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NEST SURVIVAL RELATIVE TO PATCH SIZE IN A HIGHLY FRAGMENTED SHORTGRASS PRAIRIE LANDSCAPE

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ABSTRACT.—Understanding the influences of habitat fragmentation on vertebrate populations is essential for the protection and ecological restoration of strategic sites for native species. We examined the effects of prairie fragmentation on avian reproductive success using artificial and natural nests on 26 randomly selected, privately owned patches of shortgrass prairie ranging in size from 7 to 454 ha within a cropland matrix in Washington County, Colorado, summer 2000. Survival trends of artificial and natural nests differed. Daily survival of artificial nests increased with patch size up to about 65 ha and differed little at larger patch sizes, whereas daily survival of Lark Bunting (*Calamospiza melanocorys*) and Horned Lark (*Eremophila alpestris*) nests decreased with increasing size of the grassland patch. We hypothesize that our unexpected findings of lower survival of natural nests with increasing patch sizes and different trends between artificial and natural nests are due to the particular structure of predator communities in our study area and the ways in which individual predators respond to artificial and natural nests. We recommend that the value of small habitat patches in highly fragmented landscapes not be overlooked. *Received 1 April 2004, accepted 3 November 2004.*

Understanding the influences of habitat structure and habitat fragmentation on the viability of grassland species is essential to conservation planning, especially for protection and ecological restoration of strategic sites for native species. Many grassland bird species, including those of the shortgrass prairie, have experienced population declines in the past 3 decades (Knopf 1994, Murphy 2003, Sauer et al. 2003). Between 1966 and 2002, populations of Lark Buntings (*Calamospiza melanocorys*) and Horned Larks (*Eremophila alpestris*) declined 2.0 and 1.6% per year, respectively, in the High Plains physiographic region (Sauer et al. 2003). Although mechanisms for these declines have not been identified, factors influencing reproductive success are among the possibilities. Shortgrass is the least disturbed of the three prairie types in North America, with as much as 40% remaining unplowed (Samson and Knopf 1996). Even though the extent of habitat loss is considerably less than in the tallgrass prairie (82–99%; Samson and Knopf 1996), habitat loss and fragmentation of breeding areas may contribute to population declines of shortgrass prairie birds.

Broad generalizations regarding the negative effects of habitat fragmentation on density and reproductive success of avian species are common in the scientific literature of the past 2 decades (Ambuel and Temple 1983, Herkert 1994, Donovan et al. 1995, Freemark et al. 1995). Studies on the effects of habitat fragmentation, specifically patch size and isolation, initially were stimulated by island biogeography theory (MacArthur and Wilson 1967, Diamond and May 1981) and subsequently by emerging landscape perspectives (Fahrig and Merriam 1994, Wiens 1995). When detected, patch size effects typically show that smaller habitat patches have lower habitat quality, more edge habitat, fewer species, fewer or no individuals of area-sensitive species, and/or lower reproductive output—due to increased predation and brood parasitism or decreased food abundance (Brittingham and Temple 1983, Herkert 1994, Burke and Nol 1998, Robinson 1998). These generalities are now being incorporated as assumptions in quantitative models of the effects of habitat fragmentation and edge effects on the demography of birds (Donovan and Lamberson 2001, Bollinger and Switzer 2002).

Despite broad support for these generalities, inconsistencies have been documented in well-studied systems. Although larger forest patches in forested landscapes are thought to provide better habitat (Donovan et al. 1995, Robinson et al. 1995, Thompson et al. 2002), not all studies support that pattern (Marzluff

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and Restani 1999). For example, in western forests, predation rates in fragments are often lower than in unfragmented sites (Tewksbury et al. 1998, Cavitt and Martin 2002). Current paradigms are rapidly evolving with the increased scrutiny of inconsistencies in the forest fragmentation literature (Donovan et al. 1997, Walters 1998, Marzluff and Restani 1999, Heske et al. 2001, Thompson et al. 2002). A major challenge to our understanding of the effects of habitat fragmentation on birds is the variability in their responses to fragmentation, or ''differential sensitivity'' (Walters 1998)—across regions, landscapes, habitats, species, and populations.

The effects of prairie fragmentation on reproductive success of grassland birds have been documented primarily in tallgrass prairie and in artificial nest studies. The effects are equivocal. Several bird species have experienced lower nest success in smaller grassland patches or near woody edges in field-forest ecotones (Herkert et al. 2003), but such effects do not universally apply to all grassland habitats and species (Gates and Gysel 1978, Johnson and Temple 1990, Winter and Faaborg 1999, Winter et al. 2000). Of five studies that employed artificial nest techniques in grasslands, only one (Burger et al. 1994) reported increased mortality of artificial nests with decreasing grassland patch size and distance from edges (in this case forest edges). Four of these studies reported no differences in mortality of artificial nests relative to grassland patch size or distance to edge, including forested and agricultural edges (Mankin and Warner 1992, Clawson and Rotella 1998, Pasitschniak-Arts et al. 1998, Howard et al. 2001). The lack of a patch size effect in these studies may result, in part, from the range in patch sizes being above or below a threshold at which an effect could be detected.

The search for generalities is often a search for clear and consistent trends reported by several studies. ''Similar conclusions obtained from studies of the same phenomenon conducted under widely differing conditions will give us greater confidence in the generality of those findings than would any single study'' (Johnson 2002). To contribute to our knowledge of potential effects of prairie fragmentation on birds, we conducted a study in a highly fragmented shortgrass prairie landscape (<15% grassland). The primary objective of our study was to determine the effects of patch size on reproductive success of prairie birds. We selected our study sites randomly so that we could make inferences to our entire target population (see *Site selection*) rather than just to the individual grassland patches.

METHODS

Study area.—The shortgrass prairie landscape is dominated by xeric grasses, such as buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). Common breeding birds are Horned Larks, Western Meadowlarks (*Sturnella neglecta*), Lark Buntings, Chestnut-collared Longspurs (*Calcarius ornatus*), and Grasshopper Sparrows (*Ammodramus savannarum*). Potential mammalian predators of ground-nesting birds include thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), coyotes (*Canis latrans*), swift foxes (*Vulpes velox*), long-tailed weasels (*Mustela frenata*), badgers (*Taxidea taxus*), and striped skunks (*Mephitis mephitis*). Common snake species that opportunistically prey on birds include bullsnakes (*Pituophis melanoleucus*), western hognose snakes (*Heterodon nasicus*), and prairie rattlesnakes (*Crotalus v. viridis*).

Our study was conducted during the summer of 2000 in a 4,842-km^2 agricultural region of Washington County in northeastern Colorado (39° 34′ N to 40° 27′ N; 102° 48′ W to 103° 28′ W). Land-use cover types in the study area include dryland wheat (non-irrigated wheat production in a 2-year rotation system; 73.9%), shortgrass prairie rangeland (14.3%), Conservation Reserve Program (CRP) fields (6.1%), and irrigated crops (3.7%). This agricultural area was adjacent to three large grasslands, totaling 1,689 km^2, that were not considered in this study.

Site selection.—We used satellite imagery (provided by the Colorado Division of Wildlife) to quantify land cover and restricted randomization to select study sites. Using ArcInfo, we identified all (n = 557) polygons of short- and midgrass prairie and measured corresponding area and perimeter. We calculated a diversity index (*DI*; Patton 1975) as

$$DI = \frac{TP}{2\sqrt{A\pi}},$$

where *TP* is the total perimeter of the polygon and *A* is the area of the polygon. For reference, a circle has a *DI* of 1 and a square has a *DI* of 1.3. Of the 557 identified grassland polygons, the median area was 35.7 ha (mean = 125.5 ± 367.6 SD; range 2.1–4,886.8 ha) and mean *DI* = 2.0 ± 0.7 SD. We omitted 96 polygons with *DI* >2.5 to eliminate the potentially confounding effect of highly elongated patches.

We sorted the polygons into several size classes (in increments of 10 ha between 0 and 150 ha, and in increments of 50 ha between 150 and 500+ ha) and randomly selected 2–4 from each size class as possible study sites. We ground-truthed the polygons (hereafter grassland patches) to verify their size and isolation and to update the surrounding land-use type. We considered only grassland patches that were at least 0.4 km from other grassland habitats. Grassland patches that were within 0.4 km of human habitation or riparian trees were also omitted to minimize the effects of predation by farm cats or corvids (Delisle and Savidge 1996). We obtained permission from landowners and conducted our study on 26 grassland patches ranging from 7 to 454 ha in size (mean = 106.4 ± 109.4 SD, CV = 1.03; n = 4 patches 7–20 ha, n = 6 patches 21–50 ha, n = 7 patches 50–100 ha, n = 5 patches 100–200 ha, n = 4 patches >200 ha).

Artificial nests.—Nests consisted of a scrape on the ground where we placed two fresh Japanese quail (*Coturnix japonica*) eggs and one clay egg (mean = 22 × 15 mm, n = 20) made of soft modeling compound (Sculpey III brand) to approximate the size of Lark Bunting eggs (mean = 22 × 17 mm; Baicich and Harrison 1997). Clay eggs aided in the identification of nest predators (by examining tooth impressions) and enabled us to record predation by predators too small to handle quail eggs (i.e., small rodents; Major and Kendal 1996). We inserted an orange-painted nail in the ground under the eggs to facilitate locating the nests after a disturbance. Artificial nests (n = 312) were set out at 24 sites between 31 May and 3 June and at 2 additional sites on 8 June 2000. At each site, we placed six nests near an edge (a grassland/fallow-field interface at 18 sites and a grassland/planted-field interface at 8 sites; planted sites were primarily wheat). At 100-m intervals along the edge, we paced a random distance (5–30 m) toward the interior and placed the artificial nest. We also placed six nests in the interior of each site (generally 100–500 m from the edge). In small sites, interior nests were placed as far from the edge as possible; 95% of all interior nests were ≥100 m from an edge and only one interior nest was <75 m. Interior nests were also placed 100 m apart; however, nests were placed closer together in small sites (50 m in four and 25 m in one) to enable the placement of six nests. Distance from the patch edge averaged 17.9 m ± 7.1 for edge nests and 259.1 m ± 121.1 for interior nests. For nest survival analyses, we coded distance from edge as 1 = edge, 2 = interior.

We checked nests twice, at 5 and 9 days after placement; eggs were removed from disturbed nests at the first check and from all remaining nests during the second check. Nests were classified as intact or disturbed based on signs of disturbance to either quail or clay eggs. Nests were considered disturbed if quail eggs were missing, broken, or moved, or if clay eggs were missing, moved, or had tooth impressions. We classified markings on the clay eggs as rodent, non-rodent, insect, or unknown by comparing them with known tooth impressions made from skulls in the zoology collection at Colorado State University, Fort Collins. In the absence of other signs of disturbance, nests containing clay eggs with only insect marks were considered intact.

Natural nests.—All grassland patches were systematically searched for nests by dragging a rope between two observers ~28 m apart and by observing adult behavior. We marked the location of nests with unmarked wooden stakes (2.9 × 28.5 cm) positioned 10 m from nests; painted wooden stakes (2.9 × 28.5 cm) were also placed 30 m from nests (aligned with the unmarked stake and nest) to facilitate relocating nests. When nests were found, we floated two eggs to determine their age, using a technique described by Westerskov (1950) and modified for Lark Buntings and Horned Larks. We monitored the nests and recorded numbers, ages, and status of eggs and nestlings at 2- to 4-day intervals until nests were empty. During the last nest check, we noted signs that would help determine whether young fledged (parents feeding young or call-

ing in the vicinity, fecal droppings outside of the nest [deposited only when young hop out; AAYA pers. obs.]). For each nest, we estimated distance from patch edge, coded as 1: <30 m, 2: 30–100 m, and 3: >100 m.

Vegetation sampling.—Vegetation structure and composition of grassland patches were characterized by sampling between 31 May and 7 June at six random points along line transects through the center of each site. Measurements included visual estimates of the percent cover of grasses (identified to species), sedges, forbs, shrubs, cacti, and bare ground within 5-m radius plots, as well as measurements of grass height and vegetation density at distances of 1, 3, and 5 m due east from the point. Vegetation density was recorded as the total number of vegetation hits on a 1-cm-diameter pole at intervals of 0–5, 5–10, 10–20, and 20–30 cm above ground. We constructed a variable (VegStruc) to describe overall vegetation structure as percent cover of green vegetation × median grass height × vegetation density.

Analyses.—We used Pearson correlation to assess relationships between patch area (ln-transformed to improve normality) and nine vegetation-structure variables: percent cover of grasses, forbs, shrubs, bare ground, and green vegetation (grasses, sedges, forbs, shrubs, and cacti); maximum grass height; median grass height; vegetation density; and overall vegetation structure.

We used the ''Mayfield logistic regression'' approach recently described by Hazler (2004) to examine daily survival of artificial and natural nests as a function of three variables: patch size (Patch area), distance from edge (Edge), and vegetation structure (VegStruc). Mayfield logistic regression is an alternative to typical logistic regression (i.e., 1 nest = 1 trial) because it accounts for the number of exposure days (i.e., 1 exposure day = 1 trial). We used the ''Last Active-B'' approach of Manolis et al. (2000) to calculate exposure days, and we censored the last nest check interval for nests with unknown fate (Stanley 2004). During nest checks after the fledge date, we assumed nests were successful if we observed fledglings, parental behavior near nests that suggested presence of fledglings (calling, feeding young), or fecal droppings immediately outside the nest.

We fitted models with PROC LOGISTIC (SAS Institute, Inc. 1999) and evaluated these models using AIC (Akaike 1973, Burnham and Anderson 2002) corrected for small sample size (AIC_c). The difference (Δ_i) between model i and the model with the minimum AIC_c value allows for a quick comparison and ranking of models. The model with the smallest AIC_c is the best-approximating model of the candidate models, given the data. The AIC_c weight (w_i) for model i, calculated as

$$\frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}$$

(where R is the number of candidate models in the set), is useful in assessing the weight of evidence in favor of a model. Burnham and Anderson (2002:167) recommend the use of summed Akaike weights (Σw_i) to evaluate the relative importance of variables when a balanced model set is used (e.g., in our analysis each variable appeared in four models). We computed a relative importance measure for each variable by summing Akaike weights over every model in which that variable appeared.

Because of model-selection uncertainty (it is plausible that models with ΔAIC_c values <7 are reasonable), we model-averaged the SAS-generated effect sizes ($\hat{\beta}$, regression coefficients) over the entire set of models with a weighted average based on Akaike weights (Burnham and Anderson 2002:253, equation 5.8). We computed unconditional standard errors for the effect sizes, thereby incorporating model-selection uncertainty into precision estimates, and used the Z distribution to calculate 95% confidence intervals (CI). Because PROC LOGISTIC models nest failure, signs of all coefficients were reversed to interpret effects on survival (see Hazler 2004). Herein we present a positive β to indicate increased nest survival and a negative β to indicate decreased nest survival relative to a given predictor variable. The strength of the effect ($\hat{\beta}$) is indicated by whether the 95% CI of the regression coefficient includes zero. A 95% CI where $\hat{\beta}$ does not overlap zero is analogous to $P < 0.05$, and a 90% CI where the $\hat{\beta}$ does not overlap zero is analogous to $P < 0.10$.

TABLE 1. Summary of model-selection results for survival of artificial and natural nests (Lark Bunting and Horned Lark) in Washington County, Colorado, summer 2000. Models with the lowest ΔAIC_c and the greatest Akaike weight (w_i) have the most support and are highlighted in boldface. K is the number of parameters in each model, including the intercept and each explanatory variable; n = total number of trials (nest-exposure days).

Nest survival models	Artificial nests (n = 1,492)			Lark Bunting (n = 204)			Horned Lark (n = 321)		
	K	ΔAIC_c	w_i	K	ΔAIC_c	w_i	K	ΔAIC_c	w_i
Patch area[a] + Edge + VegStruc	5	1.61	0.138	4	3.99	0.056	4	3.94	0.039
Patch area[a] + Edge	4	1.63	0.137	3	1.96	0.155	3	1.89	0.110
Patch area[a] + VegStruc	4	**0.00**	**0.308**	3	2.04	0.149	3	1.78	0.116
Edge + VegStruc	3	4.83	0.027	3	6.18	0.019	3	4.11	0.036
Patch area[a]	3	0.09	0.294	2	**0.00**	**0.414**	2	**0.00**	**0.282**
Edge	2	6.44	0.012	2	4.59	0.042	2	2.10	0.099
VegStruc	2	3.30	0.059	2	4.22	0.050	2	2.33	0.088
Constant	1	5.05	0.025	1	2.58	0.114	1	0.40	0.231

[a] We used a quadratic function of patch area in artificial nest models; patch area was used in Lark Bunting and Horned Lark models.

We ln-transformed patch area (hereafter patch area) to improve normality. Because we were unsure of the shapes of curves describing relationships between nest survival and patch area, we compared AIC values of models that included (1) patch area and (2) a quadratic function of area (patch area + patch area^2) before formalizing the candidate models. We then ran all possible additive combinations, including a constant model, for a total of eight models.

We present calculated estimates of overall nest survival, artificial nest survival for each grassland patch, and natural nest survival in small (<80 ha) and large (>80 ha) patches using the Mayfield technique (Mayfield 1975) and standard errors of the estimates following Johnson (1979). We used the 80-ha cutoff to ensure adequate sample sizes for Mayfield estimates of natural nest survival. Overall nest success was calculated as the daily survival rate (DSR) raised to the power of the length of the nesting period (21 and 20 days for Horned Larks and Lark Buntings, respectively). All estimates are reported ± SE, unless noted otherwise.

RESULTS

Vegetation composition and structure.—The dominant grasses in the study sites, in order of percent cover, were buffalograss, western wheatgrass (*Agropyron smithii*), blue grama, needleandthread (*Hesperostipa comata*), sixweeks fescue (*Vulpia octoflora*), and red threeawn (*Aristida purpurea*). Median grass height was 10.0 cm and ranged from 1 to 20 cm across all patches. There were no differences in vegetation structure that related to patch area; none of the nine vegetation structure variables was correlated with patch area ($|r| < 0.270$, $P > 0.15$ in all cases). The matrix immediately surrounding the grassland patches was primarily dryland wheat (approximately 78% of patch perimeter), CRP monocultures of smooth brome (*Bromus inermis*, 18%), and irrigated crops (4%).

The influence of grassland patch size on predation rates on artificial nests.—Mean daily survival of artificial nests across all sites was 0.834 ± 0.010 (95% CI = 0.815–0.853, n = 312). Edge nests had slightly greater daily survival than interior nests (0.841 ± 0.013; 95% CI = 0.815–0.867, n = 156 edge nests; and 0.826 ± 0.014; 95% CI = 0.799–0.853, n = 156 interior nests).

For artificial nests, we chose the quadratic rather than the linear function of patch area to represent area in the candidate models, based on relative AIC_c values of 1339.35 and 1343.75, respectively. Daily survival of artificial nests was best explained by the quadratic function of patch area and VegStruc (Table 1). Distance from edge had little influence on survival of artificial nests, as denoted by low Akaike model weights (Tables 1, 2). The predictor variables ordered by their estimated importance are area, vegetation structure, and edge, as portrayed by the summed weights (Σw_i) of 0.876, 0.532, and 0.314, respectively (Table 2).

TABLE 2. Survival of artificial nests increases with a quadratic function of patch area, up to about 65 ha, whereas survival of natural nests decreases with increasing patch area. Effect sizes ($\hat{\beta}$), standard errors (SE), 95% confidence intervals (CI), and relative importance measures (summed AIC_c weights; Σw_i) for the three explanatory variables (Patch area, Edge, and VegStruc) in the best model and across all models (model-averaged) for artificial and natural nests (Lark Bunting and Horned Lark). A positive $\hat{\beta}$ indicates increased nest survival and a negative $\hat{\beta}$ indicates decreased nest survival relative to a given predictor variable; a negative $\hat{\beta}$ of the quadratic term indicates a curve that is concave downward. Data from Washington County, Colorado, summer 2000.

	Artificial nests			Lark Bunting			Horned Lark		
Variable	$\hat{\beta}$ (SE)	95% CI	Σw_i	$\hat{\beta}$ (SE)	95% CI	Σw_i	$\hat{\beta}$ (SE)	95% CI	Σw_i
Patch area									
Best model	1.13 (0.47)	0.21, 2.03		−0.43 (0.21)	−0.85, −0.02		−0.38 (0.24)	−0.86, 0.09	
Model-averaged	1.05 (0.56)	−0.04, 2.14	0.876	−0.34 (0.26)	−0.84, 0.17	0.775	−0.21 (0.26)	−0.71, 0.30	0.546
Patch area^2									
Best model	−0.12 (0.06)	−0.23, −0.01		—			—		
Model-averaged	−0.12 (0.07)	−0.24, 0.01	0.876	—			—		
Edge									
Model-averaged	−0.03 (0.07)	−0.16, 0.10	0.314	−0.02 (0.10)	−0.22, 0.17	0.272	−0.04 (0.12)	−0.27, 0.19	0.284
VegStruct									
Best model	−0.55 (0.37)	−1.28, 0.18		—			—		
Model-averaged	−0.30 (0.39)	−1.06, 0.45	0.532	−0.06 (0.28)	−0.61, 0.48	0.275	−0.05 (0.36)	−0.76, 0.65	0.279

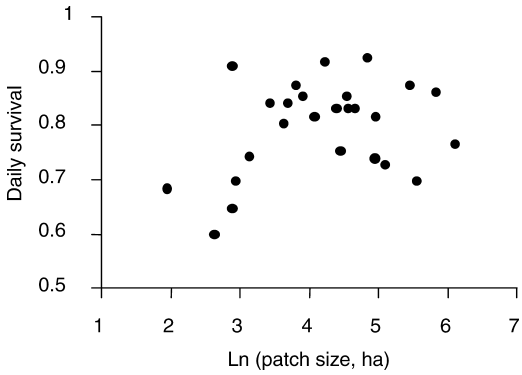

FIG. 1. Daily survival of artificial nests increased relative to ln(patch size) across 26 grassland patches in Washington County, Colorado, 2000. Artificial nest survival increased with patch area up to about 65 ha (ln65 is approximately 4.2).

Artificial nest survival increased with patch area up to about 65 ha and differed little at larger patch sizes (Fig. 1; note that ln65 is approximately 4.2). The strength of the relationship between patch area and daily nest survival is indicated by whether the 95% CI overlaps zero (Table 2). The 95% CI around the effect estimate for patch area^2 did not include 0 for the best model and slightly overlapped zero for the model-averaged estimate (that incorporates model-selection uncertainty). Nest survival increased as overall vegetation structure (VegStruc, a function of cover, height, and density) decreased, as indicated by the negative coefficients for the explanatory variable in the model-averaged estimate (Table 2); this relationship, however, is weak, as indicated by the extent of overlap of the 95% CI with zero.

Nest success of Lark Buntings and Horned Larks.—We found 36 Lark Bunting nests in 15 sites and 46 Horned Lark nests in 16 sites. Mean clutch size was 4.4 ± 0.17 (n = 22) and 3.4 ± 0.12 (n = 33) and number of young fledged per successful nest was 2.9 ± 0.26 (n = 15) and 2.8 ± 0.25 (n = 13) for Lark Buntings and Horned Larks, respectively. Daily survival rates of Lark Bunting and Horned Lark nests across all sites were 0.891 ± 0.022 (95% CI = 0.847–0.935) and 0.900 ± 0.017 (95% CI = 0.867–0.933). Overall nest survival was low, with only 10% of Lark Bunting nests and 11% of Horned Lark nests fledging at least one young. No nests were censored from analyses due to suspected abandonment. Predator sightings in the grassland sites included ground squirrels, snakes, coyotes, striped skunks, and badgers.

The total area searched by rope-dragging during the season was 1,890 ha; 42% of this effort was within 50 m of site edges. Only 12 Lark Bunting and 6 Horned Lark nests were found within 50 m of the edge, which were fewer than expected if we assumed nest distribution to be random or uniform relative to habitat edges (χ^2 = 5.6, df = 1, $P < 0.010$, and χ^2 = 14.58, df = 1, $P < 0.001$ for Lark Buntings and Horned Larks, respectively).

We chose patch area to represent area in the candidate models for Lark Buntings and Horned Larks because the quadratic form did not improve model performance (AIC_c values differed by only 0.65 and 0.04 for Lark Buntings and Horned Larks, respectively) and the use of patch area offered greater parsimony. Daily survival of both Lark Bunting and Horned Lark nests was best explained by patch area alone (Table 1). For both species, nest survival decreased with increasing patch area, as indicated by the negative coefficients ($\hat{\beta}$) for the explanatory variable in best models and model-averaged estimates (Table 2). For Lark Buntings, the 95% CI on the effect estimate for patch area did not include 0 (CI = −0.85, −0.02) in the best model but did slightly overlap zero with its model-averaged estimate (Table 2). In contrast, the 95% CI for Horned Larks barely overlapped zero in the best model and overlapped zero more so with the model-averaged estimate. The relative importance of patch area in influencing natural nest survival was stronger for Lark Buntings (Σw_i = 0.775) than for Horned Larks (Σw_i = 0.546). Edge and VegStruc had substantially smaller summed weights.

An alternative approach to examining patch-size effects on natural nest survival for this data set is to compute standard Mayfield (1975) estimates for grassland patches grouped as small (<80 ha) and large (>80 ha). Although not within the information-theoretic paradigm, the results of this analysis yielded similar results (Table 3). Nest survival was greater in small than in large patches for both species, with a somewhat stronger effect for Lark Buntings than for Horned Larks.

TABLE 3. Daily survival rates (SE, 95% CI) for Lark Bunting and Horned Lark nests were greater in small (<80 ha) than in large (>80 ha) grassland patches in Washington County, Colorado, summer 2000.

Grassland patch size	Lark Bunting			Horned Lark		
	n	Daily survival rate (SE)	95% CI	*n*	Daily survival rate (SE)	95% CI
Small (<80 ha)	15	0.925 (0.026)	0.874–0.975	25	0.912 (0.020)	0.873–0.952
Large (>80 ha)	21	0.851 (0.038)	0.776–0.925	21	0.881 (0.029)	0.824–0.937
		$t_{35} = 6.94$, $P < 0.001$			$t_{45} = 4.19$, $P < 0.001$	

DISCUSSION

Effects of prairie fragmentation on nest survival.—In this study, survival of artificial nests increased with increasing patch size. This finding is consistent with general expectations of the effects of patch size on nest survival and with findings of grassland studies that incorporated patch sizes below 31 ha (Johnson and Temple 1990, Burger et al. 1994, Clawson and Rotella 1998, Winter et al. 2000). Grassland studies with minimum patch sizes exceeding 50 ha, however, found no effect of patch size on predation rates of artificial nests (Pasitschniak-Arts et al. 1998, Howard et al. 2001).

Our finding of a positive relationship between artificial nest survival and patch size, however, is the opposite of our findings on the survival of natural nests. Nests of Lark Buntings and Horned Larks had lower survival in the more extensive grassland patches in our study area. Ours is not the only study to document this unexpected trend. Higher daily survival was experienced by Baird's Sparrows (*Ammodramus bairdii*) in smaller patches of mixed-grass prairie (S. K. Davis pers. comm.), by several species of forest birds in forest fragments in western United States (Cavitt and Martin 2002), and by American Redstarts (*Setophaga ruticilla*) breeding in small, isolated stands of quaking aspen (*Populus tremuloides*; S. J. Hannon pers. comm.).

Understanding the effects of fragmentation on predator communities.—Predator communities exert a strong influence on avian fecundity. Numerous authors recently have suggested that effects of fragmentation on avian fecundity are highly complex and depend on predator dynamics within local landscapes, varying predator responses to fragmentation, and extent of fragmentation (e.g., Tewksbury et al. 1998, Heske et al. 2001, Patten and Bolger 2003). In general, the response of nest predators to fragmentation is complex, taxon-specific, and landscape context-dependent (Chalfoun et al. 2002). Further, there are even within-species differences in responses to fragmentation and land conversion; for example, swift foxes in eastern Colorado and Wyoming tend to avoid agricultural lands (Finley 1999), whereas they do not do so in Kansas (Sovada et al. 2001b).

Once it is clearly acknowledged that predator communities differ across locales and regions, and that predator species differ in their hunting strategies and responses to habitat fragmentation (Chalfoun et al. 2002), there should be less expectation of clear and consistent relationships between fragmentation metrics and fecundity. Rather than simply asking what are the effects of fragmentation (degree of fragmentation, type of matrix, patch size, distance from edge) on avian fecundity, perhaps the pertinent questions should include: (1) what are the effects of fragmentation on predator communities, and (2) how do the resulting predator communities influence avian fecundity?

We hypothesize that our unexpected findings (of lower survival of natural nests with increasing patch area and different trends between artificial and natural nests) are due to differing composition of predator communities relative to patch sizes. Although we did not quantify predator populations, we did find patterns in artificial nest destruction relative to patch size that suggest that predator composition differs with patch size. The proportion of disturbed nests with broken quail eggs (rather than missing quail eggs or disturbed clay eggs) increased with increasing patch size ($F_{1,23} = 6.340$, $P = 0.019$). It is likely that one (or just a few) predator species are responsible for the broken eggs, assuming that egg handling varies between predator species and is consistent within species.

Additional information to support that predator community composition differs with patch size is the variation in home-range sizes and area-sensitivity of local predators. The small grassland patches may be devoid of the larger mammalian predators because small patches provide insufficient habitat not compensated for by use of the matrix (agricultural fields). That mammalian predators are absent or in lower densities in the matrix habitat than in the grassland habitats is suggested by lower predation rates on Mountain Plover (*Charadrius montanus*) nests in agricultural fields than in native prairie (F. L. Knopf and V. J. Dreitz pers. comm.), by small mammal movements out of barren cropland (Streubel and Fitzgerald 1978, Cummings and Vessey 1994), and by lower security of den sites in tilled agricultural lands.

All of our grassland patches, even the smallest 7-ha patch, contained thirteen-lined ground squirrels (average home range = 1–5 ha; Streubel and Fitzgerald 1978) and snakes. We suspect that only the larger patches are frequented by the larger mammalian carnivores, such as badgers (mean home range = 725 ha; Long 1973), striped skunks (mean home range = 378–512 ha; Wade-Smith and Verts 1982), coyotes (mean home range = 19.8 km^2; Kitchen et al. 1999), and possibly swift foxes (mean home range = 7.6 km^2; Kitchen et al. 1999). Additionally, densities of thirteen-lined ground squirrels may be greater in the smaller fragments; if larger predators are absent, numerical increases of ground squirrels may occur in a process similar to ''mesopredator release'' (Crooks and Soule 1999, Heske et al. 2001). This reasoning is consistent with Vander Haegen et al. (2002), who report that the composition of predator communities differs between fragments and contiguous tracts of shrubsteppe habitat.

Our study and other recent studies have demonstrated that trends in mortality of artificial nests do not always mimic trends of natural nests (Valkama et al. 1999, Zanette 2002, Mezquida and Marone 2003). These discrepancies may be due to differences in predator communities between treatments and the ways in which individual predators respond to artificial and natural nests. Eggs in artificial nests cannot be camouflaged by incubating adults or protected by the defensive actions of parents. In natural nest trials, on the other hand, parental presence can either attract or deter nest predators. Adult Lark Buntings, and probably Horned Larks, can deter ground squirrel nest predation; several Lark Buntings have been filmed chasing ground squirrels from their nests (J. B. Barna and A. S. Chaine pers. comm., but see Pietz and Granfors 1994). We also commonly witnessed adults of both species chasing ground squirrels. Parental behavior and scent may attract the larger mammalian predators, but nest defense probably cannot deter them. The idea that small grassland patches have greater densities of small predators or ground squirrels, which search for nests randomly, is consistent with our finding of lower survival of artificial nests in smaller patches. Likewise, the idea that larger patches have more predators that use cues of adults to find nests rather than random search is consistent with our finding of lower survival of natural nests in larger patches.

Implications for management.—For management to be effective in reversing population declines in grassland birds, the ultimate factors underlying the declines must be identified and addressed. Even if it is determined that low reproductive success due to predation in breeding areas is a primary driver of population declines, the available management tools are not extensive. Predator control as a means of improving reproductive success of songbirds is generally not advocated because removal of one subset of predators at a local site is compensated for by numerical increases or changes in foraging habits of another subset (Reitsma et al. 1990; Dion et al. 1999, 2000; Heske et al. 2001). Manipulations of habitat features at a local scale, although labor-intensive and costly, have met with some success in improving avian reproductive output (Morse and Robinson 1999, Heske et al. 2001, Sovada et al. 2001a).

Current recommendations for acquisition, restoration, and management of forest and grassland habitats are often based on patch size (Robinson et al. 1995, Heske et al. 2001), and landscape manipulations often include the protection and consolidation of large habitat tracts. This approach is justified by the many studies with positive relationships between forest area and bird abundance and/or nest survival and is especially applicable to land-

scapes with considerable native habitat remaining. We question, however, as do others (Friesen et al. 1999, Bakker et al. 2002, Cavitt and Martin 2002, Patten and Bolger 2003), whether the effects of habitat fragmentation can be generalized across regions, landscapes, and habitats—and whether the protection of only large habitat tracts is the best approach in all areas. The value of small habitat patches in agricultural landscapes is often overlooked (Friesen et al. 1999); even small patches can function as population sources in some years (S. J. Hannon pers. comm.). We do not question the value of extensive grasslands nor justify further fragmentation of native grassland, but we do encourage additional incentive programs for habitat conservation of small patches, when appropriate, in fragmented agricultural landscapes.

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