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THE HAZARDS OF NESTING NEAR SHRUBS FOR A GRASSLAND BIRD, THE McCOWN'S LONGSPUR[1]

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Abstract. Half of all nests of the McCown's Longspur (*Calcarius mccownii*) were depredated in the shortgrass prairie of northcentral Colorado, and almost all nesting failures in this species were attributable to predators, primarily the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). Nests placed beside shrubs were 2–3 times more likely to be depredated than nests associated with other types of vegetation. Half of all nests ($n = 28$) were associated with shrubs in a moderately grazed pasture, and 80% of these nests were eventually depredated. In contrast, most nests (57%, $n = 21$) were placed beside cactus in a heavily grazed pasture, which had little shrub cover. Of the 20% of nests placed beside shrubs in this pasture, however, 75% were depredated. Factor analysis of habitat variables measured at several scales around nests generated one factor that significantly explained variation in nest fate. This factor described shrub cover within 1 m of the nest and midgrass cover and degree of heterogeneity (continuity of the shortgrass matrix) at 2 m. Fine-scale (1 m) shrub cover was the most important determinant of predation risk. Nests that were depredated during incubation had six times more shrub cover within 1 m of the nest than nests depredated during the nestling period; successful nests had no measurable (≥5% total cover) shrub cover at this scale. The relationship between shrubs and an increased risk of nest predation is consistent with incidental predation by ground squirrels, which concentrate their activities beneath the cover afforded by shrubs.

Key words: Ground nests; hierarchical habitat analysis; nest microhabitat; nest predation; nest-site selection; shortgrass prairie.

INTRODUCTION

Ground-nesting passerines generally suffer high rates of nest predation, particularly in grassland systems (Martin 1988, 1993). A survey of 13 ground-nesting species in grassland/shrubsteppe habitats revealed that nearly half of all nests were depredated (Martin 1993). Nest predation obviously affects reproductive success, and thus avoidance of predation should be strongly selected for in these grassland bird species. As a consequence, features of the habitat that reduce the likelihood of nest predation should figure prominently in the selection of nest sites by grassland birds.

Our ability to characterize features of the nest microhabitat and subsequently ascribe significance to them presupposes that we are able to do so in a manner that is relevant to the species of interest; that is, that we are able to adopt a species-centered definition of habitat (Wiens 1989). Adopting species' perceptions of habitat structure is a challenge to implement, and necessitates a priori identification of habitat features that are expected to be important to the organism (e.g., availability of substrate used for nest placement) and assumes that such habitat classifications reflect scales across which habitat selection occurs (e.g., selection among habitat types within a landscape, selection of territory and nest site). One approach is to incorporate a nested hierarchy of scales in the design of a study, which facilitates the linkage of ecological patterns with underlying processes (Allen and Starr 1983, Mauer 1985, Wiens et al. 1987, Bergin 1992). This methodological approach is relevant to the hierarchical patch structure of natural systems (e.g., Kotliar and Wiens 1990), and may reflect the bird's hierarchical decision-making process in the selection of nesting habitat (Knopf and Sedgwick 1992, Kelly 1993).

The McCown's Longspur (*Calcarius mccownii*) is an endemic sparrow of the shortgrass prairie of North America (Mengel 1970). Nests

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of this species are generally placed beside vegetation or other structural features of this habitat (e.g., cattle dung pats), but nests appear exposed because they are not extensively concealed by vegetative cover (With 1994). Earlier research documented that nest microhabitat did not ameliorate climatic factors; vegetation at nest sites afforded little radiative cover (nests were shaded only 45% of daylight hours and were almost completely exposed during midday hours when solar intensity was at a maximum) and nests were not oriented with respect to associated vegetation to take advantage of wind breaks (With and Webb 1993). Consequently, avoidance of predation seemed a more important consequence of nest placement in this species, particularly given the high incidence (>50%) of nest predation reported for populations throughout its range (Felske 1971; Greer and Anderson 1989; With 1994). I therefore performed a hierarchical analysis of vegetation features across a range of spatial scales at nest sites to determine whether habitat affected the risk of nest predation.

METHODS

STUDY AREA

The Central Plains Experimental Range (CPER) is a Long-Term Ecological Research site that comprises about 6,300 ha of shortgrass steppe in the northwest corner of the Pawnee National Grassland in northcentral Colorado. The rolling topography has an average elevation of 1,650 m and the site receives about 300 mm of precipitation annually, the majority (85%) of which is received as rainfall from May through July (Milchunas and Lauenroth 1989). The CPER is divided into 130-ha pastures which have been subjected to various intensities and rotations of cattle grazing since 1939. For this study, I established a 10-ha plot (500 × 200 m; gridded at 25-m intervals) in each of two summer-grazed pastures that represented a range of shortgrass habitat used by breeding McCown's Longspurs. One pasture (26NW) was subjected to "moderate" grazing, in which 40% of annual above-ground net primary production (ANPP) was consumed by cattle. The second pasture (23E) was "heavily" grazed, with 60% of ANPP consumed by cattle annually. The shortgrass prairie is dominated by the native perennial grasses *Bouteloua gracilis* and *Buchloe dactyloides*. Embedded within this shortgrass matrix are cactus (primarily *Opuntia polyacantha*), midgrass species (e.g., *Aristida longiseta* and *Stipa comata*), shrubs (*Chrysothamnus nauseosus* and *Gutierrezia sarothrae*), and various forb species (Jameson 1969). Intense cattle grazing produces a more homogeneous habitat that is "lawn-like" in appearance and has little shrub or midgrass cover (Milchunas and Lauenroth 1989).

THE SPECIES

McCown's Longspurs arrive on their breeding grounds in the northwestern fringe of the Great Plains (northern Colorado, Wyoming, Montana and North Dakota) and the southern edge of the Canadian prairie provinces (Alberta and Saskatchewan) in April, where males establish discrete (nonoverlapping) territories about 1 ha in size (With 1994). The cup-shaped nest is built by the female within a depression she scrapes in the ground, and is usually placed next to vegetation or cattle dung pats (With and Webb 1993; With 1994). Longspurs place their nests beside a variety of available vegetation types within the habitat (Table 1). Clutch size ranges from two to four eggs; the average and modal clutch size is three eggs in northcentral Colorado (Table 2).

DATA COLLECTION

Assessment of nest fate. I located nests either during censuses conducted at least twice a week on each pasture from mid-April to early August, or incidental to other field work, in 1990 and 1991. Nests were found during censuses either by patient observation of the female's behavior, by searching the area near a song-perch or where a male made frequent aerial displays (commonly performed over the incubating female), or by flushing the female from the nest. I marked the location of the nest by driving a wood stake into the ground at least 1 m from the nest, and I monitored the status of the nest during subsequent censuses or incidental to other field work. Nests were not approached closer than 1 m and the contents were never touched. Given that a particular route was not followed during censuses or nest checks and that a large amount of activity related to field research occurred on each pasture, it is unlikely that my behavior, or that of my field assistants, could have cued potential predators to nest locations.

I found a total of 97 nests across both pastures during the two years of this study. The fate of

TABLE 1. Percentage and success rate (percentage of nests fledging at least one young) of nests associated with different vegetation types for McCown's Longspurs in two pastures subjected to different cattle-grazing intensities in northcentral Colorado.

	Moderately Grazed Pasture (n = 28 nests)		Heavily Grazed Pasture (n = 21 nests)		Total (n = 49 nests)	
Vegetation Type	Percent (n)	Success rate	Percent (n)	Success rate	Percent (n)	Success rate
Shortgrass	7.1 (2)	50.0	14.3 (3)	66.7	10.2 (5)	60.0
Cactus	14.3 (4)	50.0	57.1 (12)	41.7	32.7 (16)	43.7
Midgrass (>10 cm)	28.6 (8)	37.5	9.5 (2)	50.0	20.4 (10)	40.0
Shrub	50.0 (14)	21.4	19.0 (4)	25.0	36.7 (18)	22.2

80% of these nests (n = 78) was known and information on these nests was used to calculate the various summary statistics presented in this paper to describe predation rates and nesting success in this longspur population. Of nests that were eventually depredated, complete information as to the timing of predation was available for 49 nests (moderately grazed pasture: n = 28 nests; heavily grazed pasture: n = 21 nests). These nests thus served as the focus for this study.

Because the timing of predation may indicate the relative vulnerability of the nest site to predators, I noted whether predation occurred during incubation (first 12 days of nesting cycle) or whether predation occurred later in the nesting cycle during the nestling period when young are present in the nest (days 13–22, the 10 days following hatching before young leave the nest). Predators removed all of the nest contents, and thus it was possible to attribute a prematurely empty nest (i.e., before young could be expected to leave the nest) as a casualty of predation. Small mammals, such as thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), may not have been able to consume the entire contents of the nest at once, but I have observed them to make repeated trips to a nest until it was empty. Weather-related chilling of eggs and nestlings generally resulted in only partial clutch or brood losses; unhatched eggs were sometimes left in the nest, but weather-killed young were removed by the adults.

Measurement of nest microhabitat. I visually estimated the percent cover of various vegetation types (to the nearest 5%) at different scales for each nest site. The percent cover of shortgrass, cactus, midgrass (species such as *Aristida longiseta*; generally >10 cm in height), shrub and bareground was estimated within the area circumscribed by a fixed radius (1 m, 2 m, 4 m, and 8 m) emanating from the center of the nest. The structural simplicity of this habitat permitted the same variables to be assessed across all scales. I therefore did not have to identify different habitat variables at each scale that I expected to be important to the species in its selection of nest sites.

The spatial pattern of vegetation may be a more

TABLE 2. Measures of breeding success (mean ± SD) for McCown's Longspurs in two pastures subjected to different grazing intensities in northcentral Colorado. Successful nests are those fledging at least one young. Variable sample sizes reflect subset of total nests for which information was available to calculate parameter.

	Moderately Grazed Pasture		Heavily Grazed Pasture		Total	
Measure[a]	All nests	Successful nests	All nests	Successful nests	All nests	Successful nests
Clutch size	3.1 (0.64)	3.2 (0.69)	3.1 (0.64)	3.6 (0.52)	3.1 (0.64)	3.3 (0.65)
	n = 40	13	29	10	69	23
Hatching success (%)	60.2 (43.65)	95.5 (11.08)	78.0 (36.79)	94.2 (12.45)	67.5 (41.60)	94.9 (11.44)
	36	13	25	10	61	23
Fledging success (%)	62.1 (46.91)	93.8 (13.44)	48.8 (50.31)	97.5 (7.91)	56.6 (48.26)	95.2 (11.59)
	29	16	20	10	49	26
Reproductive success (%)	31.9 (42.86)	90.4 (15.16)	36.7 (46.58)	91.7 (13.61)	33.7 (44.03)	90.9 (14.19)
	40	13	25	10	65	23
Reproductive output	1.0 (1.35)	2.7 (0.79)	1.2 (1.66)	3.3 (0.65)	1.1 (1.47)	2.9 (0.78)
	46	16	29	11	75	27

[a] Hatching success = percentage of young hatched/eggs laid per nest; Fledging success = percentage of young fledged/young hatched per nest; Reproductive success = percentage of young fledged/eggs laid per nest; Reproductive output = number of young fledged per nest.

important determinant of the susceptibility of a nest to predation than absolute cover of vegetation (Bowman and Harris 1980, Joern and Jackson 1983). Continuity of vegetation cover (homogeneity) may afford better nest concealment (Joern and Jackson 1983), whereas heterogeneity at a broad scale (e.g., structural complexity of habitat) may disrupt search strategies of predators (e.g., by increasing search time, Bowman and Harris 1980) or diffuse predation risk by decreasing the probability that the nest will be encountered (Martin and Roper 1988). I therefore calculated an "index of homogeneity" (HI) at each scale, which measured the degree to which the shortgrass matrix was disrupted by other types of vegetation. This index was obtained by dividing the percent cover of shortgrass by the number of other vegetation types (1–5 types) that comprised at least 5% of the total cover at that scale. High values of HI were thus indicative of areas with near-uniform coverage of shortgrass (i.e., homogeneous). Although this index is not sensitive to the types of vegetation that disrupt the shortgrass matrix, it is useful for assessing the general spatial pattern of the habitat (homogeneous vs. heterogeneous).

To determine whether longspurs exhibited selective nest placement, I estimated vegetation cover at the scale extremes (1 m and 8 m) for 20 random points in the moderately grazed pasture for statistical comparisons with nest microhabitat. Random points were centered inside $6.25 \times 6.25\text{-m}^2$ cells ($39.1\ \text{m}^2$) produced by establishing a grid across the study area in each pasture. Points were chosen by randomly selecting cells from within the study grid.

DATA ANALYSIS

Effect of microhabitat on nest predation. Vegetation cover may be correlated across two or more scales (e.g., cactus cover at 4 m and 8 m exhibits a high correlation, but is uncorrelated with cactus cover at smaller scales), and may exhibit intercorrelations with certain other types of vegetation (e.g., HI is strongly correlated with midgrass cover at all scales). I therefore performed factor analysis, using a principal components solution for initial factor extraction, to elucidate the complex interrelationships among habitat features and scale and to reduce the dimensionality of habitat descriptors to a few, uncorrelated variables that were easy to interpret in this case. The number of factors retained for interpretation and subsequent analysis (see below) was determined by the number of principal components having eigenvalues >1.0. The varimax rotation method was used to facilitate the interpretation of factor loadings (Afifi and Clark 1984).

Factor analysis was initially performed on microhabitat data from all longspur nests ($n = 49$) in the two pastures. The cover of five vegetation types (shortgrass, cactus, midgrass, shrub, and bareground) was assessed at each of four scales (1 m, 2 m, 4 m, and 8 m). In addition, the degree of heterogeneity was quantified at each scale (homogeneity index, HI). Because cattle-grazing intensity affected HI and vegetation cover differentially within the two pastures, pasture was entered as a dummy variable into the factor analysis. Factors were subsequently interpreted by determining their loading scores on each of the 25 original habitat variables.

I examined whether factor variables could significantly explain nest fate (depredated during incubation, depredated during nestling period, or successful) using stepwise multiple regression analysis. Variables were retained in the regression model if $P < 0.05$ and $R^2 > 0.10$. Stepwise regression was first performed on the entire data set, and then for each pasture individually to determine whether different factor variables might explain nest fate in the two pastures.

Nest-site selection in longspurs. Factor analysis was similarly employed to reduce the dimensionality and multicollinearity of habitat variables describing nest sites ($n = 28$) and random points ($n = 20$) in the moderately grazed pasture. The cover of five vegetation types at two scales (1 m and 8 m) and the degree of heterogeneity at these scales provided the original 12 habitat variables entered into factor analysis. The resulting factor variables were used in stepwise multiple regression analysis to examine which factors significantly explained variation between nest sites and random points.

RESULTS

PREDATION EFFECTS ON NESTING SUCCESS

Predation on nest contents accounted for nearly all reproductive losses of McCown's Longspurs in this system. About half of all nests were depredated across both pastures (52.6%, $n = 78$ nests). Predators consumed the entire contents of nests, and thus partial losses were attributable to weather-related factors (e.g., chilling of one or more eggs or young because of prolonged cold, wet weather). Weather-related losses amounted to <10% of eggs laid, as indicated by the high rate of success for nests fledging at least one offspring (about 90% reproductive success for successful nests; Table 2). Thus, longspurs whose nests were not depredated enjoyed almost total reproductive success. Reproductive success (percentage of young fledged per eggs laid per nest) was similar in the two pastures, with about a third of nests successfully producing young (Table 2).

The primary nest predator in this system is most likely the thirteen-lined ground squirrel, which is diurnal and was observed depredating nests. Other known or likely predators include striped skunk (*Mephitis mephitis*), badger (*Taxidea taxus*), swift fox (*Vulpes velox*), coyote (*Canis latrans*), and perhaps deer mice (*Peromyscus maniculatus*), grasshopper mice (*Onychomys leucogaster*) and bull snakes (*Pituophis melanoleucus*). Predators took mainly nestlings in the heavily grazed pasture (70.6% of depredated nests, n = 30 nests), whereas equal numbers of eggs and nestlings were depredated in the moderately grazed pasture (n = 48 nests). Nestlings may have been the main fare in the heavily grazed pasture because of the coincidence between nesting chronology of longspurs on this pasture and the emergence of ground-squirrel litters. Longspurs in the heavily grazed pasture began nesting one week later than those in the moderately grazed pasture. Furthermore, longspurs nested synchronously on the heavily grazed pasture. A sharp peak in nest initiation (33% of all nests; n = 40) occurred in late May and again in late June (30%), such that only nestlings would have been available in July when juvenile ground squirrels emerged in late June and early July (Felske 1971). In contrast, nest initiation was continuous from mid May to late July in the moderately grazed pasture.

MICROHABITAT EFFECTS ON NEST PREDATION

Four out of five longspur nests associated with shrubs were depredated (Total Nests, Table 1). Nests placed beside shrubs were 2–3 times more likely to be depredated than nests associated with other cover types. Half of all nests in the moderately grazed pasture were placed beside shrubs, but longspurs primarily (57%) nested beside cactus in the heavily grazed pasture, perhaps owing to the paucity of shrub cover in this pasture. Nevertheless, longspurs that did nest beside shrubs in the heavily grazed pasture (19%) had the lowest success rate (25%) and their nests were about two times more likely to depredated than nests associated with other types of vegetation.

The first seven principal components met the criterion of eigenvalues >1 and together explained 86.6% of variance in nest microhabitat (Table 3). In stepwise regression analysis, only factor 7 significantly explained variation in nest fate ($F = 6.58$, $P = 0.013$, df = 1, 50, $R^2 = 0.116$). Factor 7 is a measure of fine-scale (1–2 m) heterogeneity at the nest site. It describes shrub cover in the immediate vicinity of the nest (1 m) and the degree of heterogeneity within 2 m of the nest. Midgrass cover enhances microhabitat heterogeneity, and thus is negatively correlated with HI ($r = -0.76$) and this factor in general. Shrub cover at 1 m is completely uncorrelated with midgrass cover ($r = 0.01$) and with heterogeneity ($r = -0.18$) at 2 m.

If the habitat variables comprising this factor are examined individually, the most striking result is that the amount of shrub cover within 1 m of the nest significantly affected whether and when a nest was depredated (Fig. 1). This finding is only relevant for nests in the moderately grazed

TABLE 3. Interpretation of factors resulting from the analysis of habitat variables across a range of scales (1, 2, 4, and 8 m) at nests (n = 49) of the McCown's Longspur in northcentral Colorado.

Factors	Description[a]	Percent of total variance	Percent cumulative variance
1	Pasture type, midgrass cover 2–8 m, -HI 2–8 m	22.7	22.7
2	shortgrass/-bareground matrix 1–2 m, shortgrass cover 4 m	21.7	44.4
3	shrub cover 2–8 m	14.2	58.6
4	shortgrass/bareground/cactus matrix 8 m, -bareground cover 4 m	13.5	72.1
5	HI 1 m, -cactus cover 1 m, -midgrass cover 1 m	11.0	83.1
6	cactus cover 2–4 m	11.0	94.1
7	HI 2 m, shrub cover 1 m, -midgrass cover 2 m	6.0	100.1

[a] Pasture type refers to grazing intensity (moderately grazed versus heavily grazed); HI = index of homogeneity, a measure of the degree to which the shortgrass matrix is disrupted by other types of vegetation (≥5% total cover).

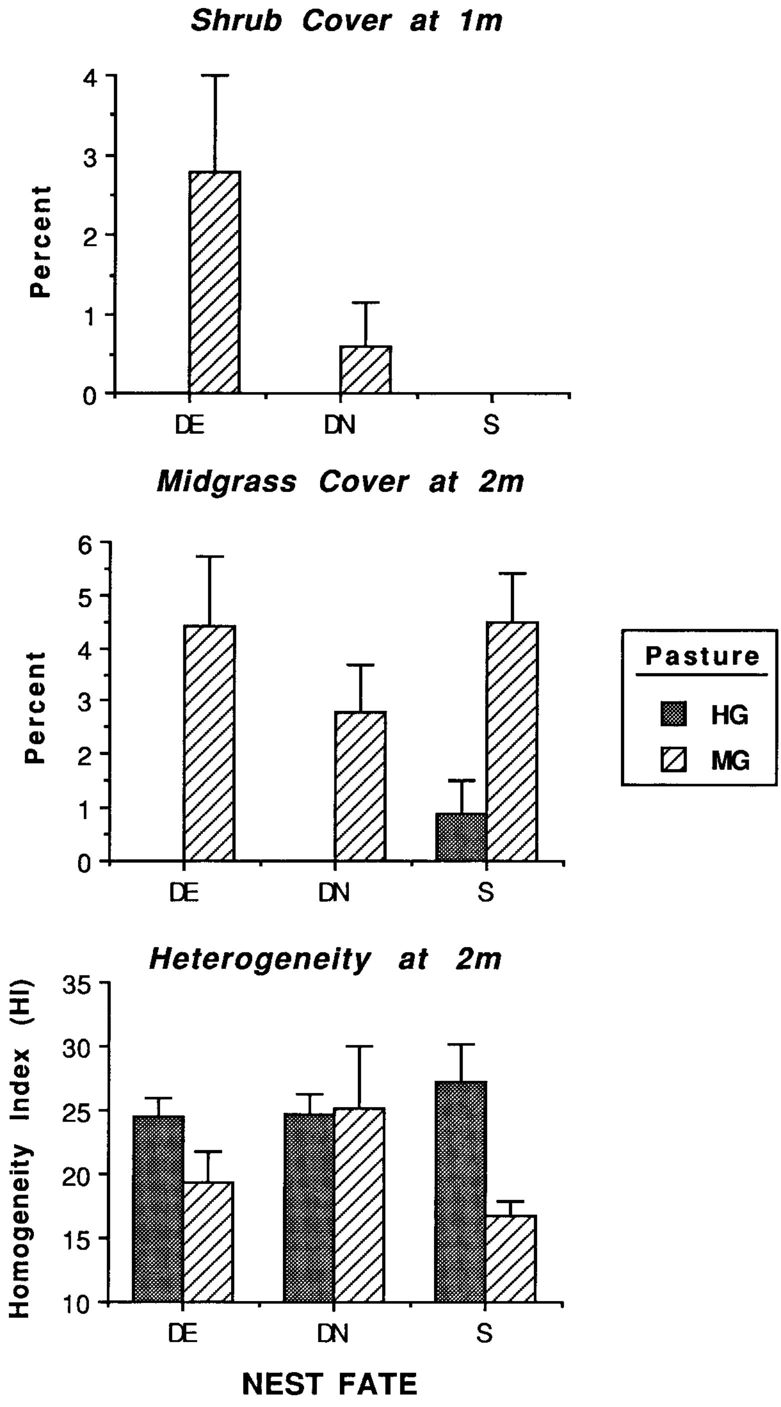

FIGURE 1. Comparison ($\bar{x}$ ± SE) of habitat variables correlated with factor 7, the habitat factor that significantly affected nesting success (DE = depredated during egg stage, DN = depredated during nestling period, and S = successful) of the McCown's Longspur in two pastures subjected to different grazing intensities in northcentral Colorado. The heavily grazed pasture (HG, n = 21 nests) was more homogeneous and structurally more simple in appearance than the moderately grazed pasture (MG, n = 28 nests).

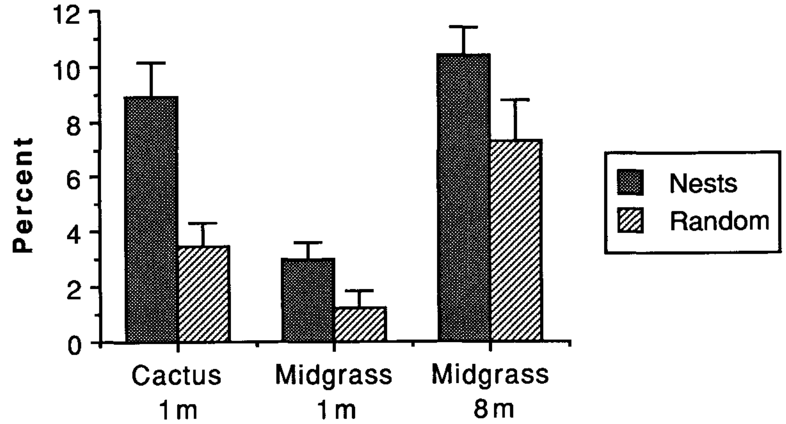

FIGURE 2. Nest-site selection by McCown's Longspurs in a moderately grazed pasture at the Central Plains Experimental Range in northcentral Colorado. Comparison ($\bar{x}$ ± SE) between nest microhabitat ($n = 28$) and random points ($n = 20$) for habitat variables that had the highest correlation with factor 2, the habitat factor generated by factor analysis that differed significantly between nest sites and random points within this pasture.

pasture, however, because nest microhabitat in the heavily grazed pasture contained no measurable (≥5%) shrub cover. Shrubs were present in low abundance and were occasionally used as nest cover in the heavily grazed pasture, however, although 75% of these nests were eventually depredated (Table 1).

Nests on the moderately grazed pasture that were depredated during incubation contained six times more shrub cover in the immediate vicinity (1 m) than nests depredated during the nestling period. Successful nests had no measurable small-scale shrub cover. Even so, some of these successful nests were placed beside an isolated, small shrub (20%, Moderately Grazed Pasture; Table 1). This demonstrates that nest predation possesses a stochastic element and that the microhabitat "patch" in which the nest is placed (1-m radius) may affect the susceptibility of the nest to predation.

It is less clear what effect midgrass cover and heterogeneity at 2 m had on nest fate in either pasture (Fig. 1). Neither of these habitat variables differed significantly among nest fates in either of the two pastures (all $P > 0.05$, MG: df = 2, 25; HG: df = 2, 21; ANOVA). The presence of shrubs in the immediate vicinity of the nest would thus appear to be the most important determinant of predation risk on nests, although again this is only applicable for birds nesting in the moderately grazed pasture. This is borne out when stepwise regression analysis is performed separately on nests from the two pastures. Factor 7 was the only significant descriptor of nest fate in the moderately grazed pasture ($F = 4.74$, df = 1, 26, $P = 0.0388$, $R^2 = 0.154$), but no factor could significantly predict nest fate in the heavily grazed pasture.

NEST-SITE SELECTION IN THE MODERATELY GRAZED PASTURE

The first four principal components met the criterion for factor extraction (eigenvalue > 1.0) and together explained 75.5% of the total variance in microhabitat of nest sites and random points. The second factor differed significantly among nest fates and random points ($F = 4.17$, df = 3, 43, $P = 0.01$) and was comprised of cactus cover at 1 m and midgrass cover at both scale extremes (1 m and 8 m). Nest microhabitat contained significantly more cactus ($F = 9.34$, df = 1, 46, $P = 0.004$) and midgrass cover (1 m: $F = 5.87$, $P = 0.019$; 8 m: $F = 6.51$, $P = 0.014$) than random points (Fig. 2). This implies that longspurs may be selecting sites that afford more cover and are more heterogeneous than the general habitat matrix of this pasture.

DISCUSSION

Predation of nest contents accounted for nearly all nesting failures of McCown's Longspurs in this grassland system. At least half of all nests were eventually depredated, which is consistent with predation rates reported for longspur populations in Wyoming (51%, Greer and Anderson 1989) and Saskatchewan (49–53%, Felske 1971), and for other ground-nesting passerines in grassland habitats (Martin 1993). Longspurs are faced with an "all-or-nothing" scenario; those individuals whose nests were not depredated enjoyed essentially complete reproductive success (Table 2). Avoidance of predation through selective nest placement would thus appear to be a potentially profitable strategy to enhance reproductive success.

Whether or not selective nest placement is an effective deterrent to predation depends upon the types of predators in the system (Martin 1987, Miller and Knight 1993), and the pattern and intensity of predation (Roseberry and Klimstra 1970, Angelstam 1986, Rotenberry and Wiens 1989, Vickery et al. 1992, Morton et al. 1993). The shortgrass prairie supports a host of generalist predators, but the primary nest predator appeared to be the thirteen-lined ground squirrel. This was certainly the most numerous of potential nest predators in this system; densities were reported to be similar in moderately and heavily grazed pastures at the CPER, ranging from 6.4 to 13.9 adults/ha during two years of study (Flake 1971). Ground squirrels are diurnal and are visually oriented foragers (Murray and Vestal 1979). Ground squirrels are not specialists on bird nests, but presumably encounter them by chance while foraging or incidental to other activities (e.g., Bridgwater 1966). This adds an element of stochasticity to the pattern of nest predation, which may render selective nest placement a less-effective anti-predation strategy than if predation were directed specifically at nests (Vickery et al. 1992).

Nevertheless, nest placement in McCown's Longspurs reflects a general predator-avoidance strategy. Longspurs generally place nests beside some type of vegetation: a clump of grass, a cactus pad, or beneath a shrub. This associated vegetation affords limited cover, and does not provide much shade or protection from ambient winds (With and Webb 1993). Placement of the nest beside some natural feature of the habitat may nevertheless serve as vertical screening or provide a disruptive effect that helps to conceal the nest and incubating female from predators (e.g., Schieck and Hannon 1993). The association of nests of Mountain Plovers (*Charadrius montanus*) with cattle dung pats at the CPER was interpreted in this context (Graul 1975). Nest concealment is only expected to be effective if visually oriented predators, such as ground squirrels or birds, are the primary concern (Reitsma et al. 1990, Clark and Nudds 1991, Holway 1991, Colwell 1992). In addition, longspurs placed nests beside a variety of vegetation types, apparently according to availability within the habitat (Table 1; With 1994); for example, in the moderately grazed pasture which was structurally more complex than the heavily grazed one, nearly three times as many nests were placed beside midgrass and shrubs as in the heavily grazed pasture (Table 1). The association of nests with a variety of vegetation types within a habitat may enhance nesting success by interfering with search patterns of predators (e.g., Storaas and Wegge 1987), or may prevent the formation of specific search images where a number of generalist predators are involved, as in this system.

The nests most susceptible to predation, however, were those associated with shrubs. In either pasture, almost all nests placed beside shrubs were depredated, and were about two times more likely to be depredated than nests associated with other cover types. The answer to the question of which nests were most susceptible to predation is complicated by the habitat context in which the bird breeds. Intense grazing reduced the structural complexity of the habitat, producing a more uniform or homogeneous landscape. Across all scales, nest microhabitat on the moderately grazed pasture was characterized by greater coverage of midgrass and shrubs. Nests that were successful in producing young had no measurable shrub cover (i.e., ≥5% total cover) within 1 m of the nest, but those depredated early in the nesting cycle (during incubation) had six times more shrub cover than nests depredated later (during the nestling period). Given that nest microhabitat on the heavily grazed pasture contained no measurable shrub cover, the finding of increased predation risk with fine-scale shrub cover (within 1-m radius of nests) is thus relevant only for nests on the moderately grazed pasture.

Why do shrubs increase the vulnerability of nests to predators? Thirteen-lined ground squirrels locate their burrow entrances near habitat features that provide substantial vertical cover, presumably to afford protection from aerial predators (Murray and Vestal 1979, Kaufman and Kaufman 1989). In the shortgrass prairie, vertical cover is provided primarily by shrubs. Shrubs additionally provide refuge while foraging, as has been noted for other quadrupedal rodents (e.g., Kotler 1984). Nests associated with shrubs are at higher risk of incidental predation by ground squirrels because squirrel activity is concentrated near shrubs. To further illustrate this point, nests of the Lark Bunting (*Calamospiza melanocorys*), a species that overlaps with the McCown's Longspur in breeding habitat, suffer greater rates of predation (about 75% of all nests) than those of longspurs, even in the same pasture (pers. observ.). Buntings prefer extensive nest cover (Pleszczynska 1978, With and Webb 1993); subsequently, nests are placed beneath either midgrass species (e.g., *Aristida*) or shrubs in this system (Creighton 1971, Creighton and Baldwin 1974), microhabitats which are expected to afford the highest risk of nest predation from thirteen-lined ground squirrels.

Nest-site selection may be viewed as a hierarchical process in which the bird focuses on particular habitat features at different scales. At the finest scale, in terms of where the nest is actually situated, longspurs prefer shrubs and half of all nests in a shrubby habitat (the moderately grazed pasture) were placed beneath shrubs. Placement of nests beside objects may generally be effective in minimizing predation risk by visually oriented predators, such as ground squirrels. This preference for disruptive nest cover is counterproductive in shrubby habitats, however. While shrubs are preferentially used by longspurs for actual nest concealment in these habitats, shrubs also harbor the most abundant nest predator in this system. Thus, nests placed beside shrubs had the greatest predation risk. In addition, nests that were placed in areas with fine-scale shrub cover (within 1 m of nest) were likely to be depredated. Longspurs appeared to be indifferent to shrub cover at this (1 m) and other scales, however, because shrub cover at nest sites did not differ significantly from random points. Fine-scale shrub cover is not correlated with any other vegetation type, nor is it correlated with shrub cover at larger scales (all $r < 0.5$). Thus, shrubs appear to be a random feature of the habitat that is preferentially utilized for nest concealment (i.e., longspurs like to nest beneath shrubs), but is not associated with the vegetation cues (e.g., areas of midgrass cover and fine-scale cactus cover) that longspurs appear to be using in their selection of the general nest site.

The habitat context in which a bird breeds is the first "decision level" in the process of nest-site selection, and which dictates the suite of predators and intensity of predation to which a nesting pair will be subjected. The McCown's Longspur is not a bird of the shrubsteppe, but is indigenous to native shortgrass prairie which historically was subjected to intense grazing over a broad scale from herbivores such as bison (*Bison bison*) and prairie dogs (*Cynomys* sp.) and to rampant wildfires (Knopf, in press). The shortgrass prairie has become a mosaic of pastures subjected to different cattle grazing intensities and fragmented by agricultural fields and areas of human development. Heavily grazed pastures therefore may best approximate the natural stature of the historical shortgrass prairie in which longspurs evolved. Nests associated with common features (e.g., cactus) in these highly disturbed habitats had the lowest rate of predation (about 40%). Areas of less-intense grazing may provide a "shrubbier" habitat in which longspurs have not evolved nest-placement strategies to reduce nest predation. Anti-predation strategies that are successful in one type of habitat may thus be ineffective in another (e.g., Rotenberry and Wiens 1989).

Nevertheless, if nests associated with shrubs typically are depredated, why don't longspurs avoid this type of cover? What are the costs associated with such imprudent choices in nest placement? While the hazards of nesting near shrubs are clear, ultimately this may have little impact on individual fitness. Longspurs attempt multiple nests per breeding season and subsequent nests may be located beneath some other cover type that affords less predation risk. McCown's Longspurs probably do not exhibit a high degree of site fidelity between years, or at least females, which are responsible for selecting the nest site, may not (With 1994). Given the mosaic nature of the modern grassland landscape, individuals may nest in different pastures during their lifetime, which would preclude the formation of nest-placement strategies that are successful only in a given habitat (e.g., avoidance of shrub cover in moderately grazed pastures). Lifetime reproductive success may not be affected and therefore the costs of occasionally nesting near shrubs would be minimal. Because of individual variability in nest placement, population output as a whole apparently is not affected either (e.g., reproductive success for populations in the two pastures was similar, Table 2). Nevertheless, assessment of how nesting strategies translate among different habitats and whether this affects reproductive output for different populations may offer important insights into the management of other species in fragmented, human-modified habitats.

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LITERATURE CITED

AFIFI, A. A., AND V. CLARK. 1984. Computer-aided multivariate analysis. Lifetime Learning Publications, Belmont, CA.

ALLEN, T.F.H., AND T. B. STARR. 1983. Hierarchy: perspectives for ecological complexity. Univ. of Chicago Press, Chicago.

ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47:365–373.

BERGIN, T. M. 1992. Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. Condor 94:903–911.

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest depredation. J. Wild. Manage. 44:806–813.

BRIDGWATER, D. D. 1966. Predation by *Citellus tridecemlineatus* on other vertebrates. J. Mammal. 47:345–346.

CLARK, R. G., AND T. D. NUDDS. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. Wildl. Soc. Bull. 19:534–543.

COLWELL, M. A. 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. Condor 94:767–772.

CREIGHTON, P. D. 1971. Nesting of the Lark Bunting in north-central Colorado. Grassland Biome, U.S. International Biological Program Technical Report No. 68, Fort Collins, CO.

CREIGHTON, P. D., AND P. H. BALDWIN. 1974. Habitat exploitation by an avian ground-foraging guild. Grassland Biome, U.S. International Biological Program Technical Report No. 263, Fort Collins, CO.

FELSKE B. E. 1971. The population dynamics and productivity of McCown's Longspur at Matador, Saskatchewan. M.Sc.thesis, Univ. of Saskatchewan, Saskatoon, Canada.

FLAKE, L. D. 1971. An ecological study of rodents in a short-grass prairie of northeastern Colorado. Grassland Biome, U.S. International Biological Program Technical Report No. 100, Fort Collins, CO.

GRAUL, W. D. 1975. Breeding biology of the Mountain Plover. Wilson Bull. 87:6–31.

GREER, R. D., AND S. H. ANDERSON. 1989. Relationships between population demography of McCown's Longspurs and habitat resources. Condor 91:609–619.

HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. Condor 93:575–581.

JAMESON, D. A. [ED.]. 1969. General description of the Pawnee site. Grassland Biome, U.S. International Biological Program Technical Report No. 1, Fort Collins, CO.

JOERN, W. T., AND J. F. JACKSON. 1983. Homogeneity of vegetational cover around the nest and avoidance of nest predation in mockingbirds. Auk 100: 497–499.

KAUFMAN, D. W., AND G. A. KAUFMAN. 1989. Burrow distribution of the thirteen-lined ground squirrel in grazed mixed-grass prairie: effect of artificial habitat structure. Prairie Nat. 21:81–83.

KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodlands. Condor 95:83–93.

KNOPF, F. L. In press. Avian assemblages on altered grasslands. Stud. Avian Biol.

KNOPF, F. L., AND J. A. SEDGWICK. 1992. An experimental study of nest-site selection by Yellow Warblers. Condor 94:734–742.

KOTLER, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65: 689–701.

KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor 89:925–928.

MARTIN, T. E. 1988. Nest placement: implications for selected life-history traits, with special reference to clutch size. Am. Nat. 132:900–910.

MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. Am. Nat. 141:897–913.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest site selection in a western population of the hermit thrush. Condor 90:51–57.

MAUER, B. A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecol. Monogr. 55:295–315.

MENGEL, R. M. 1970. The North American Central Plains as an isolating agent in bird speciation, p. 280–340. *In* W. Dort and J. K. Jones [eds.], Pleistocene and recent environments of the central Great Plains. Univ. of Kansas Press, Lawrence, KS.

Milchunas, D. G., and W. K. Lauenroth. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82–86.

Miller, C. K., and Knight, R. L. 1993. Does predator assemblage affect reproductive success in songbirds? Condor 95:712–715.

Morton, M. L., K. W. Sockman, and L. E. Peterson. 1993. Nest predation in the mountain White-crowned Sparrow. Condor 95:72–82.

Murray, G. B., and B. M. Vestal. 1979. Effects of environmental structure on the burrow distribution of thirteen-lined ground squirrels, *Spermophilus tridecemlineatus* (Sciuridae). Southwest. Nat. 24:79–86.

Pleszczynska, W. K. 1978. Microgeographic prediction of polygyny in the Lark Bunting. Science 201:935–937.

Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus,* and eastern chipmunks, *Tamias striatus,* on nest predation in a northern hardwood forest: an artificial nest experiment. Oikos 57:375–380.

Roseberry, J. L., and W. D. Klimstra. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bull. 82:243–267.

Rotenberry, J. T., and J. A. Wiens. 1989. Reproductive biology of shrubsteppe passerine birds: geographical and temporal variation in clutch size, brood size, and fledging success. Condor 91:1–14.

Schieck, J. O., and S. J. Hannon. 1993. Clutch predation, cover, and the overdispersion of nests of the Willow Ptarmigan. Ecology 74:743–750.

Storaas, T., and P. Wegge. 1987. Nesting habitats and nest predation in sympatric populations of Capercaillie and Black Grouse. J. Wild. Manage. 51:167–172.

Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecol. 3:385–397.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147.

With, K. A. 1994. McCown's Longspur, p. 1–24. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], The birds of North America, No. 96. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, DC.

With, K. A., and D. R. Webb. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. Condor 95:401–413.