

DOES HABITAT FRAGMENTATION INFLUENCE NEST PREDATION IN THE SHORTGRASS PRAIRIE?

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Abstract. We examined the effects of habitat fragmentation and vegetation structure of shortgrass prairie and Conservation Reserve Program (CRP) lands on predation rates of artificial and natural nests in northeastern Colorado. The CRP provides federal payments to landowners to take highly erodible cropland out of agricultural production. In our study area, CRP lands have been reseeded primarily with non-native grasses, and this vegetation is taller than native shortgrass prairie. We measured three indices of habitat fragmentation (patch size, degree of matrix fragmentation, and distance from edge), none of which influenced mortality rates of artificial or natural nests. Vegetation structure did influence predation rates of artificial nests; daily mortality decreased significantly with increasing vegetation height. Vegetation structure did not influence predation rates of natural nests. CRP lands and shortgrass sites did not differ with respect to mortality rates of artificial nests. Our study area is only moderately fragmented; 62% of the study area is occupied by native grassland. We conclude that the extent of habitat fragmentation in our study area does not result in increased predation in remaining patches of shortgrass prairie habitat.

Key words: *artificial nests, Conservation Reserve Program, habitat fragmentation, habitat structure, nest mortality, predation, shortgrass prairie.*

¿La Fragmentación de Hábitat Influencia la Depredación de Nidos en Praderas de Pasto Corto?

Resumen. Examinamos los efectos de fragmentación de hábitat y estructura de la vegetación sobre la tasa de depredación de nidos artificiales y naturales en praderas de pasto corto y tierras del Programa de Reserva de Conservación (CRP) en el noreste de Colorado. El CRP proporciona pagos federales para que los dueños de las tierras retiren sus cultivos de áreas agrícolas altamente erosionables. En nuestra área de estudio, las tierras de CRP han sido vueltas a sembrar principalmente con céspedes no nativos que son más altos que la vegetación nativa de las praderas de pasto corto. Medimos tres índices de fragmentación de hábitat (tamaño del parche, grado de fragmentación de la matriz, y distancia al borde), ninguno de los cuales influyó sobre la tasa de mortalidad de nidos artificiales o naturales. La estructura de la vegetación influyó la tasa de depredación de nidos artificiales: la mortalidad diaria disminuyó significativamente con incrementos en la altura de la vegetación. La estructura de la vegetación no influyó la tasa de depredación de nidos naturales. Los sitios de CRP y de pastos cortos no difirieron con respecto a la tasa de mortalidad de nidos artificiales. Nuestra área de estudio es sólo moderadamente fragmentada pues el 62% del área es ocupada por prado nativo. Concluimos que el grado de fragmentación de hábitat en nuestra área del estudio no causa aumentos en la depredación en los parches de hábitat remanentes.

INTRODUCTION

Habitat fragmentation may lower reproductive success by exposing birds in remaining habitat to higher levels of predation than those in unfragmented areas (Paton 1994, Wiens 1994). In-

creased rates of predation in small patches and near habitat edges have been documented in a variety of habitats, although most research has focused on birds in forest communities (Andrén and Angelstam 1988, Paton 1994, Keyser et al. 1998). Grassland communities may respond to fragmentation in ways unlike forest communities because of differences in species composition, predator communities, vegetation structure, and scales of disturbance.

The influence of fragmentation on predation rates of grassland birds has been investigated

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more often in tallgrass and midgrass prairies (Johnson and Temple 1990, Pasitschniak-Arts et al. 1998, Winter and Faaborg 1999) than in shortgrass (Clawson and Rotella 1998). Shortgrass is the least disturbed of the three prairie types in North America with 30% to 70% remaining unplowed (Central Shortgrass Prairie Ecoregional Planning Team 1998). Populations of grassland birds, including endemics of the shortgrass prairie, have declined dramatically in recent years (Herkert and Knopf 1998, Peterjohn and Sauer 1999). The loss of native grassland habitats has undoubtedly played a role in these declines, yet the influence of habitat fragmentation is not clear.

Some environmentally sensitive croplands have been replanted to grassland under the Conservation Reserve Program (CRP), which provides subsidies for farmers to reseed highly erodible agricultural fields with grasses or shrubs. CRP lands provide suitable nesting habitat for grassland birds in midgrass and tallgrass ecosystems (Johnson and Schwartz 1993). CRP lands in the shortgrass prairie, however, are often seeded with non-native grass species, so the vegetation is taller in CRP lands than in native shortgrass. As a result, bird and mammal species composition often differs between native shortgrass and CRP.

The objectives of this study were (1) to determine the influence of habitat fragmentation (patch size, matrix fragmentation, and distance from edge) on nest mortality of grassland birds, and (2) to determine the influence of vegetation structure (as measured by vegetation height and cover) of shortgrass and CRP lands on nest mortality of grassland birds. We examined nest mortality using both artificial and natural nests.

METHODS

STUDY AREA

Characterized by a semiarid climate, shortgrass prairie is dominated by xeric grasses such as buffalograss (*Buchloë dactyloides*) and blue grama (*Bouteloua gracilis*). Our study was conducted within a 21 600-km² area (40–41°N, 103–105°W) in Weld, Logan, and Morgan counties, Colorado. Land uses in our study area include shortgrass range (62%), crops (irrigated crops and non-irrigated wheat production in a 2-year rotation system; 29%), and CRP fields (8%; Maxwell 1996).

Common breeding birds in the study area include Lark Buntings (*Calamospiza melanocorys*), Horned Larks (*Eremophila alpestris*), McCown's Longspurs (*Calcarius mccowni*), Chestnut-collared Longspurs (*Calcarius ornatus*), Western Meadowlarks (*Sturnella neglecta*), and Grasshopper Sparrows (*Ammodramus savannarum*). Thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), deer mice (*Peromyscus maniculatus*), and swift fox (*Vulpes velox*) are the primary nest predators (Skagen et al. 1999).

SITE SELECTION

Study sites were selected randomly using satellite imagery with identified land-use types provided by the Colorado Division of Wildlife. Land sections (1 mi², equivalent to 259 ha) were the initial units of selection; grassland and CRP habitats within selected sections were designated as study sites. Because grassland patches smaller than 64.7 ha (one quarter-section) comprise less than 0.6% of the landscape (Howard 2000), we set our minimum patch size at 64.7 ha. The upper limit for patch size was truncated at 2331 ha. Matrix habitat is the mosaic of contrasting habitat types that surround each patch of grassland (Wiens 1994). The percentage of matrix intact was calculated for each site as the percentage of nine land sections (including the selected section and all adjacent sections; 2331 ha) that was intact grassland. Other land uses included occupied homes, feed lots, crops, and CRP fields. We obtained permission from public agencies and private landowners for access to 46 sites (35 shortgrass and 11 CRP) of 150 selected sites.

ARTIFICIAL AND NATURAL NESTS

We conducted an artificial nest study between 25 May and 16 July 1998. In each site, we established two parallel 800-m transect lines 400 m apart. A maximum of fourteen artificial nests (range 10–14) were placed at 100-m intervals at a random distance between 10 and 190 m from the transect line. While wearing rubber gloves to reduce human scent, we mimicked nests of Lark Buntings by creating a round depression in the litter and placing two fresh Japanese Quail (*Coturnix japonica*) and one clay egg made from Plastilina brand soft modeling compound in each nest. Quail eggs were used to mimic the food reward that pro-

tential nest predators would obtain for depredated a nest, whereas clay eggs were used to measure the activity of smaller predators unable to break a quail egg (Bayne and Hobson 1999, DeGraaf et al. 1999). We checked and removed artificial nests after 4 or 6 days. Nests were considered depredated if eggs were removed from the nest, had bite or scratch marks, or were partially or completely consumed. At the end of each trial, we quantified vegetation structure at alternating nests at each site. Maximum vegetation height was measured at 1 m and 5 m from the nest in the four cardinal directions, and percent vegetative cover was estimated visually (in 5% increments) within a 5-m radius circle around the nest. Natural nests were located by dragging a rope between 2 observers 25 m apart on the day artificial nests were established; search effort typically covered 8.4 ha. We marked the location of all active nests and recorded the status of each natural nest on the day artificial nests were removed.

STATISTICAL ANALYSES

Mean daily mortality rates and standard errors for each site were calculated using Mayfield's (1961) method as adapted by Johnson (1979). Independent variables were either site level (patch size and percent of matrix intact) or nest level (vegetation structure variables and distance from edges, including borders with roads, other land use types, and human settlements). Vegetation structure variables included vegetation height (average of maximum vegetation heights measured around the nest), and percent vegetation cover in the 5-m radius circle surrounding the nest. We calculated means by site for nest level variables so that each site had only one value for each independent variable. We modeled daily mortality as a function of each independent variable separately via weighted linear regression. We transformed daily mortality using an arcsine transformation ($y^* = \sin^{-1}y^{0.5}$). Weights consisted of the inverse of the variance for each site's estimate of daily mortality. To evaluate whether to pool shortgrass and CRP sites in these analyses, we compared daily mortality rates by land-use type (shortgrass or CRP) with two-tailed t -tests assuming unequal variances. We compared vegetation variables be-

tween land-use types with two-tailed t -tests assuming unequal variances.

We paired each natural nest with the nearest artificial nest to compare percent daily mortality rates between the two nest types using the two-population test for equality (Hensler and Nichols 1981). We conducted the same transformed, weighted linear regression analyses on natural nests that was described above for artificial nests. However, because Johnson's (1979) method does not include a variance estimate when mortality is zero, we used Hensler and Nichols's (1981) method to obtain the daily mortality and variance estimates used in the regression. We used natural nests of all species during laying and incubation stages for these analyses. Data were analyzed with SAS (1990). Means \pm SE are reported unless otherwise specified. $P < 0.05$ indicates statistical significance.

RESULTS

We placed 546 artificial nests on 46 sites. Mayfield daily mortality rates averaged 0.123 ± 0.008 , and ranged from 0.017 ± 0.017 to 0.476 ± 0.109 for each site. We found 50 natural nests in the laying and incubation stages at 30 sites. Species included Lark Buntings ($n = 36$), Mourning Doves (*Zenaida macroura*; $n = 8$), Horned Larks ($n = 4$), Western Meadowlark ($n = 1$) and Mallard (*Anas platyrhynchos*; $n = 1$). Daily mortality rates due to depredation of the Lark Bunting nests (0.091 ± 0.031) were lower but not significantly different than daily mortality rates of the nearest artificial nests (0.130 ± 0.035 , $z = 0.1$, $P > 0.4$); daily mortality rates of all 50 natural nests (0.076 ± 0.021) were significantly lower than those of the nearest artificial nests (0.145 ± 0.028 ; $z = 2.0$, $P < 0.03$). Mean daily mortality rates of artificial nests for CRP and shortgrass were 0.113 ± 0.015 and 0.126 ± 0.009 , respectively. Land use (shortgrass or CRP) had no significant effect on mortality rates of artificial nests ($t_{12} = 0.3$, $P = 0.4$) nor of all natural nests ($t_{12} = 0.1$, $P = 0.9$); we therefore used both land use types in the following analyses.

FRAGMENTATION

Patch sizes ranged from 129 ha to 2331 ha (Fig. 1a) and did not influence mortality rates of artificial nests ($t_{44} = 1.0$, $P = 0.3$), nor of natural nests ($t_{28} = -0.6$, $P = 0.6$). Percent of matrix intact in the 9 sections (2331 ha) of surrounding

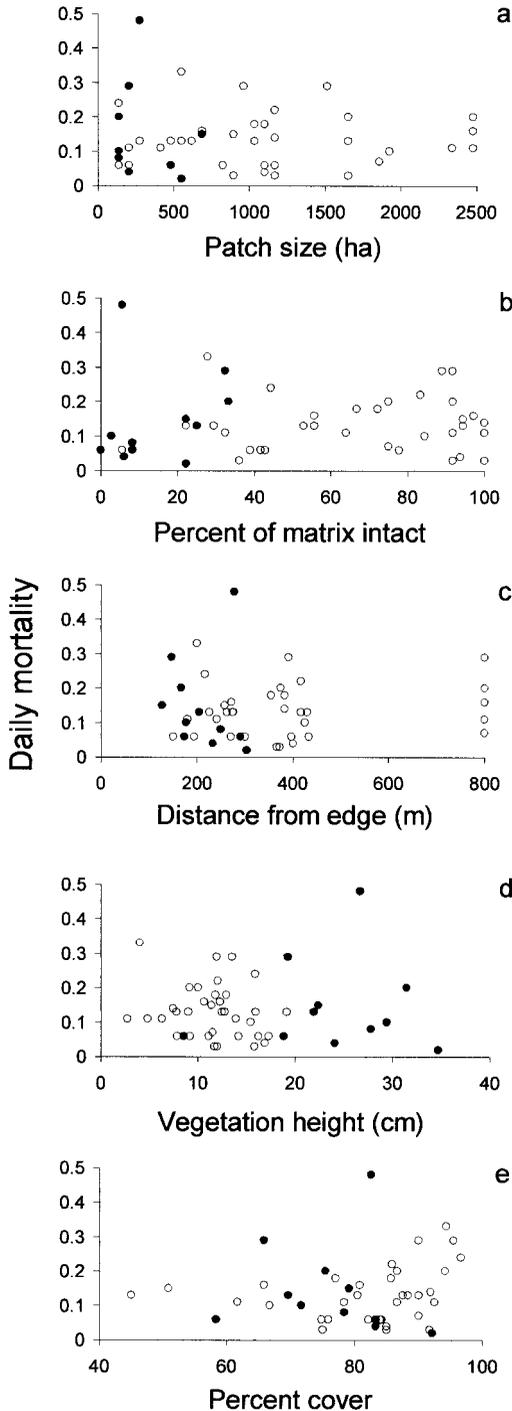


FIGURE 1. Relationship between daily nest mortality in artificial nests and (a) patch size, (b) percent matrix intact, (c) mean distance from edge, (d) maximum vegetation height, and (e) percent cover by site for 46 sites in northeastern Colorado. Conservation Reserve Program (CRP) sites are designated by solid circles and shortgrass prairie sites by unfilled circles.

landscape ranged from 0% to 100% (54 ± 5 , Fig. 1b) and did not affect daily mortality rates of artificial nests ($t_{44} = 1.4$, $P = 0.2$) nor of natural nests ($t_{28} = -0.7$, $P = 0.5$). Distance from edge of individual artificial nests ranged from 5 m to >800 m; Figure 1c depicts site averages. Distances of natural nests from the edge were not measured. Mortality rate was not significantly affected by distance from edge for artificial nests ($t_{44} = 0.9$, $P = 0.4$).

VEGETATION STRUCTURE

Vegetation height varied widely across sites (range 2.7–34.7 cm, mean 14.6 ± 1.1 cm, Fig. 1d) and was taller in CRP sites than in shortgrass sites (24.1 ± 2.2 cm and 11.6 ± 0.7 cm, respectively; $t_{12} = 5.5$, $P < 0.001$). Daily mortality of artificial nests decreased significantly with increasing vegetation height ($t_{44} = -3.2$, $P = 0.002$). Natural nest mortality was unrelated to vegetation height ($t_{28} = 0.1$, $P = 0.95$). Percent vegetation cover within sites ranged from 45% to 97% ($81 \pm 2\%$; Fig. 1e) and was not different in CRP and shortgrass sites ($76 \pm 3\%$ and $82 \pm 2\%$ for CRP and shortgrass, respectively, $t_{21} = -1.6$, $P = 0.13$). Percent vegetation cover did not affect mortality of artificial nests ($t_{44} = -1.3$, $P = 0.2$) nor of natural nests ($t_{28} = -1.4$, $P = 0.2$).

DISCUSSION

HABITAT FRAGMENTATION

In our study, mortality rates of natural and artificial nests did not vary with patch size or degree of matrix fragmentation. The shortgrass prairie in our study area is relatively intact, comprising 62% of the landscape, and minimum patch sizes are large compared with other ecosystems in North America. Moderate habitat fragmentation is defined as 45–55% habitat retention (Donovan et al. 1997). Patch-size influences on predation rates of grassland birds vary depending on species and habitat (Clawson and Rotella 1998, Winter and Faaborg 1999). Further, there may be a threshold size below which predation rates are affected. Grassland studies that have reported significant negative relationships between patch size and artificial or natural nest predation rates incorporated minimum patch sizes of 2 to 31 ha (Johnson and Temple 1990, Burger et al. 1994, Clawson and Rotella 1998, Winter et al. 2000), whereas studies with no effect had min-

imum patch sizes of 50 to 129 ha (Pasitschniak-Arts and Messier 1996, this study).

The evidence for increased predation as an edge effect in grasslands is also equivocal. Although edge effects occur along grassland-forest edges (Johnson and Temple 1990, Burger et al. 1994, Winter et al. 2000), no effect of agricultural edges on grassland predation rates has been found (Mankin and Warner 1992, Winter et al. 2000, this study).

The high variability of nest mortality in our study may have resulted in low statistical power to detect relationships between mortality and landscape variables. We did not estimate the power of our tests *a priori*, and retrospective power analyses have limited utility (Steidl et al. 1997, Gerard et al. 1998). We do not think that lack of power is the reason for our findings, however; the number of sites included in our study is greater than the number of sites used for all but one North American grassland habitat fragmentation study (Clawson and Rotella 1998).

HABITAT STRUCTURE

Our results indicate that in our study area, habitat structure is a more important determinant of nest predation than is landscape context. Taller vegetation resulted in lower mortality rates of artificial nests than shorter vegetation. Dense vegetation structure can obscure sensory cues predators use to find nests, can restrict predator movements, and can increase predator foraging costs (Martin 1993, Dion et al. 2000). Vegetation structure may also influence the species composition and density of predator communities (Grant and Birney 1979), which in turn may affect reproductive success of birds. Although the literature on the effects of vegetation structure on predation is equivocal, our findings are consistent with those studies that report negative associations between vegetation density, height, or cover and predation rates (DeLong et al. 1995, Clawson and Rotella 1998, Ardizzone and Norment 1999). Although we did not see an effect of vegetation height on predation of natural nests, we expect this is an artifact of small sample sizes.

The economy and versatility of artificial nests makes them useful in elucidating patterns of avian nest predation, despite justifiable concerns regarding their validity (Major and Kendal 1996, King et al. 1999, Lindell 2000). Artificial nests

consistently show greater mortality than real nests (Major and Kendal 1996, King et al. 1999, Zannette and Jenkins 2000), possibly because of the lack of parental defense. In our artificial nest experiment, we matched the predator assemblage (small mammals) with the egg models (Rangen et al. 2000) in our effort to measure the relative predation pressure between different landscape and habitat variables (Butler and Rotella 1998, Wilson et al. 1998). In doing so, we were able to account for one source of bias of artificial-nest studies.

As noted by Tewksbury et al. (1998), landscape-level processes determining predation pressure may be more complex than is often appreciated. Predation patterns in any landscape depend on the response of different predator species to landscape composition and habitat structure, and on the relative effects of these predators on different bird species. We concur with them that generalizations about the effects of fragmentation are difficult to develop because they are a complex function of habitat structure, landscape context and the predator community.

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