			7	.0268
Lepidoptera	1	.0152	7	.1120	10	.2921	3	.0363	3	.0650
Orthoptera	5	.1121	19	.5235	5	.3543	27	1.0028	7	.4059
Unident.					5	.2527				
Totals	28	.2809	39	.9249	34	1.0019	34	1.1092	26	.6506

*See text for definition of diurnal periods.

**Expressed in grams. Dry weights obtained from a regression curve from representative samples of each order.

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Table 15. Average diurnal diet returned to nestlings by male Horned Larks at the Pawnee Site.

	Diurnal Period*									
	1		2		3		4		5	
Order	No.	Dry Wt.**	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.
Araneida					1	.0057			1	.0043
Coleoptera	3	.0236	5	.0651	11	.3574	13	.1364	6	.0370
Diptera							4	.0077		
Hemiptera			1	.0011					3	.0034
Homoptera			1	.0016						
Hymenoptera			6	.0108	3	.0351	7	.0097	4	.0164
Lepidoptera	1	.0075	2	.0185	4	.0658	6	.0283	2	.0165
Orthoptera			3	.1081	5	.0658	4	.0474	3	.0686
Totals	4	.0311	18	.2196	25	.5298	34	.2295	19	.1462

*See text for definition of diurnal periods.

**Expressed in grams. Dry weights obtained from a regression curve from representative samples of each order.

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Table 16. Average diurnal diet returned to nestlings by male McCown's Longspurs at the Pawnee Site.

Order	Diurnal Period* 1		2		3		4		5	
	No.	Dry Wt.**	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.
Araneida							1	.0057	1	.0099
Coleoptera	6	.0544	3	.0310	8	.0837	12	.2649	7	.1575
Diptera							2	.0018		
Hemiptera							1	.0060		
Homoptera										
Hymenoptera					4	.0095	4	.0157	3	.0207
Lepidoptera	2	.0118	6	.0435	4	.0264	4	.0205	1	.0033
Orthoptera	3	.0435	15	.2127	9	.1200	9	.0722	9	.1003
Totals	11	.1097	24	.2872	25	.2396	33	.3868	21	.2917

*See text for definition of diurnal periods.

**Expressed in grams. Dry weights obtained from a regression curve from representative samples of each order.

Table 17. Average diurnal diet returned to nestlings by male Chestnut-collared Longspurs at the Pawnee Site.

Order	Diurnal Period* 1		2		3		4		5	
	No.	Dry Wt.**	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.	No.	Dry Wt.
Araneida			1	.0406	2	.0231			1	.0043
Coleoptera			9	.0966	15	.2749	14	.2837	7	.0450
Diptera					3	.0017	1	.0013		
Hemiptera									1	.0022
Homoptera			1	.0008						
Hymenoptera					2	.0106	8	.0456	2	.0069
Lepidoptera			3	.0186	2	.0211	1	.0059	3	.0115
Orthoptera	12	.2430	13	.2956	21	.4538	11	.0937	7	.0644
Totals	21	.2430	27	.4522	45	.7852	35	.4302	21	.1343

*See text for definition of diurnal periods.

**Expressed in grams. Dry weights obtained from a regression curve from representative samples of each order.

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the portions of day when illumination and temperature are highest (Verner, 1965). On a daily average, male Lark Buntings returned a significantly greater ($p < 0.05$) amount of food to nestlings than males of the other species although the actual number of feeding trips to nests were not different between species.

The per cent representation of prey item orders in the diets of nestling Horned Larks, Chestnut-collared and McCown's Longspurs were relatively constant when food items were grouped by biweekly periods. Numerical representation fluctuated although dry weight contributions did not. A clear difference is seen if foods of nestling Lark Buntings are grouped in the same way (Figure 22). A definite temporal component is present in their diet. During the early part of their nesting periods, Lark Buntings exploited a variety of orders fairly equally, but later in the breeding season nestlings were maintained on a diet consisting largely of orthopterans to the exclusion of other orders. By the end of summer, orthopterans accounted for 85% of the total dry weight in the diet of nestlings.

Habitat Partitioning

The guild concept provides a mechanism for ecological investigations of sympatric species exploiting similar resources by enumerating the various ways a habitat can be partitioned. Partitioning by a guild implies that species divide up the habitat in such a way that each

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Figure 22. Biweekly variation in the composition of nestling Lark Buntings' diet at the Pawnee Site, 1971-72. Dry weight contributions of the major prey items to the total dry weight of the nestling diet were used to determine percent of total diet.

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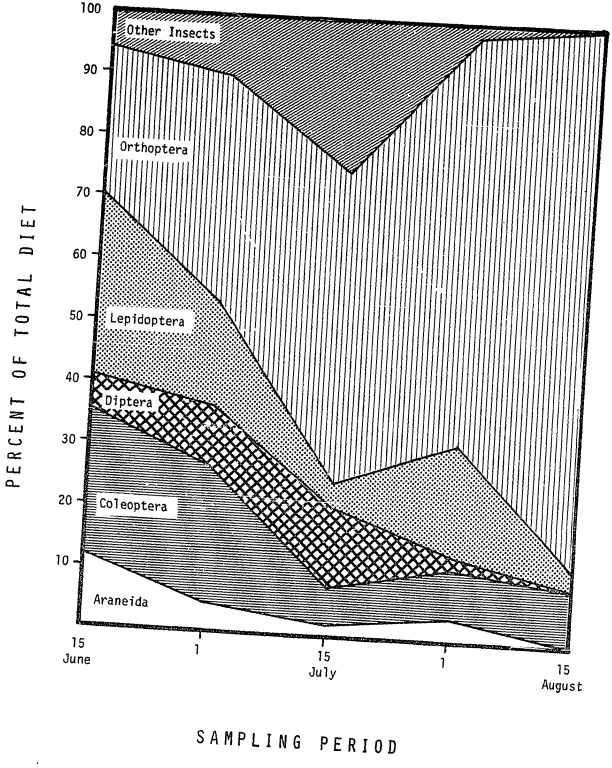

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species is limited by a different resource (MacArthur, 1958). These resources may have both a spatial and temporal component, and habitat partitioning is achieved by a guild through combinations of adjustments and divergences in use of time, space and food. What should be stressed is that partitioning is not usually obtained by only one type of species' adjustment; rather, a complex of compromises is necessary to reduce the intensity of competition between species exploiting the same habitat. The important contribution of the guild concept is that it focuses attention on the functional relationships of species—species exploiting a habitat in similar ways are members of the same guild, not occupants of the same niche.

Patterns of habitat partitioning by guild members can be compared by the degree of overlap occurring between members in utilization of the same habitat parameter. Table 18 summarizes the overlap values occurring within the guild in use of space, time and food. The greatest degree of similarity occurs between the two longspurs as demonstrated by high overlap values in times of nesting, exploitation of food resources, and selection of prey item size. This similarity between the McCown's and Chestnut-collared Longspurs reflects close taxonomic relationships and conforms with the observation that intrageneric competition tends to be stronger than between unrelated species. However, this similarity of exploitation patterns of the longspurs must be superimposed on the type of habitat being

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Table 18. Summary of overlap values between guild members.

Type of overlap	Species-Pair Compared: Horned Lark (HL)	Lark Bunting (LB)	McCown's Longspur (ML)	Chestnut-collared Longspur (CL)	
Spatial	--	.45	.85	.45	HL
	.45	--	.11	.75	LB
(value of	.85	.11	--	-.52	ML
association)	-.02	.75	-.52	--	CL
Temporal	--	.66	.68	.81	HL
	.66	--	.82	.75	LB
	.68	.82	--	.83	ML
	.81	.75	.83	--	CL
Food	--	.81	.91	.82	HL
	.81	--	.93	.95	LB
	.91	.93	--	.97	ML
	.82	.95	.97	--	CL
Food Length	--	.69	.74	.73	HL
	.69	--	.73	.73	LB
	.74	.73	--	.78	ML
	.73	.73	.78	--	CL

exploited. There is a highly significant disassociation between these two species--where McCown's Longspurs occur, Chestnut-collared Longspurs do not, and vice versa. Species clearly can have very similar exploitation patterns if the same habitat is not being exploited. Because of the patchiness of the grassland (areas of shortgrass interspersed with midgrass), these two species exhibit geographic overlap combined with habitat exclusion. Chestnut-collared Longspurs' nests are closely associated with nest-protective vegetation which is usually mid-sized bunchgrass while McCown's Longspurs' nests are not usually associated with protective vegetation. Felske (1971) suggested that McCown's Longspurs prefer exposed shortgrass areas because those areas allowed earlier nesting and favorable supplies of food during the early breeding season. At the Pawnee Site, although Chestnut-collared Longspurs may begin nesting before McCown's Longspurs, the median date of nest initiation of McCown's Longspurs is two weeks in advance of the Chestnut-collared Longspurs. Bhatnagar and Pfadt (1973) found that population densities of grasshoppers also increased earlier in shortgrass areas than in midgrass, therefore apparently Felske's suggestions are confirmed.

Slight differences in spatial utilization by Horned Larks and Chestnut-collared Longspurs, and by Lark Buntings and McCown's Longspurs would also promote coexistence between these species.

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For species exploiting the same habitat, temporal segregation of reproductive demands would assist coexistence. In short grass areas, the temporal differences between nest initiation of Horned Larks and McCown's Longspurs are sufficient to provide separation of maximum exploitation pressures associated with care of nestlings. The mean nesting peak of Horned Larks occurs 2 weeks earlier than that of McCown's Longspurs, and because incubation and nestling periods are of the same duration this staggering is maintained during the nesting season. Temporal overlap is relatively higher between Lark Buntings and Chestnut-collared Longspurs, although nesting of the buntings is much more concentrated in time than that of the longspurs. Coexistence may be promoted between these two species by the dilution of longspur demands over a longer period of time. By longspurs maintaining a constant but reduced level of reproduction throughout the breeding season, intense interspecific competition may be avoided.

Temporal segregation is most pronounced between Horned Larks and Lark Buntings with each species exploiting different portions of the total breeding season. It is significant that overlap values are relatively low between Horned Larks and Lark Buntings for all habitat parameters compared. Of the entire ground-foraging guild, these two species apply the greatest numerical pressure on the resources of the grassland, and a montage of adjustments would favor coexistence and mutual exploitation.

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It is interesting to note that Lark Buntings arrive later in the spring at the Pawnee Site that other guild members, and then concentrate reproduction during a small portion of the total breeding season. This would suggest that perhaps reproduction in Lark Buntings is closely attuned to some proximate factor. It was also noted in the last chapter that later Lark Buntings nestlings are maintained on a diet of orthopterans almost exclusively. Figure 23 shows dates of nest initiation of Lark Buntings and increase in numbers of grasshoppers (data are from Figure 1 of Bhatnagar and Pfadt, 1973) at the Pawnee Site. A striking similarity of peaks exist. The correlation between numbers of Lark Bunting nests initiated per week and the number of grasshoppers present is significant at the 95% confidence level ($R = 0.86$). No such correlation exists between nest initiations of Horned Larks ($R = 0.08$), McCown's Longspurs ($R = -0.18$) and Chestnut-collared Longspurs ($R = 0.08$) with increasing numbers of grasshoppers.

Habitats lacking vertical stratification provide a greater potential for exploitation of the same food resources than would spatially complex areas. In comparing the foods delivered to nestlings of guild members, high values of overlap of taxa exploited were found to exist between all species. However, if prey items are procured in roughly the same frequency that they are encountered in a given area, it is not only the dietary composition which is important to habitat

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Figure 23. Temporal relationship of Lark Bunting nest initiations and density of grasshoppers within the primary study area at the Pawnee Site. Grasshopper densities were derived from Bhatnager and Pfadt (1973).

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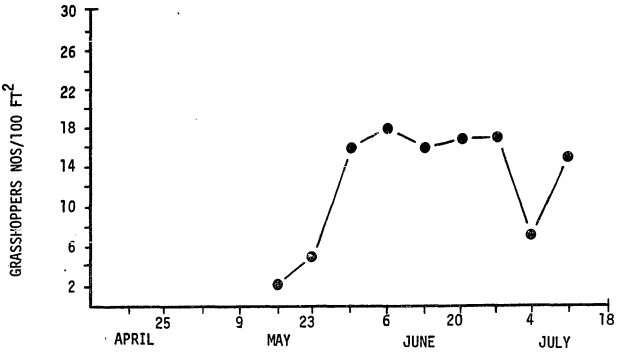

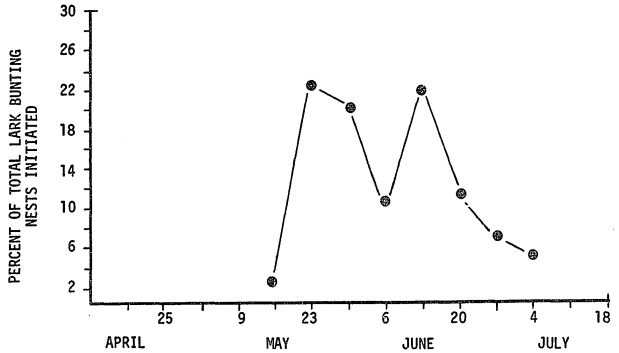

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partitioning, but also a consideration of the tactics employed by guild members to capture the items. Three different prey capture techniques are employed by species in the ground-foraging guild:

Maneuver	Position of Prey	Position of Bird
Stalking	on the ground	on the ground
Hawking	in the air	in the air
Gleaning	in vegetation	on or near vegetation

An axiom in geometry states that the sum of three perpendicular distances from an interior point to the sides of an equilaterial triangle is equal to the length of one side and is independent of the position of the interior point; thus the proportion of prey capture techniques employed by guild members can be demonstrated within a triangle (Figure 24), as MacArthur (1958) and Root (1967) have. Horned Larks foraged mainly on the ground, capturing most of their items by gleaning and stalking. Cody (1968) characterized Horned Larks as predominantly employing aerial prey capture techniques. Although aerial prey capture is the most conspicuous tactic, in Horned Larks it actually accounted for very few items. Techniques employed by Lark Buntings are again most dissimilar to those of Horned Larks, as bunting capture most prey items by stalking and hawking. The tactics employed by McCown's and Chestnut-collared Longspurs are similar. There are relatively greater differences in the food capture techniques of species occupying the same habitat than between those

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Figure 24. Foraging tactics employed by members of the ground-foraging guild. The length of the arms toward each coordinate represents the frequency that each maneuver was performed as a percent of total prey capture tactics in the foraging regime of each species.

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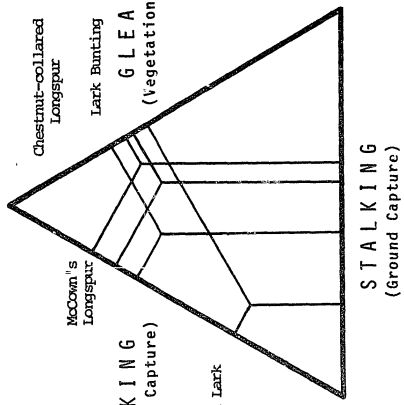

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of species occupying different habitats. The result is that while food overlap is considerable, guild members are being exposed to items in different ways, and capturing prey by unique patterns.

Mechanisms of habitat partitioning, summarized in Table 19, can then be described for members of the ground-foraging guild. Horned Larks and McCown's Longspurs are associated in shortgrass areas. Coexistence between these species is achieved by temporal segregation and differences in prey capture techniques. McCown's and Chestnut-collared Longspurs avoid competitive interactions by exploiting very dissimilar grassland areas, although otherwise resembling each other in habitat exploitation patterns. A complete spectrum of adaptations is present in relationships of Horned Larks and Lark Buntings. These species divide the habitat by combinations of temporal and spatial segregation, selecting different prey sizes, and employing divergent prey capture techniques. Habitat partitioning between McCown's Longspurs and Lark Buntings, and Horned Larks and Chestnut-collared Longspurs is achieved by clear spatial segregation. McCown's Longspurs and Horned Larks are associated with shortgrass areas while Lark Buntings and Chestnut-collared Longspurs are found in midgrass locations. The greatest potential for competitive interactions occurs between Lark Buntings and Chestnut-collared Longspurs because both species occur in similar areas, nest at the same time, and exploit the same food resources.

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Table 19. Mechanisms of habitat separation in the ground-foraging guild at the Pawnee Site.

	Species-Pair Compared		
	Horned Lark		
Lark Bunting	TFS	Lark Bunting	
McCown's Longspur	TF	S	McCown's Longspur
Chestnut-collared Longspur	S	T	S

The above symbols indicate the following means of separation:

S: spatial segregation
T: temporal segregation of nest initiation
F: food segregation, either by prey-capture mechanism, dietary composition or prey size

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The most apparent adjustment between these species is the even distribution of reproductive demands over a longer period during the breeding season by Chestnut-collared Longspurs while breeding is concentrated in a relatively short time by Lark Buntings.

The interplay of these partitioning mechanisms between various species-pairs dramatizes the dynamic nature of guild relationships. The habitat is partitioned by a union of different species and the integrity of the union, an ecological guild, is maintained by slight variations in exploitation patterns of the guild members.

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SUMMARY

The shortgrass prairie of northcentral Colorado is utilized in similar ways by four species of songbirds; Horned Larks, Lark Buntings, McCown's Longspurs, and Chestnut-collared Longspurs. Because the same class of environmental resources are being exploited in similar fashions, these species qualify for membership in an ecological guild. Mechanisms of habitat partitioning by members of the ground-foraging guild were investigated in this study by isolating differences in feeding behavior, and spatial and temporal utilization.

The ground-foraging guild was studied as part of the International Biological Program's Grassland Biome Study at the Pawnee Site on the Pawnee National Grassland of Colorado. Over 2000 hours were spent in actual observation during breeding seasons of three different years. Time budgeting techniques were employed to quantify variations in foraging regimes and behavioral schedules of guild members. In addition, the vegetative parameters associated with each species, reproductive success, nestling foods, and general life history of guild members were studied. Some of the conclusions stemming from this study are as follows:

1. Discrete vegetational associations with species composing the ground-foraging guild are found, and spatial segregation is an

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important adjustment permitting species coexistence. The two taxonomically closely-related species, McCown's and Chestnut-collared Longspurs, inhabit vastly different microhabitats. Also, the vegetation associated with the two most abundant species, Horned Larks and Lark Buntings, is again different. McCown's Longspurs and Horned Larks are commonly associated with shortgrass and sparcely vegetated areas, while Chestnut-collared Longspurs and Lark Buntings are found in mid and bunchgrass locations.

2. Resources of the habitat are partitioned by guild members extracting their necessary requisites, associated with reproduction, at different times. Dates when first eggs were laid were used to indicate temporal overlap. McCown's Longspurs and Horned Larks, which are spatially associated, have a low index of temporal overlap. Overlap between Lark Buntings and Chestnut-collared Longspurs is somewhat higher, but competition between these species may be reduced by the longspur distributing a reduced intensity of nesting over a longer period of time. An index of seasonal utilization was developed as a measure of this relative dispersion. Overlap was low between Horned Larks and Lark Buntings, and was an additional mechanism of habitat partitioning by these two species.

3. The total amount of time spent foraging and the number of feeding trips to the nest by males in the guild were not significantly different. However, male Lark Buntings returned significantly greater amounts of food to nestlings than males of other species.

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4. Nestling foods were used as an indicator of food specialization. Over 1600 prey items were recorded by a photographic method and about 200 additional items were obtained by throat collar techniques. Acridid grasshoppers formed the bulk of nestling diets for Lark Buntings, and McCown's and Chestnut-collared Longspurs while coleopterans formed a significant portion of nestling Horned Lark diet. Size of food items fed to nestling buntings was larger than items fed to nestling of other guild members. Dietary overlap was lowest between Lark Buntings and Horned Larks, and between Horned Larks and Chestnut-collared Longspurs; reflecting, in part, the habitat differences associated with these species. Although remaining fairly constant for the other three species, the dietary diversity of nestling Lark Buntings decreased as the breeding season progressed demonstrating an increased utilization of grasshoppers by the bunting.

5. Techniques used for procuring prey items by guild members contribute to the efficiency of habitat partitioning. The foraging regime of Horned Larks, resembling that of Chestnut-collared Longspurs, is unlike the foraging repertoires of Lark Buntings and McCown's Longspurs. Differences in the frequency that various prey capture tactics are employed, while reflecting the morphological variation present in the guild, permit prey items to be encountered and extracted in ways promoting species coexistence.

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6. The combination of varied methods each species employ to exploit time, space, and food structures the guild, forming a dynamic pattern of habitat partitioning.

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