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Management and Conservation Article

Land Use and Small Mammal Predation Effects on Shortgrass Prairie Birds

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ABSTRACT Grassland birds endemic to the central shortgrass prairie ecoregion of the United States have experienced steep and widespread declines over the last 3 decades, and factors influencing reproductive success have been implicated. Nest predation is the major cause of nest failure in passerines, and nesting success for some shortgrass prairie birds is exceptionally low. The 3 primary land uses in the central shortgrass prairie ecoregion are native shortgrass prairie rangeland (62%), irrigated and nonirrigated cropland (29%), and Conservation Reserve Program (CRP, 8%). Because shortgrass–cropland edges and CRP may alter the community of small mammal predators of grassland bird nests, I sampled multiple sites on and near the Pawnee National Grasslands in northeast Colorado, USA, to evaluate 1) whether small mammal species richness and densities were greater in CRP fields and shortgrass prairie–cropland edges compared to shortgrass prairie habitats, and 2) whether daily survival probabilities of ground-nesting grassland bird nests were negatively correlated with densities of small mammals. Small mammal species richness and densities, estimated using trapping webs, were generally greater along edges and on CRP sites compared to shortgrass sites. Vegetation did not differ among edges and shortgrass sites but did differ among CRP and shortgrass sites. Daily survival probabilities of artificial nests at edge and CRP sites and natural nests at edge sites did not differ from shortgrass sites, and for natural nests small mammal densities did not affect nest survival. However, estimated daily survival probability of artificial nests was inversely proportional to thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) densities. In conclusion, these data suggest that although land-use patterns on the shortgrass prairie area in my study have substantial effects on the small mammal community, insufficient data existed to determine whether land-use patterns or small mammal density were affecting grassland bird nest survival. These findings will be useful to managers for predicting the effects of land-use changes in the shortgrass prairie on small mammal communities and avian nest success.

KEY WORDS Conservation Reserve Program, edge effects, grassland birds, nest survival, Pawnee National Grassland, shortgrass prairie, small mammals.

Birds endemic to the central shortgrass prairie ecoregion of the United States have experienced steep and widespread declines in recent decades, with some species of ground-nesting grassland birds such as lark buntings (*Calamospiza melanocorys*), chestnut-collared longspurs (*Calcarius ornatus*), and McCown's longspurs (*Calcarius mccownii*) declining 68–91% (Knopf 1994, Herkert and Knopf 1998, Peterjohn and Sauer 1999, Sauer et al. 2007, North American Bird Conservation Initiative 2009). Although mechanisms for these declines have not been identified, factors influencing reproductive success have been implicated (Knopf and Rupert 1996, Skagen et al. 2005, Yackel-Adams et al. 2007). Nest predation is the major cause of nest failure in passerines (Martin 1993), and nesting success of ground-nesting grassland birds in the shortgrass prairie is exceptionally low. In northeastern Colorado (USA) in 1998, Howard et al. (2001) found nesting success for lark buntings to be 15% (assuming 12-day incubation and 8-day nestling stages), and in 2000 Skagen et al. (2005) estimated nesting success of lark buntings and horned larks (*Eremophila alpestris*) to be 10% and 11%, respectively. Yackel-Adams et al. (2007) reported nesting success for lark buntings in northeastern Colorado between 1997 and 2003 to be <31% every year during that period. Historical records of nesting success for lark buntings and horned larks in this region were 63% and 43%, respectively (Creighton and Baldwin 1974).

Land-use patterns in the shortgrass prairie may be contributing to declines of shortgrass prairie birds. The 3 primary land uses in the central shortgrass prairie ecoregion are native shortgrass prairie (rangeland, 62%), irrigated and nonirrigated cropland (29%; mostly corn and wheat), and Conservation Reserve Program (CRP, 8%; Maxwell 1996). Conservation Reserve Program lands provide good habitat for grassland birds in mid- and tallgrass prairies where it mimics the structure of the native prairies (Johnson and Schwartz 1993). However, it is unclear whether CRP provides suitable nesting habitat for shortgrass prairie birds. Moreover, the increased vegetative structure on CRP lands relative to shortgrass prairie, and increased seed availability at shortgrass–cropland interfaces (hereafter, edges), may host greater species richness and densities of potential mammalian predators of ground-nesting grassland birds, including the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), deer mouse (*Peromyscus maniculatus*), and northern grasshopper mouse (*Onychomys leucogaster*; Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003, Grant et al. 2006). Because local environmental characteristics can influence predator abundance and activity, and because birds nesting in areas with high abundance and activity of nest predators often experience a high probability of nest predation (Cain et al. 2006), it is reasonable to predict that CRP or edges will negatively affect grassland bird nest survival in the shortgrass prairie. Whereas the relationship between small mammal density and nest survival has been evaluated in mixed-grass prairie (Grant et al. 2006) and pastureland (Renfrew et al. 2005), more studies evaluating these factors are required in different cover types (Ribic et al. 2009). I am not aware of any studies that simultaneously evaluated small mammal nest-predator densities and avian nest survival in natural and human-altered sites in the shortgrass prairie.

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I evaluated the working hypothesis that land-use patterns in the shortgrass prairie region altered small mammal communities and this alteration has increased, in turn, predation rates on nests of ground-nesting grassland birds. Consequently, my objectives were to evaluate the following predictions: 1) small mammal species richness and densities are greater in CRP fields and shortgrass prairie–cropland edges compared to interior (i.e., nonedge) shortgrass habitats, and 2) daily survival probabilities of ground-nesting grassland bird nests are negatively correlated with densities of small mammals.

STUDY AREA

I conducted my study in Logan, Morgan, and Weld counties in northeastern Colorado, USA, on and near the United States Forest Service Pawnee National Grassland (PNG) between 40°N and 41°N latitude and 103°W and 105°W longitude. Land use in this area was predominantly shortgrass rangeland dominated by buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia opuntia*). On CRP fields smooth brome (*Bromus inermis*) and wheatgrass (*Agropyron* spp.) were predominant.

METHODS

I collected data for comparing shortgrass prairie and CRP in this study in 1999 as a companion study to Howard et al. (2001). Howard et al. (2001) used satellite imagery to randomly select 150 shortgrass prairie and CRP sites and subsequently obtained permission from public agencies and private landowners to sample 35 shortgrass prairie sites and 11 CRP sites. From the Howard et al. (2001) sites I randomly selected 8 shortgrass prairie sites and 8 CRP sites.

For the comparison of shortgrass prairie interior and edge habitat, I collected data in 2000 and 2001. In early spring, 2000, I surveyed approximately 90% of the PNG by vehicle to locate 1.6 × 1.6-km sections of shortgrass prairie where ≥1 edge interfaced active or fallow cropland. From the resulting sampling frame of 44 sites, I randomly selected 16 study sites (8 sites for 2000 and 8 sites for 2001) for sampling.

Sampling

I sampled small mammals by placing trapping webs at study sites (Anderson et al. 1983, Wilson and Anderson 1985). During their 1998 field season, Howard et al. (2001) established 2 parallel, 800-m transect lines, 400 m apart, at each study site. I partitioned the 800 × 400-m area flanked by these transects into 4 200 × 400-m parcels, and then randomly selected a parcel for small mammal sampling. I placed the center (i.e., focus) of the circular trapping web near the geometric center of the randomly selected parcel. During the 2000 and 2001 field seasons, I placed the focus of a circular trapping web 300 m from the edge and placed 2 semicircular trapping webs with their foci 300 m apart at the edge (Fig. 1).

Circular trapping webs consisted of 8 primary spokes and 8 secondary spokes, whereas semicircular trapping webs consisted of 5 primary spokes and 4 secondary spokes. When setting up a trapping web, the first spoke I established was a primary spoke and I aligned it with 1 of the 4 cardinal directions (N, S, E, or W). I offset the second spoke, always a secondary spoke, by 22.5°. I repeated this alternating pattern of primary and secondary spokes until I placed all spokes. For circular trapping webs, the end result was 8 primary spokes oriented in the 4 cardinal and 4 ordinal directions (e.g., N, NE, E) and 8 secondary spokes oriented equidistant between the cardinal and ordinal direction (e.g., NNE, ENE). On primary spokes I placed 20 Sherman live traps (7.5 × 8.75 × 22.5 cm) at 5-m intervals beginning at 2.5 m and ending at 97.5 m. On secondary spokes I placed 10 live traps at 10-m intervals beginning at 7.5 m and ending at 97.5 m. Thus, circular webs had 240 traps and semicircular webs had 140 traps. I baited traps using a 4-way grain mix (rolled corn, barley and oats, and molasses; Northern Colorado Feeders Supply, Inc., Fort Collins, CO).

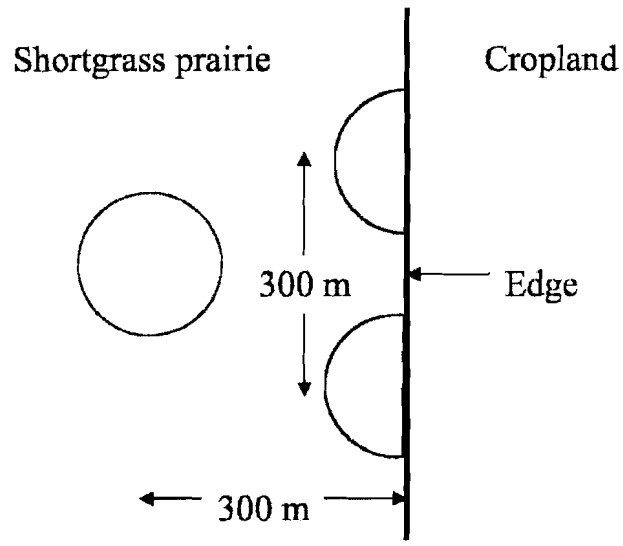

Figure 1. Spatial configuration of circular and semicircular trapping webs I used to estimate small mammal densities in shortgrass prairie and at the shortgrass prairie–cropland edge interface I sampled in 2000 and 2001, northeastern Colorado, USA.

Due to logistical constraints, I could only simultaneously operate 2 circular trapping webs or 1 circular trapping web and 2 semicircular trapping webs. Consequently, during the 1999 field season, I randomly paired a shortgrass site with a CRP site and ran trapping webs on the pair for approximately 1 week. Pairing shortgrass and CRP sites helped ensure that factors such as weather, vegetation phenology, and emergence of young did not confound estimated land-use effects. At the end of the week I moved trapping webs to the next randomly selected pair and sampled those sites for approximately 1 week. I repeated this until I sampled all 8 pairs. During the 2000 and 2001 field seasons, I simultaneously operated the interior and edge trapping webs for one site for approximately 1 week, and after that week I moved webs to the next randomly selected

site. During all field seasons I conducted trapping from May to mid-July.

To reduce mortality from heat stress, I set traps in the evening after 1800 hours and checked them in the morning and closed them before 1200 hours. Upon first capture, I provided all individuals uniquely numbered ear tags (one for each ear) or marked them ventrally with a red permanent marker and weighed, sexed, and identified them to species. I recorded date of first capture and all recaptures for each individual, as well as the location of the trap. I released individuals at the point of capture.

In 1999 I randomly selected 8 points/trapping web for vegetation sampling. In 2000 and 2001, I randomly selected 10 points/circular trapping web and 5 points/semicircular trapping web for vegetation sampling. At each point I determined by ocular estimation percentage of bare ground, grasses, forbs and shrubs, cactus, and green vegetation in a 1-m-radius circle centered on the point. In addition, at each point I obtained 2 visual obstruction readings from 2 opposing cardinal directions (i.e., N and S or E and W) to assess vegetation standing crop (Robel et al. 1970).

Artificial and Natural Nests

During all years, I constructed artificial nests at each of the random points selected for vegetation sampling to monitor nest predation. I constructed artificial nests by creating a small depression in the soil near vegetation in a manner emulating the nest of a ground-nesting grassland bird, then placing a nail beneath the soil at the center of the nest and placing upon that one Japanese quail egg (*Coturnix japonica*). The nail allowed observers to confirm the location of an artificial nest in the event the egg was missing during a subsequent check. I constructed artificial nests the same day I set up the trapping web, and I rechecked nests daily for predation until I moved the trapping web to the next site. I did not replace eggs once they were depredated.

During the 1999 field season I recorded incidental detections of natural nests on interior and CRP sites. During the 2000 and 2001 field seasons, I conducted standardized searches for natural nests on the interior and edge trapping webs. I marked nests I found by placing a stake 5 m from the nest in the direction of the east–west axis of the web, and I aged the nest by floating 2 randomly selected eggs (Westerskov 1950) or by noting feather development of nestlings. I rechecked nests daily while the trapping web was in operation and at irregular intervals upon removal of the trapping web.

Analysis

I obtained site-specific values for species richness by counting the number of distinct species captured at a site. I used this method, in lieu of the Nichols et al. (1998) method that accounts for detection probabilities, because data were too sparse to obtain site-specific estimates under the Jackknife estimator. I estimated small mammal density for species with a sufficient number of first captures using Program DISTANCE (Buckland et al. 1993). I pooled data for the 2 semicircular webs at the edge, within a site, before analysis and, when necessary, I pooled trapping-web data within species across sites to estimate the detection function. To fit the detection function, I evaluated the uniform and half-normal keys, with cosine adjustments up to order 3. I selected the detection function for estimation using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In the analysis, I corrected for differences in area sampled because the 2 semicircular trapping webs collectively sampled a slightly larger area than one circular trapping web.

I estimated daily survival probabilities for artificial and natural nests using the Stanley (2000) model with a logit link to incorporate covariates. Under this model unbiased estimates of stage-specific (e.g., incubation and nestling stages) daily survival probabilities are obtained even when the day of transition from one stage to the next or the day a nest fails between visits are unknown. This typically occurs when nests are checked at irregular intervals exceeding 1 day, as was the case for natural nests in my study. The logit link allows daily survival probabilities to be explicitly modeled as a function of variables hypothesized to affect survival (e.g., land use, predator density). I evaluated models with and without stage-specificity and covariates. I used Akaike's Information Criterion corrected for small samples (AIC_c) to select the model best supported by the data (Burnham and Anderson 2002).

I evaluated shortgrass versus CRP and shortgrass versus edge by computing mean differences and placing 95% confidence intervals on the means because sites were paired. Thus, for example, if y_{i1} and y_{i2} represent small mammal density on the ith pair of shortgrass and CRP sites (i = 1, ..., 8), then mean difference is

$$\bar{d} = \frac{1}{8}\sum_{i=1}^{8}(y_{i1} - y_{i2}).$$

In some cases it was desirable to model a dependent variable (e.g., small mammal density) as a function of certain predictor variables (e.g., vegetation characteristics), which I accomplished in a general linear models (GLM) framework using SAS Proc GLM (SAS Institute Inc., Cary, NC), after taking differences between paired dependent variables and paired predictor variables. For example, let y_{i1} and y_{i2} be paired density estimates (i.e., the dependent variables), as described above, and let x_{i1} and x_{i2} be similarly defined paired predictor variables. Then the GLM is $(y_{i1} - y_{i2}) = (\beta_{01} - \beta_{02}) + \beta_1(x_{i1} - x_{i2}) + (\varepsilon_1 - \varepsilon_2)$, which can be written more compactly as: $d_i = \beta_0 + \beta_1(x_{i1} - x_{i2}) + \varepsilon$. Here, d_i is the difference between the ith pair of dependent variables, β_0 is the mean difference between paired sites (or here, mean difference between paired shortgrass and CRP sites), β_1 is the effect of the predictor x on the dependent variable y (β_1 is assumed constant across sites), and $\varepsilon \sim N(0, \sigma^2)$. If we view the differences being taken in the ys and xs as a pair-specific normalization (or rescaling), then as with typical GLMs for unpaired data a positive β_1 means y is directly proportional to x, and a negative β_1 means y is inversely proportional to x. I used AIC_c for all model selection (Burnham and Anderson 2002).

Table 1. Species-specific counts of the number of distinct small mammal individuals I captured at shortgrass prairie and Conservation Reserve Program (CRP) sites sampled in 1999, northeastern Colorado, USA.

Species	Shortgrass	CRP
Thirteen-lined ground squirrel	91	17
Grasshopper mouse	11	24
Deer mouse	7	85
Silky pocket mouse (*Perognathus flavus*)	1	0
Plains pocket mouse (*Perognathus flavescens*)	0	3
Hispid pocket mouse (*Chaetodipus hispidus*)	0	3
Prairie vole (*Microtus ochrogaster*)	0	9
Plains harvest mouse (*Reithrodontomys montanus*)	0	1
Total count	110	142

RESULTS

Shortgrass Versus CRP

During the 1999 field season, I captured 110 individual small mammals from 4 species at shortgrass sites and 142 individuals from 7 species at CRP sites (Table 1). Mean species richness/shortgrass site was 2.0 (SE = 0.3) and mean richness/CRP site was 3.1 (SE = 0.3), which yielded a mean (95% CI) paired difference (shortgrass minus CRP) of −1.1 (−2.5 to 0.2). Sufficient trapping-web data existed to estimate densities for 3 mammal species. For thirteen-lined ground squirrel and deer mouse, AIC selected the uniform key with zero cosine adjustments for the best fit model; for grasshopper mouse, AIC selected the half-normal key with one cosine adjustment. Goodness-of-fit tests for the selected models ranged from $P = 0.136$ to 0.706, indicating models provided an adequate fit to the data (assumed under the null hypothesis), and estimated detection probabilities ranged from 0.492 to 1.00. Thirteen-lined ground squirrel and deer mouse had 95% confidence intervals on paired differences that did not cover zero (Table 2).

All vegetation measures differed among shortgrass and CRP sites (Table 3), whereas daily survival probabilities of artificial nests did not. Mean (95% CI) daily survival probability for artificial nests was 0.920 (0.882–0.957) on shortgrass sites and 0.904 (0.827–0.981) on CRP sites, and the mean paired difference was 0.016 (−0.087–0.119). I could not rigorously estimate natural nest survival due to small sample sizes (e.g., 1–3 nests/species) for all species.

I regressed small mammal density against 4 vegetation predictor variables: percent grasses, percent forbs and shrubs, percent cactus, and visual obstruction reading, as well as all pair-wise combinations of these variables to yield 10 models. Model selection using AIC_c resulted in simple models containing only one vegetation parameter (Table 4). The best model retained a term for visual obstruction reading for thirteen-lined ground squirrel ($\beta = 0.41$, 95% CI = 0.10–0.72) and grasshopper mouse ($\beta = -1.33$, 95% CI = −2.86 to 0.20). For deer mouse the best model retained a term for percent grasses ($\beta = 0.17$, 95% CI = 0.06–0.28). For both thirteen-lined ground squirrel and deer mouse the 95% confidence interval on the vegetation parameter did not cover zero. Regression of artificial nest survival against thirteen-lined ground squirrel, grasshopper mouse, and deer mouse densities yielded parameter estimates near zero (Table 5).

Interior Versus Edge

I found no evidence for year effects on any of the variables I investigated, so for all results I pooled data across 2000 and 2001. I captured more individuals and more species along edges than interior sites (Table 6). Mean species richness was 2.1 (SE = 0.3) for interior sites and 3.6 (SE = 0.4) for edge sites, which yielded a mean (95% CI) paired difference (interior minus edge) of −1.5 (−2.0 to −1.0). There were sufficient trapping-web data to estimate densities for 3 mammal species. For thirteen-lined ground squirrel and grasshopper mouse AIC selected the half-normal key with one or 2 cosine adjustments as the best fit model, and for deer mouse AIC selected the uniform key with one cosine adjustment for the best fit model. Goodness-of-fit tests for selected models ranged from $P = 0.148$ to 0.948, and

Table 2. Mean small mammal densities (no./ha) and 95% confidence intervals (95% CI) for shortgrass prairie and Conservation Reserve Program (CRP) sites sampled ($n = 8$) in 1999, northeastern Colorado, USA.

	Shortgrass		CRP		Paired differences (shortgrass − CRP)	
Species	Mean density	95% CI	Mean density	95% CI	Mean density	95% CI
Thirteen-lined ground squirrel	1.83	1.14–2.52	0.34	0–0.71	1.49	0.76–2.21
Grasshopper mouse	0.68	0–1.51	1.87	0–4.73	−1.19	−4.19–1.81
Deer mouse	0.34	0–0.82	3.38	0.37–6.39	−3.04	−5.91 to −0.17

Table 3. Mean vegetation differences and 95% confidence intervals (95% CI) for shortgrass prairie and Conservation Reserve Program (CRP) sites sampled ($n = 8$) in 1999, northeastern Colorado, USA.

	Shortgrass		CRP		Paired differences (shortgrass − CRP)	
Vegetation variable	Mean difference	95% CI	Mean difference	95% CI	Mean difference	95% CI
Bare ground (%)	22.0	18.2–25.8	41.9	37.0–46.7	−19.8	−26.0 to −13.7
Grasses (%)	60.2	55.6–64.9	51.6	47.0–56.2	8.6	1.9–15.3
Forbs and shrubs (%)	12.1	9.2–15.0	6.5	3.9–9.1	5.6	1.6–9.6
Cactus (%)	4.9	3.1–6.6	0.4	0–0.9	4.4	2.7–6.1
Green (%)	77.0	73.2–80.7	57.9	53.1–62.7	19.1	12.9–25.2
Visual obstruction reading (dm)	0.5	0.4–0.7	1.8	1.4–2.1	−1.3	−1.7 to −0.8

Table 4. Model selection results from a regression analysis of small mammal density against vegetation variables[a] on shortgrass prairie and Conservation Reserve Program sites I sampled in 1999, northeastern Colorado, USA. Results include the difference in Akaike's Information Criterion corrected for small samples (AIC_c) relative to the best model (ΔAIC_c), the model weight (w_i), and the number of estimated parameters (K) for models with $w_i \geq 0.05$ (i.e., 5%).

Model	AIC_c	ΔAIC_c	w_i	K
Thirteen-lined ground squirrel				
VOR	2.5	0.0	0.44	3
Forbshrb	3.2	0.7	0.31	3
Grass	4.4	1.7	0.17	3
Grasshopper mouse				
VOR	28.2	0.0	0.43	3
Forbshrb	28.7	0.5	0.34	3
Cactus	30.9	2.7	0.11	3
Grass	31.2	3.0	0.09	3
Deer mouse				
Grass	22.8	0.0	0.82	3
Forbshrb	27.1	4.2	0.10	3

[a] % grasses (grass), % forbs and shrubs (forbshrb), % cactus (cactus), and visual obstruction reading (VOR).

Table 5. Results of a regression analysis of artificial nest daily survival probabilities against densities of thirteen-lined ground squirrel, grasshopper mouse, and deer mouse on shortgrass prairie and Conservation Reserve Program sites sampled in 1999, northeastern Colorado, USA.

Predictor variable	Parameter estimate	95% CI
Thirteen-lined ground squirrel density	−0.068	−0.168 to 0.032
Grasshopper mouse density	0.012	−0.013 to 0.037
Deer mouse density	0.003	−0.026 to 0.032

estimated detection probabilities ranged from 0.162 to 0.451. Two species had 95% confidence intervals on the paired differences that did not cover zero (Table 7).

Neither vegetation measures (Table 8), nor artificial nest predation rates, differed among interior and edge sites. Mean (95% CI) daily survival probability for artificial nests was 0.939 (0.907–0.971) on interior sites and 0.944 (0.920–0.967) on edge sites, and the mean paired difference was −0.005 (−0.041 to 0.032). Natural nest data pooled over 2000 and 2001 allowed estimation of daily nest survival probabilities for lark buntings, McCown's longspurs, and horned larks (Table 9). There was no evidence that daily nest survival probabilities differed between interior and edge sites for any of these species or for these species pooled.

As done for the shortgrass versus CRP analyses, I regressed small mammal density against 4 vegetation predictor variables: percent grasses, percent forbs and shrubs, percent cactus, and visual obstruction reading, as well as all pair-wise combinations of these variables yielding 10 models. Model selection using AIC_c resulted in simple models containing few vegetation parameters (Table 10). For thirteen-lined ground squirrel the best model retained a term for percent forbs and shrubs (β = 0.56, 95% CI = 0.02–1.11) and a term for percent grasses (β = 0.43, 95% CI = 0.05–0.81). For grasshopper mouse the best model retained a term for visual obstruction reading (β = 2.58, 95% CI = 0.63–4.53), and for deer mouse the best model retained a term for percent grasses (β = −0.16, 95% CI = −0.38 to 0.07). For thirteen-lined ground squirrel and grasshopper mouse the 95% confidence intervals on vegetation parameters did not cover zero.

Regression of artificial nest survival against thirteen-lined ground squirrel, grasshopper mouse, and deer mouse densities revealed an inverse relation between survival and thirteen-lined ground squirrel densities. For grasshopper mouse and deer mouse 95% confidence intervals on density parameters covered zero (Table 11). A species-specific analysis of natural nest survival using densities of thirteen-lined ground squirrel, grasshopper mouse, and deer mouse as a covariate was not possible due to small sample sizes; hence, I pooled data for lark buntings, McCown's longspurs, and horned larks prior to analysis. None of the parameters from this analysis differed from zero (Table 11).

DISCUSSION

Small Mammals

My prediction that small mammal densities would be greater in CRP fields and edges when compared to shortgrass habitats was supported by my data. Densities of deer mouse were higher in CRP and edges compared to

Table 6. Species-specific counts of the number of distinct small mammal individuals I captured at shortgrass prairie interior and shortgrass prairie–cropland edge sites I sampled in 2000 and 2001, northeastern Colorado, USA.

	2000		2001	
Species	Interior	Edge	Interior	Edge
Thirteen-lined ground squirrel	43	73	34	74
Grasshopper mouse	11	14	14	26
Deer mouse	3	49	5	30
Silky pocket mouse	0	0	0	5
Plains pocket mouse	2	5	0	5
Hispid pocket mouse	0	3	0	4
Ord's kangaroo rat (*Dipodomys ordii*)	0	9	0	9
Prairie vole	3	12	0	13
Plains pocket mouse	0	0	0	1
Western harvest mouse (*Reithrodontomys megalotis*)	0	3	1	10
Meadow vole (*Microtus pennsylvanicus*)	0	0	0	1
Northern pocket gopher (*Thomomys talpoides*)	0	0	1	0
Total count	62	168	55	178

Table 7. Mean mammal densities (no./ha) and 95% confidence intervals (95% CI) for shortgrass prairie interior and shortgrass prairie–cropland edge sites I sampled (n = 16; data pooled across yr) in 2000 and 2001, northeastern Colorado, USA.

	Interior		Edge		Paired differences (interior − edge)	
Species	Mean density	95% CI	Mean density	95% CI	Mean density	95% CI
Thirteen-lined ground squirrel	2.51	1.39–3.62	6.29	3.83–8.76	−3.79	−6.53 to −1.04
Grasshopper mouse	2.16	0.98–3.34	2.90	0.97–4.82	−0.74	−1.96–0.48
Deer mouse	0.31	0–0.68	2.35	0.36–4.34	−2.04	−4.06 to −0.02

Table 8. Mean vegetation differences and 95% confidence intervals (95% CI) for shortgrass prairie interior and shortgrass prairie–cropland edge sites I sampled (n = 16; data pooled across yr) in 2000 and 2001, northeastern Colorado, USA.

	Interior		Edge		Paired differences (interior − edge)	
Vegetation variable	Mean difference	95% CI	Mean difference	95% CI	Mean difference	95% CI
Bare ground (%)	7.3	4.1–10.5	7.0	3.1–10.8	0.3	−3.1–3.7
Grasses (%)	84.6	80.8–88.4	85.1	81.3–88.8	−0.5	−5.3–4.3
Forbs and shrubs (%)	6.0	2.9–9.1	5.7	2.5–8.9	0.3	−2.9–3.6
Cactus (%)	2.5	0.8–4.1	1.7	0.5–2.9	0.8	−0.3–1.9
Green (%)	79.3	69.1–89.6	78.0	69.3–86.6	1.4	−3.3–6.1
Visual obstruction reading (dm)	0.8	0.5–1.0	0.8	0.4–1.3	−0.1	−0.4–0.2

shortgrass prairie, and thirteen-lined ground squirrel densities were higher in edges than in shortgrass prairie. There was no evidence that grasshopper mouse densities differed in either case. More generally, when counts for deer mouse, thirteen-lined ground squirrel, and grasshopper mouse (the 3 species for which density estimates were possible) are removed from the species-specific counts (i.e., Tables 1 and 6), I only captured one additional individual on shortgrass sites, whereas I captured 16 individuals of 4 species on the CRP sites. Furthermore, I captured only 7 individuals of 4 species on interior shortgrass sites, whereas I captured 80 individuals of 8 species on edge sites (counts pooled across yr). Hall and Willig (1994) found a similar pattern, wherein more individuals were captured at CRP sites than at shortgrass sites, though in that study *Reithrodontomys* spp. were the most common species captured, whereas in my study thirteen-lined ground squirrel was the most commonly captured species. Likewise, in comparing interior to riparian edge habitats in West Virginia, USA, Osbourne et al. (2005) found small mammal diversity and abundance of some species was greater in edge habitat. In contrast, in a study of grassland interior and edge habitat in Boulder, Colorado, Bock et al. (2002) found total captures of native rodents were higher in interior than in edge plots. Plots in that study were tallgrass prairie or mixed grassland, and edges were formed by the interface of grassland and suburban habitat. Bock et al. (2002) speculated that domestic and human-commensal predators might explain the negative edge effect in that study. Plots in my study were rural and most were on the PNG so such an effect seems unlikely, though there is evidence from tallgrass prairie–forest edges that mid-sized carnivores, which are potential small mammal predators, preferentially forage near forest edges (Winter et al. 2000).

Species diversity and composition are commonly used as indicators of environmental well-being and are often the targets of restoration efforts (Jordan et al. 1987, Magurran 1988, Hall and Willig 1994, Olson and Brewer 2003). Hall and Willig (1994) found no significant differences in small mammal diversity in comparisons of CRP and shortgrass, but those authors did find differences in species composition. In my study species richness was lower at shortgrass sites compared to CRP or edges, and species composition differed. At CRP sites I captured 7 distinct species compared to 4 species at shortgrass sites, and at edges I captured 11 species compared to 7 species at interior shortgrass sites. Thus, from a restoration perspective (i.e., where the goal would be to restore species richness and composition to its original state), my results and those of Hall and Willig (1994) suggest that for small mammals

Table 9. Mean daily natural nest survival probabilities, number of nests in the sample n, and 95% confidence intervals (95% CI) for shortgrass prairie interior and shortgrass prairie–cropland edge sites I sampled (data pooled across yr) in 2000 and 2001, northeastern Colorado, USA. The difference parameter represents the change in daily survival probability, on a logit scale, due to nesting at an edge site (a positive value means daily survival probabilities were higher at edge sites).

	Interior			Edge			Difference parameter	
Bird species	Mean survival probability	95% CI	n	Mean survival probability	95% CI	n	Mean survival probability	95% CI
Lark bunting	0.959	0.911–0.981	15	0.975	0.900–0.994	17	0.517	−0.690–1.724
McCown's longspur	0.934	0.878–0.965	15	0.985	0.880–0.998	5	1.536	−0.551–3.623
Horned lark	0.929	0.802–0.977	4	0.951	0.586–0.996	3	0.390	−1.946–2.726
Species pooled	0.946	0.916–0.966	34	0.973	0.932–0.990	25	0.733	−0.116–1.582

Table 10. Model selection results from a regression analysis of small mammal density against vegetation variables[a] on shortgrass prairie and shortgrass–cropland edge sites I sampled in 2000 and 2001, northeastern Colorado, USA. Results include the difference in Akaike's Information Criterion corrected for small samples (AIC_c) relative to the best model (ΔAIC_c), the model weight (w_i), and the number of estimated parameters (K) for models with $w_i \geq 0.05$ (i.e., 5%).

Model	AIC_c	ΔAIC_c	w_i	K
Thirteen-lined ground squirrel				
Grass + forbshrb	56.6	0.0	0.31	4
Grass	57.8	1.2	0.17	3
Cactus	58.9	2.3	0.10	3
Forbshrb	59.0	2.4	0.09	3
VOR	59.1	2.5	0.09	3
Grass + VOR	59.3	2.7	0.08	4
Cactus + VOR	59.9	3.3	0.06	4
Forbshrb + VOR	60.1	3.5	0.05	4
Grasshopper mouse				
VOR	26.0	0.0	0.59	3
VOR + forbshrb	27.2	1.2	0.32	4
Deer mouse				
Grass	47.2	0.0	0.32	3
VOR	48.5	1.3	0.16	3
Cactus	49.4	2.2	0.10	3
VOR + grass	49.5	2.3	0.10	4
Grass + forbshrb	49.5	2.3	0.10	4
Forbshrb	49.6	2.4	0.09	3
Grass + cactus	50.5	3.3	0.06	4

[a] % grasses (grass), % forbs and shrubs (forbshrb), % cactus (cactus), and visual obstruction reading (VOR).

CRP is clearly not an acceptable substitute for shortgrass prairie. However, considering that CRP in my study system was a replacement for cropland that was formerly shortgrass prairie, and that most species present on shortgrass sites were also present on CRP sites, then arguably conversion of cropland to CRP may be a beneficial management activity in shortgrass systems. Such activities, however, would also need to consider potential effects on birds and other taxa.

Nest Survival

I assessed effects of mammal density on nest survival using both artificial and natural nests. Use of artificial nests has been much scrutinized in recent years, with many studies concluding that results based on artificial nests may be misleading (Rangen et al. 2000, Zanette 2002, Burke et al. 2004, Moore and Robinson 2004). However, as Villard and Pärt (2004) point out a broader perspective is needed. Specifically, we must "...realize that progress depends on developing model systems that, although not faithful replicas of the in vivo environment, enable the easy and repeatable study of biological phenomena" (Bull and Levin 2000:1409). I discovered few natural nests on trapping webs, which limited inferences about factors associated with nest survival. Hence, artificial nests were useful because they facilitated the study of predation phenomena across habitats.

Daily survival probabilities of artificial nests did not differ in CRP or edge sites compared to shortgrass sites. These results are concordant with Howard et al. (2001), who found no differences in artificial nest predation between CRP and shortgrass sites but differ from Winter et al. (2000), who found survival of artificial nests was lower within 30 m of a tallgrass–forest edge. These contradictory results with respect to edge effects are in line with synthetic reviews of the literature where authors claim field studies do not support the hypothesis that nest predation increases near habitat edges (e.g., Lahti 2001; synthesis of 54 study sites) or that field studies do support the hypothesis that nest predation increases near habitat edges (e.g., Batáry and Báldi 2003; meta-analysis of 64 experiments). Despite the lack of an effect across habitats, artificial nest survival in my study was inversely proportional to thirteen-lined ground squirrel densities in interior shortgrass and edge habitats. Whereas this result is consistent with other studies describing thirteen-lined ground squirrel as an important nest predator (With 1994, Dion et al. 2000, Pietz and Granfors 2000, Renfrew and Ribic 2003), I did not observe a similar effect in grassland and CRP habitats. Although natural nest data in my study were too sparse to analyze at grassland and CRP sites, Howard et al. (2001) found no differences in natural nest survival across shortgrass prairie and CRP sites. Analysis of natural nest data at interior shortgrass and edge sites showed that, in contrast to my prediction, natural nest survival was slightly higher on edges for 3 bird species (Table 9), though confidence intervals in all cases covered zero. A similar pattern of higher nest survival along woodland edges in the mixed-grass prairie was reported by Grant et al. (2006). In that study thirteen-lined ground squirrel was the most common predator of eggs and young, but unlike in my study, abundance of thirteen-lined ground squirrel was lower near edges. My data thus do not support the prediction that daily survival probabilities of ground-nesting grassland bird nests are negatively correlated with densities of small mammals. However, this conclusion must be tempered by the fact that sample sizes for natural nests were small and insufficient power may have existed to detect differences.

Table 11. Results of a regression analysis of artificial nest and natural nest (data pooled for lark buntings, McCown's longspurs, and horned larks) daily survival probabilities against densities of thirteen-lined ground squirrel, grasshopper mouse, and deer mouse on shortgrass prairie and shortgrass–cropland edge sites I sampled in 2000 and 2001, northeastern Colorado, USA.

Predictor variable	Parameter estimate	95% CI
Artificial nests		
Thirteen-lined ground squirrel density	−0.009	−0.014 to −0.003
Grasshopper mouse density	−0.010	−0.026 to 0.007
Deer mouse density	0.004	−0.007 to 0.014
Natural nests		
Thirteen-lined ground squirrel density	−0.059	−0.167 to 0.049
Grasshopper mouse density	−0.092	−0.241 to 0.057
Deer mouse density	0.307	−0.024 to 0.638

MANAGEMENT IMPLICATIONS

My data strongly support the notion that land-use patterns on the shortgrass prairie alter the small mammal community. One implication of my results is that CRP, from a

management standpoint, should not be considered a replacement for shortgrass prairie even though it may represent a marked improvement over the cropland it replaces as a cover type. A second implication is that if a management objective is to maintain small mammal communities on the shortgrass prairie in their original state, then efforts should be focused on preventing the conversion of shortgrass prairie to cropland, because such prevention will reduce habitat loss and creation of edges that alter the mammal community and potentially other biological responses.

Nesting data in my study—at the spatial scale and sample sizes I examined—failed to support the hypothesis that ground-nesting grassland bird nest survival is reduced at high small mammal densities. The implication is that managers should not assume undertaking management activities that alter the small mammal community will have no effect on avian nesting success. Rather, it would be prudent for managers to execute management activities in tandem with well-designed field studies that monitor effects of the management activity on avian nest survival.

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