

# RELATIONSHIPS BETWEEN POPULATION DEMOGRAPHY OF McCOWN'S LONGSPURS AND HABITAT RESOURCES<sup>1</sup>

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*Abstract.* The relationships between habitat quality and population demography of McCown's Longspurs (*Calcarius mccownii*) were studied on a mixed-grass prairie in southeastern Wyoming. McCown's Longspurs were censused and their breeding territories delineated on four 9-ha plots in 1986 and 1987. Vegetation characteristics and arthropod biomass were quantified on 97 McCown's Longspur territories and on 65 areas unoccupied by McCown's Longspurs. Stepwise regression analysis indicated that vegetation features were generally poor predictors of prey biomass throughout the study area. The harsh climate may erode coupling of the arthropod and vegetation communities. Vegetation structure may therefore provide poor guidance to McCown's Longspurs in their evaluation of food resource availability. Because no differences in total arthropod biomass and only moderate differences in vegetation structure were shown between territorial and nonterritorial areas, most of the habitat may be suitable for nesting by McCown's Longspurs. Nesting success was not related to arthropod productivity and was only moderately related to vegetation structure on the territory. Neither territory size nor population density was related to prey productivity which is consistent with the view that all individuals were able to occupy suitable habitat. Territory size did not differ between years and was not associated with the number of McCown's Longspur territories per study plot, suggesting a lower limit to territory size in an unsaturated habitat with unlimited food resources. No association was demonstrated between territory size and nesting success, and predation was responsible for almost all nest failures. This suggests that predation, rather than food resources, determined nesting productivity.

*Key words:* McCown's Longspurs; population demography; habitat selection; vegetation structure; prey productivity; territory size.

## INTRODUCTION

Birds select breeding habitat that provides a favorable environment for their survival and reproduction (Hilden 1965). Because habitats may differ in structural configuration, food productivity, and range of competitive interactions (Cody 1981), they may also differ in suitability (Wiens and Rotenberry 1981). If birds attempt to maximize their fitness or reproductive success by selecting habitat of optimal quality or suitability (Fretwell 1972) and if variation in resource availability affects fitness, then resource differences should be evident between these habitats and habitats of poorer intrinsic quality not selected by the species.

Fretwell and Lucas (1970) proposed the "ideal-free distribution" model of habitat selection where the habitat suitability defined in terms of fitness declined with increasing population den-

sity, i.e., density-dependent habitat selection (O'Connor and Fuller 1983, Rosenzweig 1985). This model is based on two assumptions: (1) ideal behavior in that individuals select the most suitable habitat for survival and reproduction, and (2) individuals are freely able to occupy any habitat regardless of the presence of other members of the species.

In this model, equal fitness is conferred to individuals settling at higher densities in "good" habitat or lower densities in "poor" habitat. Birds sequentially settle in the best habitat, compress their territory sizes to saturate the habitat up to the point where fitness is reduced, and then initiate occupancy in the next best habitat. Therefore, in the ideal-free distribution model, density of individuals in an area reflects local habitat quality.

Cody (1981) concurred that bird species may respond to varying habitat quality by tracking limited resources via spatial and temporal adjustments in population distributions and densities. On western grasslands, unstable climate causes unpredictable resources, and Cody (1985b)

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suggested that resident bird species opportunistically use habitats of higher resource productivity. These bird communities are locally saturated with species that are optimally adapted to the current environment, and coexistence among species is achieved through partitioning of limited resources (Cody 1968).

In contrast, Wiens and Rotenberry (1981) stated that the ideal-free distribution may not be applicable to bird populations, especially in variable environments. Birds may not select optimal habitat because fluctuating environmental factors may prevent them from closely tracking resources, and generally superabundant resources may place no fitness costs on individuals that do not exploit them optimally (Wiens 1977a). Also, selection for optimal behavior and morphology because of limited resources may occur during the nonbreeding season (Fretwell 1972). In a variable environment, as is typical of the mixed-grass prairie, bird populations may be held below equilibrium or carrying capacity levels, and local density patterns may merely reflect stochastic distribution of individuals within a regional setting (Wiens 1986). If this is true, optimal habitats may not be fully saturated and density or territory size may be a poor index of habitat quality.

In this study, we will examine mechanisms underlying habitat selection of McCown's Longspurs (*Calcarius mccownii*) on a mixed-grass prairie. Our goal is to determine the relationship between habitat resources (i.e., vegetation structure and food availability) and population demographic features. For this purpose, the following questions will be addressed:

- (1) Is there a relationship between habitat structure and arthropod biomass?
- (2) Do vegetation characteristics and prey productivity differ between territorial and non-territorial areas?
- (3) What effects do habitat structure and prey biomass within the territory have on nesting success?
- (4) Is population density related to prey productivity?
- (5) What is the relationship between territory size and year of survey, population density, prey productivity, and nesting success?

## METHODS

### SPECIES DESCRIPTION

McCown's Longspurs are ground-nesting sparrows which breed on short-grass and mixed-grass

prairies of western North America (Mickey 1943) and prefer dry sites with low vegetation cover for nesting (Dubois 1935). In southeastern Wyoming, males arrive at breeding areas during the first week of April, and are followed by females in the third week of April (Mickey 1943). By the last week of April, McCown's Longspurs begin to establish territories with their unique aerial song and display (Mickey 1943, Finzel 1962). Territories have a semicolonial distribution, with each pair occupying its own territory within a disjunct flock (Mickey 1943, Felske 1971). The species is double brooded and breeds from early May through July in the study area (Mickey 1943, Greer 1988). McCown's Longspurs are primarily insectivorous during the nesting season (Mickey 1943, Baldwin 1973), with orthopterans and coleopterans composing a large portion of their diets (Felske 1971, Creighton and Baldwin 1974, Maher 1979, Greer 1988). McCown's Longspurs generally forage within their territory, and both adults feed and brood their young (Mickey 1943).

### STUDY AREA

The study was conducted during 1986 and 1987 on a mixed-grass prairie located 7 km south of Laramie, Wyoming (41°14'N, 105°37'W) at an elevation of 2,185 m. The vegetation is dominated by the short-grass blue grama (*Bouteloua gracilis*), and mid-grasses: needle-and-thread grass (*Stipa comata*), western wheatgrass (*Agropyron smithii*), Junegrass (*Koeleria cristata*), Indian ricegrass (*Oryzopsis hymenoides*), and bluegrasses (*Poa* spp.).

Four 300- × 300-m (9-ha) plots were established within the study area prior to the 1986 breeding season. On each plot, numbered wooden stakes were set at 50-m intervals. Criteria for plot location included relatively flat topography to facilitate observation of bird movement and minimal shrub cover to simplify interpretation of bird-habitat relationships (Cody 1968, 1985b).

### CENSUSING AND TERRITORY DELINEATION

McCown's Longspurs were censused during the peak of their breeding season from 22 May through 18 June 1986 and from 12 May through 30 June 1987 using the territory flush technique (Wiens 1969). Territory boundaries were determined by plotting the locations of males that were consecutively flushed throughout their generally exclusive territories. Perimeters of the territories were typically defined by tracing flight

paths, but also included outermost sight, call, and song observations. Simultaneous singing by adjacent males assisted in boundary definition. Only those territories with over half their areas encompassing a study grid were included in the analysis. A digital planimeter was used to calculate territory size.

#### NESTING SUCCESS

Nests of McCown's Longspurs were located directly by systematically searching the study plots, and incidentally while bird censusing and quantifying vegetation structure and arthropod productivity. Nests were visited approximately 5 days per week and the nesting chronology was recorded. Ages of nestlings were determined by hatch date or plumage, openness of eyes, and alertness (Mickey 1943). A nest was assumed to be successful if at least one nestling was in the nest on the eighth day of the nestling period, i.e., the earliest departure described by Mickey (1943). All other nesting outcomes were considered failures.

#### VEGETATION STRUCTURE AND ARTHROPOD PRODUCTIVITY

Vegetation characteristics and arthropod biomass were quantified for each territorial area and for areas displaying no occupancy by McCown's Longspurs during May, June, and July in 1986 and 1987. We and two technicians collected the data with the methodology thoroughly described in Greer (1988). Care was taken to disperse the sampling among plots, dates, and time of day (08:00 through 15:00). Within each territorial and nonterritorial area, 10 samples were collected by quantifying vegetation and arthropods every 5 m along two 25-m transects oriented in opposite directions. Transect starting points for McCown's Longspur territories ( $n = 97$ ) were territory centers or nest sites. For the unoccupied areas, transect starting points were either Horned Lark (*Eremophila alpestris*) ( $n = 38$ ) or Chestnut-collared Longspur (*Calcarius ornatus*) ( $n = 3$ ) territory centers, or were centers of 1,963-m<sup>2</sup> (25-m radius) circular plots within which no territorial behavior by any bird species was observed ( $n = 24$ ). The Horned Lark and Chestnut-collared Longspur territories did not appear to be avoided by McCown's Longspurs because of their occupancy; we observed high territorial overlap among these species and a scarcity of interspecific aggression (Greer 1988).

Vegetation structure was characterized using a

modification of techniques developed by Wiens (1969) and Rotenberry and Wiens (1980) for studying habitat relationships of shrubsteppe and grassland birds. At each of the 10 sampling points, percentage cover was estimated within a 50- × 20-cm Daubenmire frame (Daubenmire 1959) for the following habitat variables: short grass, mid grass, cactus, shrub, forb, lichen, litter, ground, and cattle dung. The coverage class values were 2.5 for 0–5% coverage, 15 for 5–25% coverage, 37.5 for 25–50% coverage, 62.5 for 50–75% coverage, 85 for 75–95% coverage, and 97.5 for 95–100% coverage. For each occupied and unoccupied area, the 10 coverage values were averaged.

The vertical structure of the vegetation was examined using two methods. The first involved recording the number of vegetation contacts within 10-cm intervals along a 5-mm wide rod set into ground 2 cm from each corner of the Daubenmire frame. For the second method, a 8.7-cm wide board divided into 5-cm intervals was vertically placed at each end of the Daubenmire frame. From a distance of 5 m, a standing observer estimated coverage of vegetation within each 5-cm interval using coverage class values described above. At each sampling point, mean vertical structure values were determined for each method and interval. For each occupied and unoccupied area, the means of the 10 samples were calculated.

Horizontal structure or patchiness of vegetation was determined on each area by measuring the variation in vertical structure between the 10 sampling points. This was estimated using the coefficient of variation of the mean number of vegetation contacts and coefficient of variation in mean coverage class values within the first three height intervals of their respective sampling methods.

The 17 vegetation variables were reduced to 12 variables which remained relatively uncorrelated ( $r < 0.60$ ) and allowed for meaningful interpretation. The vertical vegetation contact data were summed to one value because the number of contacts in the second and third 10-cm intervals was low, 0.10 and 0.01 contacts per sample, respectively. For these reasons, the corresponding coefficient of variation variable was deleted. The vertical coverage variable for interval two was deleted because of high correlation ( $r = 0.83$ ) with interval one, and interval three was removed from analysis because its mean was less than 2% coverage.

Arthropod productivity per territorial and nonterritorial area was quantified by collecting all individuals within 10 0.1963-m<sup>2</sup> metal cylinders positioned on the ground along the transects. Each cylinder, measuring 50 cm in diameter by 10 cm in height, was initially covered with mosquito netting to prevent evasion by mobile arthropods. All arthropods enclosed by the cylinder were dispatched with a wooden dowel if necessary, collected with forceps, and immersed in a vial containing 70% ethyl alcohol. Arthropods flushed prior to the proper positioning of the cylinder or escaping with the cylinder in place on the ground were recorded.

In the laboratory, arthropod lengths were measured, and biomass per individual was determined using length-weight regression models developed by Rogers et al. (1976) and Rogers et al. (1977). Arthropods were grouped by order and life stage (adult or immature). Total biomass per territory or nonterritory for each taxon was determined by summing the values from each of the 10 samples (total ground area sampled = 1.963 m<sup>2</sup>). The following eight taxa contributing independently at least 1% to the total biomass of arthropods were considered for further analysis: Orthoptera, adult Coleoptera, adult Diptera, adult Lepidoptera, Hemiptera, Homoptera, Araneida, and Hymenoptera.

#### ANALYSES

Due to deviations from normal distributions (Zar 1974), the percentage cover variables were transformed using the arcsine square root transformation; and the number of vegetation contacts, territory size, and arthropod biomass variables were transformed using the base 10 logarithmic transformation. Untransformed means and standard deviations are shown, but the probability values (*P*) are based on transformed variables.

To assess whether McCown's Longspurs may be able to detect differences in potential prey biomass in an area using vegetation cues, the relationship between prey biomass and vegetation characteristics for all territorial and nonterritorial areas was examined with stepwise multiple regression analyses (SPSS<sup>+</sup> 1983). Hymenoptera, particularly Formicidae, are of minimal value as nestling food but may be important in the adult diet (Greer 1988). Therefore, total arthropod biomass and this value excluding Hymenoptera biomass were used as dependent variables in the regression analyses.

Variables potentially important in the habitat-selection process were investigated by comparing territorial with nonterritorial areas in terms of vegetation and arthropod characteristics. Differences between means for vegetation variables, arthropod taxon biomass, total arthropod biomass, and total biomass excluding Hymenoptera were compared using Student's *t*-tests (SPSS<sup>+</sup> 1983). Analysis of covariance was performed to test for differences between territorial and nonterritorial areas in total arthropod biomass and total biomass excluding Hymenoptera after adjusting for the covariates of collection date and time.

In addition, discriminant function analyses were employed to compare territorial and nonterritorial areas using all significant (*F* to enter 1.0) vegetation and arthropod biomass variables. Prior probabilities of group membership were assumed to be equal. Box's *M*-tests were used to test for equality of the group covariance matrices based on the discriminating variables. Because discriminant function analysis is robust to departures from the assumption of equal covariance matrices (Nie et al. 1975, Johnson 1981) and because ecological significance is of primary concern, results are discussed based on the ecological interpretability regardless of Box's *M*-test outcome (Green 1974). However, note Williams (1983) concerning interpretation problems with departures from this assumption. Student's *t*-tests were also used to compare the total arthropod biomass and total biomass excluding Hymenoptera between McCown's Longspur territories (*n* = 97) and areas not occupied by any bird species (*n* = 24).

To examine effects of territorial features on nesting outcomes, vegetation and arthropod variables were compared between successful and unsuccessful territories using Student's *t*-tests and discriminant function analyses. The association between nesting success per plot (number successful/total nests) and number of McCown's Longspur territories per plot was examined with correlation analysis. The relationships between number fledged per successful nest and total arthropod biomass and total biomass excluding Hymenoptera were evaluated with correlation analyses.

McCown's Longspur territory sizes were compared between 1986 and 1987, and between successful and unsuccessful territories using Student's *t*-tests. The associations between territory

size and total arthropod biomass and total biomass excluding Hymenoptera were investigated with correlation analyses. Correlation analysis was also used to determine the association between mean territory size and number of McCown's territories per plot in 1986 and 1987. Associations between the number of McCown's Longspur territories per plot and mean total arthropod biomass per sampled area (territories and nonterritories) per plot, and mean total biomass excluding Hymenoptera were examined with correlation analyses.

## RESULTS

### TERRITORIAL AND NONTERRITORIAL AREAS

Vegetation features were generally poor predictors of arthropod biomass on the 162 territorial and nonterritorial areas. Stepwise regression analyses demonstrated only 9% and 8% of the variance (adjusted  $R^2$ ) in total arthropod biomass and total excluding Hymenoptera, respectively, were accounted for by structural vegetation characteristics. In the former model, percentage ground (Beta = 0.28,  $P < 0.01$ ), total vegetation contacts (Beta = 0.21,  $P < 0.01$ ), and percentage cactus (Beta = 0.18,  $P = 0.02$ ) were positively related to total prey biomass. In the latter model, total vegetation contacts (Beta = 0.27,  $P < 0.01$ ) and percentage ground (Beta = 0.19,  $P = 0.01$ ) were positively related to total biomass excluding Hymenoptera.

Territories and nonterritorial areas were similar in total arthropod biomass and arthropod biomass by taxon. Student's  $t$ -tests revealed no significant differences between territorial and nonterritorial areas in either total prey biomass ( $P = 0.26$ ) ( $n = 97$ ,  $\bar{x} = 46.64$  mg, SD = 98.14 and  $n = 65$ ,  $\bar{x} = 29.79$  mg, SD = 46.59, respectively), or total biomass excluding Hymenoptera ( $P = 0.76$ ) ( $n = 97$ ,  $\bar{x} = 33.92$  mg, SD = 98.08 and  $n = 65$ ,  $\bar{x} = 19.91$  mg, SD = 40.71, respectively). Analysis of covariance also demonstrated no significant differences between territorial and nonterritorial areas in total arthropod biomass ( $F = 2.00$ ,  $P = 0.16$ ) or total biomass excluding Hymenoptera ( $F = 0.40$ ,  $P = 0.53$ ) after adjusting for the effects of collection date and time. The biomass values of all eight arthropod taxa were also not significantly different between groups (all  $P > 0.21$ ) (Table 1). Moreover, the discriminant function maximizing area group differences based on the individual taxa biomass values was

TABLE 1. Biomass of arthropod taxa (mg dry weight) examined for McCown's Longspur territories ( $n = 97$ ) and nonterritorial areas ( $n = 65$ ). Means<sup>1</sup> ( $\bar{x}$ ), standard deviations<sup>1</sup> (SD), and probability values<sup>2</sup> ( $P$ ) are shown.

	Territories		Nonterritories		$P$
	$\bar{x}$	SD	$\bar{x}$	SD	
Orthoptera	15.12	88.66	9.51	37.84	0.21
Lepidoptera (adult)	0.54	2.06	0.89	2.82	0.28
Hymenoptera	12.73	14.44	9.87	9.07	0.41
Hemiptera	1.64	2.59	1.19	1.49	0.46
Homoptera	1.69	3.75	2.43	5.30	0.52
Coleoptera (adult)	8.91	33.61	3.64	12.60	0.65
Araneida	1.14	3.00	1.37	4.28	0.71
Diptera (adult)	0.19	0.91	0.48	2.62	0.85

<sup>1</sup> Untransformed variables.

<sup>2</sup> Student's  $t$ -test of transformed variables.

not significant (Wilk's lambda = 0.98,  $\chi^2 = 3.92$ ,  $df = 3$ ,  $P = 0.27$ ). Box's  $M$ -test indicated group covariance matrices were not equal ( $P = 0.01$ ). No significant differences were demonstrated between McCown's Longspur territories and areas not occupied by any bird species in terms of total arthropod biomass ( $P = 0.67$ ) ( $n = 97$ ,  $\bar{x} = 46.64$ , SD = 98.14 and  $n = 24$ ,  $\bar{x} = 25.71$ , SD = 21.16, respectively), and total biomass excluding Hymenoptera ( $P = 0.62$ ) ( $n = 97$ ,  $\bar{x} = 33.92$ , SD = 98.08 and  $n = 24$ ,  $\bar{x} = 15.28$ , SD = 16.69, respectively) based on Student's  $t$ -tests.

However, subtle differences were shown between territorial and nonterritorial areas in terms of vegetation structure. Student's  $t$ -tests revealed significant differences ( $P < 0.05$ ) between the area means of coverage by the first 5 cm of vegetation and percentage cover by cattle dung, lichen, and forbs (Table 2). Stepwise discriminant function analysis showed that the group means were significantly different (Wilk's lambda = 0.85,  $\chi^2 = 24.63$ ,  $df = 6$ ,  $P < 0.01$ ). Group covariance matrices were not equal as shown by Box's  $M$ -test ( $P = 0.03$ ). Six vegetation variables were retained in the function. Structure coefficients, or correlations between the variables and the discriminant function, expressed the function as a continuum from higher number of vegetation contacts to higher coverage by cattle dung, lichen, shrubs, bare ground, and cactus (Table 3). Group centroids (area means) on the function demonstrated that McCown's Longspur territories were associated with more vegetation contacts (centroid =  $-0.34$ ), and areas not occupied

TABLE 2. Vegetation structure variables examined for McCown's Longspur territories ( $n = 97$ ) and nonterritorial areas ( $n = 65$ ). Means<sup>1</sup> ( $\bar{x}$ ), standard deviations<sup>1</sup> (SD), and probability values<sup>2</sup> ( $P$ ) are shown.

	Territories		Nonterritories		$P$
	$\bar{x}$	SD	$\bar{x}$	SD	
Vegetation coverage in first 5 cm (%)	26.49	11.91	20.80	12.17	0.01
Cattle dung percentage	1.41	1.88	2.07	2.06	0.01
Lichen percentage	14.11	13.39	19.89	14.85	0.01
Forb percentage	7.36	3.99	8.77	4.16	0.03
Total number of vegetation contacts	1.52	0.50	1.40	0.39	0.10
Litter percentage	14.84	3.59	13.96	3.97	0.12
Shrub percentage	6.74	4.01	7.51	4.48	0.23
Short grass percentage	22.86	12.55	25.19	15.26	0.49
Bare ground percentage	38.10	13.79	38.97	13.95	0.66
Vegetation coverage (coefficient of variation)	0.71	0.20	0.70	0.24	0.79
Mid grass percentage	27.11	9.32	27.06	10.38	0.92
Cactus percentage	1.04	1.77	0.92	1.53	0.97

<sup>1</sup> Untransformed variables.<sup>2</sup> Student's  $t$ -test of transformed variables.

by the species were associated with the remaining five variables (centroid = 0.50).

The adequacy of the discriminant function in separating the two groups was also shown by the classification results which predicted the group that each area most likely resembled based on the six vegetation variables (Table 4). The accuracy of discrimination and group distinction are demonstrated by the percentage of areas classified correctly (Klecka 1980). Because just 70% of the sampled areas were correctly classified, territorial and nonterritorial areas differed only moderately with respect to the measured vegetation variables.

#### SUCCESSFUL AND UNSUCCESSFUL NESTING

Territories successfully fledging McCown's Longspurs were similar to unsuccessful territories in terms of both prey and vegetation characteristics. Total prey biomass was not signifi-

cantly different ( $P = 0.22$ ) between successful and unsuccessful territories ( $n = 33$ ,  $\bar{x} = 65.11$  mg, SD = 147.182, and  $n = 36$ ,  $\bar{x} = 27.44$  mg, SD = 36.71, respectively). Total biomass excluding Hymenoptera also showed no significant difference ( $P = 0.17$ ) between successful and unsuccessful territories ( $n = 33$ ,  $\bar{x} = 55.24$  mg, SD = 148.84 and  $n = 36$ ,  $\bar{x} = 14.61$  mg, SD = 33.68, respectively). Number fledged per successful nest was also not related to either total arthropod biomass ( $r = 0.29$ ,  $P = 0.11$ ) or total biomass excluding Hymenoptera ( $r = 0.30$ ,  $P = 0.10$ ).

No significant differences were shown between territories fledging and those not fledging young for any arthropod taxon biomass (all  $P > 0.29$ ) or vegetation characteristic (all  $P > 0.09$ ). The discriminant function maximizing the separation between successful and unsuccessful territories was not significant when examining arthropod taxa biomass values (Wilk's lambda = 0.98,  $\chi^2 = 1.11$ , df = 1,  $P = 0.29$ ). Box's  $M$ -test indicated group covariance matrices were equal ( $P = 0.06$ ). The discriminant function separating

TABLE 3. Structure coefficients for vegetation variables from discriminant function analysis of territorial ( $n = 97$ ) and nonterritorial ( $n = 65$ ) areas. These coefficients are correlations between the transformed vegetation variables and the function.

Variable	Structure coefficient
Cattle dung percentage	0.52
Lichen percentage	0.48
Total number of vegetation contacts	-0.32
Shrub percentage	0.23
Ground percentage	0.08
Cactus percentage	0.01

TABLE 4. Classification results from discriminant function analysis of McCown's Longspur territorial ( $n = 97$ ) and nonterritorial ( $n = 65$ ) areas based on transformed vegetation variables. The percentage (number) of areas correctly and incorrectly classified by the discriminant function is shown.

Actual group	Predicted group	
	Territory	Nonterritory
Territory	68.0 (66)	32.0 (31)
Nonterritory	26.2 (17)	73.8 (48)

successful and unsuccessful territories was significant for the structural vegetation features (Wilk's lambda = 0.84,  $\chi^2 = 11.61$ ,  $df = 5$ ,  $P = 0.04$ ). Box's *M*-test showed group covariance matrices were equal ( $P = 0.63$ ). However, only 68% of the territories were classified into the correct success group. No association was shown between nesting success per plot and number of McCown's Longspur territories per plot ( $r = 0.05$ ,  $P = 0.91$ ).

#### TERRITORY SIZE

No relationships were indicated between territory size and census year, nesting success, population density, or prey productivity. Student's *t*-tests revealed no significant difference ( $P = 0.87$ ) between territory size in 1986 ( $n = 31$ ,  $\bar{x} = 0.55$  ha,  $SD = 0.11$ ) and 1987 ( $n = 43$ ,  $\bar{x} = 0.58$  ha,  $SD = 0.22$ ), nor a significant difference ( $P = 0.12$ ) in size between successful ( $n = 25$ ,  $\bar{x} = 0.62$  ha,  $SD = 0.21$ ) and unsuccessful territories ( $n = 26$ ,  $\bar{x} = 0.53$  ha,  $SD = 0.18$ ). Mean territory size per plot was not associated with the number of McCown's Longspur territories per plot ( $r = 0.24$ ,  $P = 0.57$ ). Territory size was not related to total prey biomass within the territory ( $r = 0.06$ ,  $P = 0.59$ ) or total biomass excluding Hymenoptera ( $r = 0.10$ ,  $P = 0.38$ ).

#### POPULATION DENSITY

The population density of McCown's Longspurs was not related to prey productivity per plot. Mean total arthropod biomass per territorial and nonterritorial area per plot and mean total biomass excluding Hymenoptera demonstrated no association with number of McCown's Longspur territories per plot ( $r = 0.28$ ,  $P = 0.51$  and  $r = 0.18$ ,  $P = 0.67$ , respectively).

#### DISCUSSION

Although birds may select territories based on proximate factors (e.g., vegetation cues) which ensure that ultimate factors (i.e., food supply) are met (Hilden 1965, Smith and Shugart 1987), this study showed that vegetation characteristics were generally poor indicators of prey biomass. The distribution and abundance of insects may be affected by the taxonomic composition and physical structure of the vegetation (Anderson 1964) through their coevolution and coadaptation (Hodkinson and Hughes 1982). Insects may therefore select specific microhabitats associated with vegetation that provide suitable substrate,

microclimate, background for crypsis, food availability, olfactory and visual stimulation, and oviposition sites (Joern 1982, 1987).

However, local insect populations are also regulated by weather conditions. Temporal fluctuations in weather can cause dramatic variation in insect populations and produce spatial patchiness in plant-insect systems (Kareiva 1986). These climatic factors influence not only endocrine system activity, survival, development, and reproduction of insects directly (Varley et al. 1973), but by causing changes in the vegetation composition and structure, indirectly affect insect populations (Anderson 1964). On the mixed-grass prairie, the climate is severe and unstable during the breeding season (Wiens 1974, Cody 1985b). These conditions, acting as episodic selecting agents, may have eroded close coupling of the insect community with the associated vegetation. Therefore, vegetation structure may provide poor guidance to McCown's Longspurs in their evaluation of territory quality with respect to prey abundance within the relatively homogeneous study area.

Birds should select territorial areas that provide the most abundant and exploitable food supply, and substrates which allow the most efficient foraging, except when either competition, predation, absence of nest sites, or social requirements decreases the habitat's suitability (Martin 1986). However, this study demonstrated no differences in prey biomass and only moderate differences in vegetation structure between territorial and nonterritorial areas. Thus, a gradient in habitat quality may not be easily recognized by McCown's Longspurs upon arrival at this breeding area; most of the habitat may have appeared suitable for nesting although some selection was exercised.

Because McCown's Longspur territories did not saturate the study area (Greer 1988), along with their potentially unlimited supply of food (Wiens 1977b, Greer 1988), this species may generalize in selection of breeding habitat based on prey availability. At low densities, individuals may not discriminate between habitat patches as long as minimal limiting factors to foraging and reproductive potential are met (Rosenzweig 1985), and all may exercise optimal habitat selection (Wiens et al. 1985). Thus, short-lived birds with a high annual mortality rate may breed in vacant, optimal habitat each year (O'Connor 1985). Felske (1971) also found that ideal nesting

habitat was apparently available but not occupied by McCown's Longspurs.

McCown's Longspurs did, however, moderately respond to variation in vegetation structure in their selection of territory sites. Seastedt and MacLean (1979) also suggested that Lapland Longspurs (*Calcarius lapponicus*) selected breeding territories in relation to the composition of the habitat instead of directly monitoring prey density. In the present study, the subtle statistical patterns of vegetation structure are difficult to interpret biologically, as are many proximate factors to which species respond (Hilden 1965, Cody 1985a). The areas occupied by McCown's Longspurs may have provided more suitable nesting substrate affecting microclimate (Zimmerman 1982), lower predation risk, or more efficient foraging (Martin 1986). These preferences may reflect adaptations by the species in the absence of direct competitive relationships (Wiens 1984, Greer 1988).

Martin (1986) stated that territories with more abundant food, allowing an increased feeding rate and more time for other nesting activities, may improve the reproductive success of birds. In addition, vegetation characteristics may influence nesting outcome through degree of concealment from predators (Wray and Whitmore 1979) or favorability of microclimate (Zimmerman 1971). But this study demonstrated that the nesting success of McCown's Longspurs was not related to prey productivity and was only moderately related to vegetation structure. This observation is possibly due to the small proportion of available prey biomass on the mixed-grass prairie that is consumed by either nestlings (Greer 1988) or adults (Wiens 1977b), and the seemingly abundant supply of similar nesting habitat (Finzel 1962) affording equal protection from predators and the elements. A potentially unlimited supply of food and nesting habitat may not require optimal selection of habitat (Wiens 1977a). Therefore, nesting success may not necessarily vary with habitat resource quality.

The major factor influencing reproductive success of McCown's Longspurs in the study area was predation, most likely mammalian (Greer 1988). Although predation on eggs or nestlings was never observed, the abundant thirteen-lined (*Spermophilus tridecemlineatus*) and Wyoming (*S. elegans*) ground squirrels were probably the major causes of nest failure (i.e., missing eggs and nestlings). On several occasions, we ob-

served territorial McCown's Longspurs hovering immediately over ground squirrels, presumably recognizing their potential as predators. Dubois (1935, 1937) and Mickey (1943) also presumed that ground squirrels were nest predators of McCown's Longspurs. In our study area, other species capable of exploiting nest contents were coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*), badgers (*Taxidea taxus*), and red (*Vulpes vulpes*) and swift (*V. velox*) foxes. Also, groups of McCown's Longspurs were often seen mobbing Swainson's Hawks (*Buteo swainsoni*) and California Gulls (*Larus californicus*).

Predators accounted for the failure of 51% of 73 attempted nestings by this species in 1986 and 1987; only one nest was unsuccessful due to other factors. The advantage of selecting higher quality breeding sites, in terms of vegetation structure or food abundance, may be completely overridden by stochastic, catastrophic mortality factors (Bedard and Lapointe 1984). In concurrence, Zimmerman (1971) suggested that high predation rates may obscure the relationship between Dickcissel (*Spiza americana*) fledgling production and vegetation features as ultimate environmental factors.

Despite a 169% increase in the number of McCown's Longspur territories from 1986 to 1987 on all four plots (Greer 1988), territory size remained similar between years. This suggests an optimal, possibly lower, limit to territory size for the species in this unsaturated habitat with abundant food resources. Territory size was not related to the number of McCown's Longspur territories per plot because all suitable habitat was not occupied, individuals were freely able to select preferred habitat, and no compression of territory size was necessary to accommodate other territorial conspecifics (Huxley 1934).

Similarly, neither territory size nor population density of McCown's Longspurs per plot was related to prey productivity. In contrast, other studies (see reviews in Verner 1977, Myers et al. 1979, Martin 1986, Smith and Shugart 1987) have found an inverse correlation between territory size and food abundance, and propose two generally accepted hypotheses to explain this pattern. One is that birds assess the local food supply and adjust their territory sizes to include sufficient resources for energetic requirements. The other hypothesis is that competition for higher quality habitat reduces territory sizes because of increased defense costs (Smith and Shugart 1987).



However, Wiens (1977a) stated that because individuals may not saturate all suitable habitat in variable environments, the relationship between territory size or population density and food resources may be obscured, and the Fretwell-Lucas model of habitat selection may not apply. An ideal-free distribution of McCown's Longspur territories, with density depicting habitat quality, would not be demonstrated until the species reached higher densities and saturated the mixed-grass prairie habitat. In addition, local variation in food abundance, predation rate, and environmental conditions may erode the relationship between population density and habitat quality (Van Horne 1983). Results of the present study support this contention.

The high prey density relative to consumption by McCown's Longspurs (Wiens 1977b, Greer 1988) may prevent a need for territory size modification based on food resources; a minimal territory size may supply adequate resources for reproduction. Maclean and Seastedt (1979) concur that small territories may be sufficient for reproductive output in years of high food abundance. In addition, intraspecific competition for preferred habitat and consequent territory size reduction may not occur if all individuals are able to occupy suitable habitat. We also demonstrated the absence of a relationship between territory size of McCown's Longspurs and nesting outcome. No nests appeared to be unsuccessful because of starvation; again, predation was responsible for almost all failures.

Maclean and Seastedt (1979) discussed the function of territorial behavior in regions with high yearly variation in resource productivity. They suggested that this behavior was a mechanism for sustaining reproduction during years of low resource productivity, and small territories may suffice for reproduction in favorable years. This indeed may have been the case for McCown's Longspurs on the mixed-grass prairie during our brief period of study.

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