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RESEARCH ARTICLE

Importance of agricultural landscapes to nesting burrowing owls in the Northern Great Plains, USA

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Abstract Anthropogenic habitat loss and fragmentation are the principle factors causing declines of grassland birds. Declines in burrowing owl (*Athene cunicularia*) populations have been extensive and have been linked to habitat loss, primarily the decline of black-tailed prairie dog (*Cynomys ludovicianus*) colonies. Development of habitat use models is a research priority and will aid conservation of owls inhabiting human-altered landscapes. From 2001 to 2004 we located 160 burrowing owl nests on prairie dog colonies on the Little Missouri National Grassland in North Dakota. We used multiple linear regression and Akaike's Information Criterion to estimate the relationship between cover type characteristics surrounding prairie dog colonies and (1) number of owl pairs per colony and (2) reproductive success. Models were developed for two spatial scales, within 600 m and 2,000 m radii of nests for cropland, crested wheatgrass (*Agropyron cristatum*), grassland, and prairie dog colonies. We also included number of patches as a metric of landscape fragmentation. Annually, fewer than 30% of prairie dog colonies were occupied by owls. None of the models at the 600 m scale explained variation in number of owl pairs or reproductive success. However, models at the 2,000 m scale did explain number of owl pairs and reproductive success. Models included cropland, crested wheatgrass, and prairie dog colonies. Grasslands were not included in any of the models and had low importance values, although percentage grassland surrounding colonies was high. Management that protects prairie dog colonies bordering cropland and crested wheatgrass should be implemented to maintain nesting habitat of burrowing owls.

Keywords Athene cunicularia · Black-tailed prairie dog · Burrowing owl · Crested wheatgrass · *Cynomys ludovicianus* · Fragmentation · Grassland · Habitat selection

Introduction

Anthropogenic habitat loss and fragmentation are the principle causes of species declines worldwide. Fragmentation typically decreases amount of available habitat and increases degree of isolation and edge/area ratios of remaining patches (Wilcove et al. 1986; Saunders et al. 1991; Andrén 1994; Wiens 1994; Fahrig 2003). Within the Great Plains of North America, over 80% of native grasslands have been lost. In the most impacted areas of the tallgrass

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prairie, less than 0.1% of original grassland persists; most has been put into agricultural production (Sampson and Knopf 1994; Vickery et al. 1999; Askins et al. 2007). Moreover, remaining grassland patches often become unsuitable with time because of fire suppression, removal of native grazers, pollution, and species introductions. As a consequence, grassland birds have shown the most consistent, widespread declines of any avian assemblage (Knopf 1994; Peterjohn and Sauer 1999; Vickery and Herkert 2001; Brennan and Kuvlesky 2005; Askins et al. 2007). Species vulnerability seems to be related to habitat use, with specialists showing the swiftest and sharpest declines [e.g., Cassin's sparrow (*Aimophila cassinii*) and grasshopper sparrow (*Ammodramus savannarum*)]. In contrast, some generalists seem to benefit from human-altered landscapes that create a mosaic of habitats, particularly those species associated with woody or brushy edges [e.g., red-winged blackbird (*Agelaius phoeniceus*), brown-headed cowbird (*Molothrus ater*)].

Deteriorating status of burrowing owl (*Athene cunicularia*) populations coincides with the declines of other grassland birds. Burrowing owls are extirpated from Manitoba, Minnesota, and eastern North Dakota, and current populations in Alberta and Saskatchewan are 85–95% smaller than those that existed in the late 1980s (Martell et al. 2001; Murphy et al. 2001; Shyry et al. 2001; Skeel et al. 2001; Wellicome and Holroyd 2001). There is mounting evidence that declines of burrowing owls reflect decreases in populations of fossorial mammals, primarily black-tailed prairie dogs (*Cynomys ludovicianus*) and ground squirrels (*Spermophilus* spp.), species on which owls rely for nest burrows (Haug et al. 1993; Desmond et al. 2000; Restani et al. 2001; Smith and Lomolino 2004). Range of prairie dogs after a century of poisoning, habitat conversion, and sylvatic plague (*Yersinia pestis*) is 2–10% of the historic distribution (Miller et al. 1994; Forrest 2005). Increasing the distribution and abundance of prairie dogs to improve status of owls, however, is unlikely to occur because state and federal natural resources agencies are pressured to keep prairie dog populations at or below existing levels.

Although burrowing owls in the Great Plains are highly dependent upon prairie dogs for nest sites, foraging activity during the breeding season is not restricted to the immediate nest area. For example, owls nesting in agroecosystems devoid of prairie dogs will travel nearly 3 km to foraging sites and their home range size averages over 2 km^2 (Haug and Oliphant 1990; Gervais et al. 2003). We are unaware of any studies reporting foraging behavior of radio-tagged burrowing owls nesting in prairie dog colonies, but it is likely that landscape structure surrounding nests also plays an important role in decisions regarding habitat use. In Colorado, the percentage of shortgrass prairie in the landscape surrounding prairie dog colonies occupied by nesting owls is less than that surrounding unoccupied colonies (Orth and Kennedy 2001). In Saskatchewan north of prairie dog range, owls also nest in grassland patches embedded within an agricultural matrix (Warnock and James 1997). Although these studies determined factors affecting occupancy, the relationship between demographic parameters and landscape structure remains unknown but is needed to guide conservation by identifying high quality habitat.

A hierarchy of decisions is thought to govern habitat selection (Hildén 1965; Johnson 1980), and biologists must consider habitat attributes at several spatial scales when developing conservation plans for declining and rare species (Wiens 1994). For example, mostly intact grasslands may be important to burrowing owls at the largest spatial scales of the geographic range (i.e., first-order selection), but a mixture of vegetation types accompanying fragmentation may be important at smaller spatial scales around the nest within the home range (i.e., third order selection, Johnson 1980). We evaluate aspects of this hypothesis by examining habitat use and reproductive success of nesting owls at two spatial scales on the Little Missouri National Grassland (hereafter, Little Missouri) in North Dakota. Parcels of public land of native prairie exist in a matrix of private landownership dominated by varying mixture of cropland and exotic grassland typical of the northern Great Plains. The multiple-use landscape includes activities along a continuum of intensity, from recreation to cattle grazing to row crop farming. Despite a 90% decline of prairie dogs on the Little Missouri since the late 1800s (Bishop and Culbertson 1976; Sidle et al. 2001), the species continues to provide the vast majority of burrows used by nesting owls (Murphy et al. 2001; Davies and Restani 2006). However, each year less than half of the colonies are occupied by owls, so the presence of nest burrows alone is an insufficient cue during habitat selection. We predicted that burrowing owls would nest most often and have higher reproductive success on prairie dog colonies embedded within more fragmented grasslands because agroecosystems rather than intact grasslands often contain higher abundance of small mammals, passerines, and insects (Best et al. 1997; Jonsen and Fahrig 1997; Sissons et al. 2001; Olson and Brewer 2003; Moulton et al. 2006), the primary prey of nesting owls.

Methods

Study area

We conducted research on the Little Missouri, an area in western North Dakota, USA (47°15′ N, 103°30′ W) administered by the U.S. Forest Service. Severe drought in the 1930s combined with poor landuse practices led to purchase of the grasslands under the Bankhead-Jones Farm Tenant Act of 1937. East to west contraction of burrowing owl range has encroached on the Little Missouri, where the owl is considered a "sensitive species" (Murphy et al. 2001; Wellicome and Holroyd 2001). Approximately 62% of total land area (8,620 km^2) within the boundaries of the Little Missouri was managed by state and federal natural resource agencies: U.S. Forest Service (87%), North Dakota (8%), and National Park Service (5%) (Murphy et al. 2001). The remainder was privately owned. Land use across public and private lands included livestock grazing, dryland farming (mostly hay land and small grains, some configured in strips), oil drilling and extraction, and a national park. Recreational shooting of prairie dogs occurred throughout the year, but was concentrated from late May to mid-June.

Black-tailed prairie dog colonies occupied approximately 1,800 ha on the Little Missouri (Sidle et al. 2001; Davies and Restani 2006). Topography was flat to rolling mixed-grass prairie interspersed with rugged badlands, with elevations ranging from 600 to 900 m. Prairie vegetation was dominated by grasses (*Bouteloua*, *Pascopyrum*, and *Stipa* spp.) and shrubs (*Artemisia*, *Shepherdia*, and *Symphoricarpos* spp.). Riparian areas supported plains cottonwood (*Populus deltoides*), box elder (*Acer negundo*), and willows (*Salix* spp.), whereas open stands of ponderosa pine (*Pinus ponderosa*) and juniper (*Juniperus scopulorum*) dominated hillsides within badlands. Climate was semi-arid, with mean annual precipitation of about 35 cm.

Field procedures

We conducted field research from early May to late August 2001–2004. We used spotting scopes (15–45×) and binoculars (10×) to survey prairie dog colonies for nesting burrowing owls, concentrating effort in early morning (05:00–10:00 MDT) and late afternoon (17:00–22:00), daytime periods when owls are most active and visible (Haug and Oliphant 1990). We repeatedly surveyed colonies in May and June from a vehicle and on foot and used presence of owls, whitewash, shredded cow dung, and owl pellets to identify colonies occupied by nesting owls (Restani et al. 2001). We defined an owl pair (i.e., a nesting attempt) as a male and female owl regularly associated with a burrow (Desmond and Savidge 1996). The locations of nest burrows were recorded using a Global Positioning System (GPS) (Garmin, Olathe, KS, USA). We did not survey prairie dog colonies on state and private lands and did not search for owls off of prairie dog colonies. Nest burrows were repeatedly revisited in mid to late July to estimate brood size when young averaged 31–39 days old (Davies and Restani 2006). We estimated reproductive success from brood size by observing nest burrows for at least 30 min during mornings, and recorded the maximum number of young observed outside the burrow at one time. Although our maximum counts likely underestimated brood size (Gorman et al. 2003), we believe detectability was similar among nests because of the uniform, low height of vegetation on prairie dog colonies.

Habitat analysis

We defined burrowing owl habitat as the sum total of characteristics of an area (e.g., prey, nest burrows) that produced occupancy (Hall et al. 1997; Jones 2001). In our study, habitat use was equated with the distribution of burrowing owl nests on prairie dog colonies. Habitat quality varied along a continuum from poor to high, and was ranked based on owl reproductive success (i.e., brood size) not nesting density (Van Horne 1983; Hall et al. 1997), although the two parameters are often positively correlated (Bock and Jones 2004).

We obtained Geographic Information System (GIS) data of land cover types and prairie dog colonies on the Little Missouri from the U.S. Forest Service. Land cover data of 30-m spatial resolution were generated using Satellite Imagery Land Cover (SILC) obtained in 2000. These data were ground-truthed by the U.S. Forest Service. Perimeters of prairie dog colonies were mapped in 2001 on foot or by driving an all terrain vehicle along the edge of the colony while plotting boundary locations of active prairie dog burrows (i.e., fresh diggings and scat) with a gimbal-mounted GPS unit. We used ArcGIS 9.0 (ESRI 2004) to analyze cover type data.

We categorized SILC data by life form into eight cover types: cropland (hay land and small grains), grassland, shrubland [primarily sagebrush (*Artemisia* spp.)], crested wheatgrass (*Agropyron cristatum*), broadleaf forest, coniferous forest, badlands, and water. We created 600-m and 2,000-m buffers around a point centered within prairie dog colonies with and without nesting owls (Orth and Kennedy 2001), and used the intersect tool (ArcGIS) to determine area (ha) of the eight land cover types within buffers. We used the same technique to determine area of prairie dog colonies within the buffers. Radii of 600 m and 2,000 m had biological significance because burrowing owls spent approximately 95% of their time foraging within 600 m of nests (Haug and Oliphant 1990), and because maximum range from nests during foraging on the Little Missouri was approximately 2,000 m (R. Olson, unpublished data). The 600-m radius was embedded within the 2,000-m radius.

Cover type variables in our models only included cropland (CR), crested wheatgrass (CW), grassland (GR), and prairie dog colony habitat (PD). We incorporated native vegetation, which was composed of shrubland and grassland, into a grassland category (shrubland averaged only 12–15% of the combined category). We selected these four cover types because of their demonstrated or presumed relationship to habitat use of nesting burrowing owls (Rich 1986; Warnock and James 1997; Clayton and Schmutz 1999; Desmond et al. 2000; Orth and Kennedy 2001). We expected that increasing grassland and prairie dog area would promote owl use. Crested wheatgrass may mimic natural grasslands when birds select nesting habitat (Sutter and Brigham 1998; Davis and Duncan 1999; Lloyd and Martin 2005), so we assumed it also would increase probability of owl use. Burrowing owl nest sites in other study areas were often surrounded by fragmented habitat containing cropland, and biologists have speculated that prey abundance may be greater in fragmented grasslands, thus prompting selection by owls for these landscapes (Rich 1986; Orth and Kennedy 2001; Moulton et al. 2006). However, the relationship between amount of cropland in the landscape and owl use was likely quadratic, with intermediate levels of cropland around prairie dog colonies supporting a higher density of owls than either very low or very high amounts of cropland (e.g., Schmutz 1989). We expected that area (ha) of prairie dog colonies would be positively correlated with owl use because this habitat feature was strongly correlated with size and trend of burrowing owl populations in the central Great Plains (Desmond et al. 2000). Finally, we included number of different cover type patches (NP) (i.e., the number of polygon pieces) within buffers as a direct measure of landscape fragmentation (Gutzwiller and Barrow 2002). Landscape fragmentation increased with number of patches.

Statistical analysis

All five explanatory variables had reasonable ranges in value at both spatial scales (Table 1), which is a prerequisite for model building (Hirzel and Guisan 2002). Before developing models, we determined if any variables were correlated within and across spatial scales (Table 2). High positive correlations existed between similar habitat variables measured at the 600-m and 2,000-m scales ($CR = 0.82$, $CW = 0.75$, $GR = 0.60$, $PD = 0.84$, $NP = 0.52$), probably because of non-independence (i.e., the 600-m radius was embedded in the 2,000-m radius). Therefore, we did not include in the list of candidate models any with the same variables at both spatial scales. Moreover, we did not include models containing the following pairs of variables because they were highly correlated (each negatively): GR and CW at 600 m, GR and PD at 600 m, and CR and GR at 2,000 m. Given these constraints, we derived a suite of 20 candidate models, of the general form:

$$\mathrm{Owl}_{\mathrm{pairs}} = \left(e^{\beta_0+\beta_1 CR+\beta_2 CW+\beta_3 PD+\beta_4 NP+\beta_5 GR}\right) - 1. \tag{1}$$

Finally, we did not examine interactions among variables given the relatively small sample size.

Table 1 Summary statistics for variables considered in modeling habitat use by burrowing owls on the Little Missouri National Grassland, North Dakota, 2001–2004

Buffer radius	Cover type variable	Mean	Minimum		Median		Maximum (100 percentile)
			(0 percentile)	(25 percentile)	(50 percentile)	(75 percentile)	
600 m	CR	2.0	0.0	0.0	0.0	0.0	32.7
	CW	13.1	0.0	0.0	3.2	18.7	87.2
	GR	65.1	17.7	48.0	67.0	84.9	100.4
	PD	20.4	0.3	7.3	14.2	26.3	85.8
	NP	26.8	10	20	26	34	57
2,000 m	CR	76.5	0.0	0.0	0.4	83.5	850.3
	CW	93.6	0.0	10.0	40.4	129.6	463.6
	GR	845.3	223.2	767.8	884.2	978.3	1121.2
	PD	31.2	0.3	8.9	19.6	49.9	121.9
	NP	157.2	57	117	152	187	325

Sample size: $n = 72$ prairie dog colonies

CR = Cropland, CW = Crested wheatgrass, GR = (Shrubland + grassland), PD = Prairie dog colony, NP = Number of patches; CR, CW, GR, and PD in ha

Table 2 Correlation matrix for variables considered in modeling habitat use by burrowing owls on the Little Missouri National Grassland, North Dakota, 2001–2004

	GR	CW	PD	NP
600-m radius				
CR	−0.40	0.27	−0.03	0.02
GR		−0.60	−0.51	−0.19
CW			−0.21	−0.33
PD				0.23
2,000-m radius				
CR	−0.76	0.21	−0.08	−0.31
GR		−0.43	0.15	0.01
CW			−0.05	−0.47
PD				−0.21

Sample size: $n = 72$ prairie dog colonies

CR = Cropland, CW = Crested wheatgrass, GR = (Shrubland + grassland), PD = Prairie dog colony, NP = Number of patches

We initially considered using Poisson or negative binomial distributions in a generalized linear modeling framework because the response variable for each year was a count of the number of burrowing owl pairs within a prairie dog colony (McCullagh and Nelder 1989). However, we chose to define the response variable as the mean number of owl pairs across the four study years because (1) surrounding habitats did not change year-to-year from estimates obtained in 2000 and (2) because our main interest was addressing "On average, how many owl pairs can be expected to occupy a prairie dog colony based on surrounding cover types?". Therefore, based on Johnson (1995), we used multiple linear regression with ordinary least squares (Freund and Littell 2000) to model mean number of owl pairs as a function of CR, CW, GR, PD, and NP. We log-transformed the mean number of owl pairs to accommodate a few prairie dog colonies that consistently had high numbers of owl pairs. A value of 1.0 was added to all owl pairs prior to transformations to accommodate prairie dog colonies that never were occupied by nesting owls (Steel and Torrie 1980). Although 60% of colonies never had owls, we did not use logistic regression to model presence-absence of owl pairs because our interest focused on modeling numbers of owls not simply likelihood of occurrence.

We conducted the same modeling to determine the mean brood size of burrowing owls based on surrounding cover types and number of patches. Prior to modeling, we averaged brood size for each occupied colony across the four years of study to obtain an estimate of reproductive success.

We used an information-theoretic model selection approach (Burnham and Anderson 2002) and PROC REG (SAS 2004) to estimate the relationship between explanatory variables and burrowing owl pairs or reproductive success. We did not split the data into a training data set and test data set, but rather used all observations for model building and report two summary statistics, adjusted R^2 and adjusted PRESS R^2 (Myers et al. 2002), to assist in evaluating the overall fit of candidate models.

In some models the number of samples was small relative to the number of parameters ($n/K < 40$), so we used Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_C}$) during model selection procedures (Burnham and Anderson 2002). Models with the lowest $\Delta\mathrm{AIC_C}$ values (<3) were considered the most parsimonious and received the strongest support. We also calculated Akaike's weights (w_i) and the relative importance of each habitat variable (i.e., by summing w_i values), which provided better insight for the importance of a single variable than from what could be surmised from the entire model set (Burnham and Anderson 2002). To estimate final model parameters, we calculated model-averaged parameter estimates based on re-scaled Akaike weights (Burnham and Anderson 2002) across all candidate models. Standard errors of model-averaged parameter estimates were calculated from unconditional variances across all candidate models including model uncertainty.

Results

From 2001 to 2004, we searched for nesting burrowing owls on 72 prairie dog colonies, averaging 24.6 ± 3.2 ha, located on public land of the Little Missouri. Colonies were dispersed across the 8,620 km^2 Little Missouri and totaled approximately 1,745 ha. Number of nesting pairs varied from 31 in 2001 to 47 in 2003 and 2004 (Table 3). Each year, 40–65% of colonies occupied by owls contained only one breeding pair (range 1–13 pairs per colony, Fig. 1). Size of prairie dog colony was a poor predictor of nesting density ($r^2 = 0.20$, $P < 0.001$, $y = -0.003x + 0.25$, $n = 72$). Grassland was the most common cover type surrounding nests at both spatial scales.

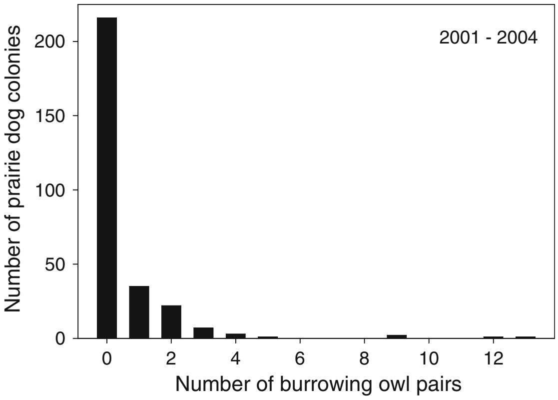

Fig. 1 Number of burrowing owl pairs per black-tailed prairie dog colony on the Little Missouri National Grassland, North Dakota, 2001–2004. The number of colonies per year ($n = 72$) was summed across years

Owls produced a mean 3.4 ± 0.4 young per pair in 2001 (range 0–7, $n = 31$), 3.7 ± 0.3 young per pair in 2002 (range 0–9, $n = 35$), 2.6 ± 0.3 young per pair in 2003 (range 0–7, $n = 47$), and 3.5 ± 0.3 young per pair in 2004 (range 0–7, $n = 47$). Seven pairs failed to fledge young in 2001, three pairs failed in 2002, 12 pairs failed in 2003, and six pairs failed in 2004.

Two of the 20 candidate models predicting number of owl pairs per colony had $\Delta\mathrm{AIC_C}$ values <3.0 (Table 4). All other models had $\Delta\mathrm{AIC_C}$ values >9.0, and therefore provided little insight into habitat use by nesting burrowing owls. Cropland, crested wheatgrass, and prairie dog colonies had the highest relative importance values of the five variables considered (Table 5). The two top ranked models explained >50% of the observed variation in number of burrowing owl pairs (adjusted R^2), and >40% of the variation in predicted owl pairs (adjusted PRESS R^2). Only one of the 20 candidate models predicting

Table 3 Distribution and abundance of burrowing owls nesting on the Little Missouri National Grassland, North Dakota, 2001–2004

Year	Number of owl pairs	Nearest neighbor distance (km)		% of prairie dog colonies occupied by nesting owls
		Mean (SE)	Range	
2001	31	4.5 (1.5)	0.035–38.0	28 (20 of 72 colonies)
2002	35	2.3 (1.0)	0.020–26.3	24 (17 of 72 colonies)
2003	47	1.4 (0.6)	0.045–23.3	21 (15 of 72 colonies)
2004	47	1.7 (0.6)	0.041–23.2	28 (20 of 72 colonies)

Table 4 Results of the best five habitat use models for predicting number of owl pairs (log [burrowing owl pairs + 1.0], top) and reproductive success (log [mean brood count + 1.0], bottom) based on $n = 72$ prairie dog colonies on the Little Missouri National Grassland, North Dakota, 2001–2004

Buffer	Model	K	RSS	Log L	$\Delta \mathrm{AIC}_{\mathrm{C}}$	w_{i}	Adj. R^2	PRESS Adj. R^2
Number of pairs								
2,000 m	CR + PD + CW	5	6.98	84.00	0.00	0.5758	0.52	0.43
2,000 m	CR + CW	4	7.28	82.51	0.65	0.41571	0.51	0.43
2,000 m	GR + NP	4	8.20	78.23	9.22	0.00573	0.45	0.38
2,000 m	GR + PD + NP	5	8.16	78.41	11.18	0.00216	0.44	0.36
2,000 m	CR + NP	4	8.92	75.18	15.33	0.00027	0.40	0.30
Reproductive success								
2,000 m	CR + PD + CW	5	19.03	47.90	0.00	0.94570	0.44	0.36
2,000 m	CR + CW	4	21.70	43.18	7.12	0.02687	0.37	0.32
2,000 m	GR + PD + CW	5	21.07	44.24	7.32	0.02438	0.38	0.29
600 m	CR + PD + CW	5	22.61	41.69	12.41	0.00191	0.33	0.25
2,000 m	GR + CW	4	23.82	39.82	13.85	0.00093	0.30	0.25

CR = Cropland, CW = Crested wheatgrass, GR = (Shrubland + grassland), PD = Prairie dog colony, NP = Number of patches

Table 5 Importance values and model averaged parameter estimates (2,000-m buffer only) for habitat use by burrowing owls on the Little Missouri National Grassland, North Dakota, 2001–2004

Cover type variable	Relative importance	Parameter (SE)
Number of pairs		
CR	0.99190	0.00132 (0.00025)
CW	0.99171	0.00191 (0.00034)
PD	0.57817	0.00209 (0.00124)
NP	0.00825	−0.00392 (0.00077)
GR	0.00806	−0.00123 (0.00024)
Intercept	–	−0.01020 (0.08474)
Reproductive success		
CW	0.99783	0.00297 (0.00056)
CR	0.97255	0.00140 (0.00040)
PD	0.97020	0.00631 (0.00205)
GR	0.02550	−0.00087 (0.00042)
NP	0.00020	−0.00380 (0.00137)
Intercept	–	−0.02580 (0.13330)

CR = Cropland, CW = Crested wheatgrass, GR = (Shrubland + grassland), PD = Prairie dog colony, NP = Number of patches

reproductive success of owls had a $\Delta \mathrm{AIC}_{\mathrm{C}}$ value <3.0 (Table 4), and it also included cropland, crested wheatgrass, and prairie dog colonies. The model explained 44% of the observed variation in reproductive success of burrowing owl pairs (adjusted R^2), and 36% of the variation in predicted reproductive success (adjusted PRESS R^2). Cropland, crested wheatgrass, and prairie dog colonies also had the highest importance values (Table 5).

Discussion

Each year, burrowing owls nested on a minority (<30%) of prairie dog colonies on the Little Missouri and landscape composition surrounding colonies at the 2,000-m scale correlated with both the number of owl pairs per colony and their reproductive success. Landscapes composed of relatively high amounts of crested wheatgrass, cropland, and prairie dog colonies predicted owl distribution and productivity, whereas the amount of grassland and the number of habitat patches, a metric of landscape fragmentation, were unimportant at both spatial scales. All of the models at the 600-m scale failed to predict owl use or reproductive success.

Burrowing owls nesting in the northern Great Plains are closely associated with prairie dogs (Murphy et al. 2001; Restani et al. 2001; Davies and Restani 2006). However, on the Little Missouri, only one habitat use model at the 2,000-m scale revealed a positive effect of prairie dogs on the number of owls nesting per colony. It appeared, therefore, that once requirements of a nest burrow were met at the local scale, prairie dogs became relatively unimportant in habitat use at larger scales, such as that associated with foraging. Many studies have shown that owls nested on prairie dog colonies in areas of low vegetative cover and high prairie dog density (30–75 m radius from nests) (Plumpton and Lutz 1993; Desmond and Savidge 1996; Restani et al. 2001; Lantz et al. 2007). These characteristics apparently improved nest success by reducing predation on incubating females and flightless young (Desmond and Savidge 1999) and by providing habitat for young during the post-fledging period (Davies and Restani 2006). Our data further supported these observations because model importance value of prairie dog colonies was much higher for reproductive success than for number of owl pairs per colony.

Although prairie dog colonies on the Little Missouri comprise the smallest percentage of cover types around nests at the 2,000-m scale, presence of prairie dogs in models for both number of owls per colony and reproductive success supports the proposition that prairie dogs have disproportionate effects on grassland ecosystems by maintaining high biological diversity (Miller et al. 1994; Smith and Lomolino 2004). Protecting and fostering growth of existing prairie dog colonies and promoting new colonies through translocation would contribute significantly to owl conservation. During this study, occupied range of prairie dogs in western North Dakota was approximately 10% of historic distribution (Bishop and Culbertson 1976; Sidle et al. 2001). Any future loss of colonies from poisoning, habitat conversion, or sylvatic plague will likely threaten population persistence of burrowing owls (Desmond et al. 2000; Restani et al. 2001). Owl range has contracted hundreds of kilometers from north to south and from east to west within the northern Great Plains during the past 50 years (Murphy et al. 2001; Shyry et al. 2001; Skeel et al. 2001; Wellicome and Holroyd 2001), probably from the combined effect of converting native prairies to agricultural cover types and suppressing prairie dog populations.

Crested wheatgrass often is a component of seed mixtures planted as part of the Conservation Reserve Program (CRP) in western prairies. Although CRP functions primarily to control erosion by retiring unproductive agricultural lands, it also is habitat for nesting birds (Johnson and Schwartz 1993; Best et al. 1997; Coppedge et al. 2001). Crested wheatgrass is an exotic species and is popular among farmers because of its growth characteristics, grazing tolerance, and relatively inexpensive cost. How well monocultures of crested wheatgrass mimic native grassland, however, remains largely unresolved and a source of conservation concern (Deluca and Lesica 1996; Christian and Wilson 1999). For example, chestnut-collared longspurs (*Calcarius ornatus*) do not discriminate between crested wheatgrass and native grasses when selecting nest sites, but nesting pairs suffer lower productivity in the exotic habitat type, which may have dire consequences for persistence of this declining grassland obligate (Lloyd and Martin 2005). In contrast, crested wheatgrass was positively associated with the number of burrowing owl pairs per colony and reproductive success on the Little Missouri, and at least two possibilities existed for this pattern. First, owls may have been unable to detect a difference between crested wheatgrass and native grasses because of their similar structure and appearance. Alternatively, owls may have nested in prairie dog colonies near fields of crested wheatgrass because they provided increased prey abundance or availability. Crested wheatgrass began growing earlier than native grasses, and harbored higher numbers of mammalian prey than native grassland in spring (R. Olsen, unpublished data), a critical time period when female owls mobilize resources for egg production. Moreover, crested wheatgrass monocultures contained high proportions of bare ground (Sutter and Brigham 1998; Christian and Wilson 1999), a condition which has facilitated detection of invertebrate prey by foraging birds (Atkinson et al. 2004; Butler and Gillings 2004).

Presence of cropland surrounding prairie dog colonies also was a strong predictor of the number of owl pairs per colony and reproductive success, and the variable had high model importance values. Although amount of cropland surrounding nests was small relative to most other cover types, its occurrence may have been important because owl prey species (e.g., small mammals, passerines, insects) have occurred at highest abundance in areas containing a mixture of native grasslands and cropland (Jonsen and Fahrig 1997; Robinson et al. 2001; Sissons et al. 2001; Olson and Brewer 2003; Moulton et al. 2006). Moreover, owls preferred to forage along habitat edges (Rich 1986; Haug and Oliphant 1990; Rosenberg and Haley 2004), and consumed more small mammals following crop harvest, presumably because of increased prey vulnerability (Bellocq 1997).

Although the percentage of grasslands surrounding colonies was the highest of all cover types at both spatial scales, grassland was not included in any of the top models and had low importance values. Percentage grassland also was unimportant in core owl habitat at either 2.7-km or 20-km radius scales in Saskatchewan (Warnock and James 1997), and colonies occupied by owls in Colorado had a smaller percentage of the surrounding landscape in shortgrass prairie than unoccupied colonies (Orth and Kennedy 2001). Burrowing owls nested in intensive agroecosystems in California (Rosenberg and Haley 2004) and Idaho (Moulton et al. 2006) that were outside the range of prairie dogs, which suggested native vegetation was not necessary to support owl populations as long as some nest burrows were available. Historically, in the Great Plains, however, amount of grassland was probably closely tied to prairie dogs and declines in the latter were highly correlated with loss of owls in Nebraska (Desmond et al. 2000). Burrow availability on prairie dog colonies is high and allows groups of owls to nest semi-colonially, a condition generally different from that found in agroecosystems.

The number of patches of different cover types, an indicator of landscape fragmentation, did not affect habitat use or reproductive success at either spatial scale. In contrast to our findings, burrowing owls in Colorado and Saskatchewan nested within more fragmented landscapes at the 2.0 to 20-km radius spatial scales (Warnock and James 1997; Orth and Kennedy 2001). Differences in the amount of different cover types within 2,000 m of nests among the study areas may have contributed to the varying effects reported. On the Little Missouri, approximately 70% of the area within 2,000-m radii of nests was grassland (not including prairie dog colonies), which was higher than that reported from Colorado (about 60%) (Orth and Kennedy 2001).

How much landscape in the northern Great Plains can be converted to agricultural cover types before negatively impacting burrowing owls remains unknown and needs to be determined. In general, many species, such as prairie dogs, decline with increasing agricultural intensification (review by Benton et al. 2003). Most of the landscape on the Little Missouri remains in native condition, and it appears that the current level of heterogeneity derived from cropland and crested wheatgrass on private lands adjacent to prairie dog colonies on the Little Missouri is beneficial to owls. The mechanism driving this association remains unknown. Although intensive agricultural landscapes contain less spatial and temporal heterogeneity than natural landscapes, a species that requires heterogeneous landscapes can meet its needs by exploiting different cover types across short time scales or by using different cover types as they become available (Benton et al. 2003). We are currently evaluating which strategy radio-tagged burrowing owls employ when foraging on the Little Missouri.

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