Do land-use patterns influence nest-site selection by burrowing owls (*Athene cunicularia hypugaea*) in northeastern Colorado?

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Abstract: Populations of western burrowing owls (*Athene cunicularia hypugaea*) are declining. In the Great Plains this decline maybe related to a decline in black-tailed prairie dog (*Cynomys ludovicianus*) towns that the owls use for nest sites. One potential cause of prairie dog decline is conversion of native prairie to agriculture. We predicted that owl-occupied prairie dog towns would be in less fragmented landscapes that contain more prairie then owl-unoccupied prairie dog towns. To test this prediction, we used a geographic information system and spatial analysis metrics to examine the landscape within 1000 and 2500 m radius circles surrounding prairie dog towns in the shortgrass prairie in northeastern Colorado. We compared landscape features of irrigated cropland, non-irrigated cropland, and shortgrass patches around owl-unoccupied (N = 7) and owl-occupied (N = 15) prairie dog towns at these two spatial scales. Contrary to our predictions, at the 2500-m scale burrowing owls prefer to nest in towns surrounded by a landscape in which shortgrass patches were a smaller percentage of the total landscape, relatively far apart from other shortgrass patches, and more numerous then crop patches. At the 1000-m scale owls nested in towns in which shortgrass patches were a smaller percentage of the total surrounding landscape. In Logan County owls may select nest sites in prairie dog towns in more fragmented landscapes because prey availability maybe higher than in less fragmented landscapes and (or) prairie dog control programs may be more active on shortgrass rangelands than in croplands. In addition, the level of fragmentation in our study area (62% of the study area is occupied by native grassland) may not be high enough to have negative consequences on nest occupancy of burrowing owls. However, it is difficult to generalize about the effects of landscape fragmentation on burrowing owls because any effects are probably a complex function of local habitat structure, landscape structure, and local prey and predator availability.

Résumé : Les populations de la Chevêche des terriers de l'ouest (*Athene cunicularia hypugaea*) sont en déclin. Dans les Grandes Plaines, il se pourrait que ce déclin soit relié à la diminution du nombre de villages de Chiens-de-prairie à queue noire (*Cynomys ludovicianus*) qui servent de sites de nidification aux chevêches. L'une des causes probables du déclin des chiens-de-prairie est la conversion de la prairie originale en terres agricoles. Nous avons prédit que les villages de chiens-de-prairie utilisés par les chevêches étaient plus susceptibles de se trouver dans des paysages moins fragmentés contenant plus de prairie que de villages inoccupés de chiens-de-prairie. Pour vérifier cette prédiction, nous avons utilisé un système d'information géographique et des mesures d'analyse spatiale pour faire l'examen du paysage dans un rayon de 1000 à 2500 m de villages de chiens-de-prairie dans la prairie d'herbe courte du nord-est du Colorado. Nous avons comparé les caractéristiques du paysage dans des terres cultivées irriguées, des terres de culture non irriguées et des zones d'herbes courtes autour de villages de chiens-de-prairie non occupés par des chevêches (N = 7) et des villages occupés (N = 15) à ces deux échelles spatiales. Contrairement à nos prédictions, à l'échelle de 2500 m, les chevêches préfèrent nicher dans des villages entourés de paysages dans lesquels les zones d'herbes courtes représentent un pourcentage moins élevé du paysage entier, relativement éloignées des autres zones d'herbes courtes et sont plus nombreuses que les zones cultivées. À l'échelle de 1000 m, les chevêches nichent dans des villages dans lesquels les zones d'herbes courtes occupent un pourcentage moins élevé du paysage environnant global. Dans le comté de Logan, les chevêches choisissent des sites de nidification dans des villages de chiens-de-prairie situés dans des paysages plus fragmentés parce que la disponibilité des proies y est probablement supérieure à celle des paysages moins fragmentés et (ou) parce que les programmes de lutte aux chiens-de-prairie sont plus dynamiques dans les zones d'herbes courtes que dans les zones cultivées. De plus, la fragmentation au site étudié (62 % de ce site est couvert de prairie indigène) n'est peut-être pas suffisamment importante pour avoir des effets négatifs sur l'occupation du site par les chevêches. Cependant, il est difficile de tirer des conclusions au sujet des effets de la fragmentation du paysage sur les

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chevêches, parce que tous les effets sont probablement une fonction complexe de la structure locale de l'habitat, de la structure du paysage et de la disponibilité des prédateurs et des proies localement.

[Traduit par la Rédaction]

Introduction

Population reductions of the burrowing owl (*Athene cunicularia*) have been reported throughout its range (Rodriguez and Rubio 1993; DeSante et al. 1997; James and Espie 1997; Desmond et al. 2000; but for description of an increasing population in Florida see Millsap and Bear 2000). The species is considered endangered in Canada and a species of special concern in many midwestern and western U.S. states (Sheffield 1997).

Western burrowing owls (*Athene cunicularia hypugaea*, hereinafter referred to as burrowing owls) depend on burrowing mammals for nest burrows (Haug et al. 1993; Desmond et al. 1995). Burrowing owls prefer nest sites in grassland habitat, and in the Great Plains nest sites are most common in colonies of black-tailed prairie dogs (*Cynomys ludovicianus*, hereinafter referred to as prairie dogs) (Butts 1973; Desmond and Savidge 1996). Thompson and Anderson (1988) and Hughes (1993) noted that all owl nests observed in Wyoming and Colorado, respectively, were located in abandoned prairie dog burrows within active colonies.

Several authors have proposed that owl abundance is controlled by burrow availability (Columbe 1971; Green and Anthony 1989; Desmond et al. 1995, 2000). Prairie dogs historically covered tens of millions of acres (Summers and Linder 1978; Anderson et al. 1986). However, land conversion of grassland habitat to agriculture, sylvatic plague (*Yersinia pestis*), and control programs reduced prairie dog populations by an estimated 90–98% since the turn of the century (Summers and Linder 1978; Miller et al. 1994; Desmond et al. 2000). If loss of suitable nest sites alone, however, was responsible for declines in populations of burrowing owls, competition for remaining adequate nest sites should be high. However, this does not appear to be the case. Although prairie dog towns still exist in the grasslands of Colorado, many prairie dog towns are not chosen as nest sites by burrowing owls (Plumpton and Lutz 1993; this study).

Plumpton and Lutz (1993) investigated characteristics of prairie dog towns to determine if towns chosen as nest sites by owls differed from towns not occupied by owls. They found no significant differences across years in burrow density, distance to road, town size, percentage of forb cover, percentage of bare ground, forb height, and vertical density at burrows between towns with and without owls. Studies of burrowing owls in other parts of their range also report no differences (Schmutz 1997) or only differences in a few variables (Rich 1986; Green and Anthony 1989; J.R. Belthoff and R.A. King, unpublished data) when comparing habitat variables of owl nests and unoccupied burrows. However, these investigators only focused on the spatial scale immediately surrounding the nest burrow (when the burrow was not excavated by prairie dogs) or within town characteristics (when the nest was within a prairie dog town). They did not compare landscape characteristics surrounding owl-occupied and owl-unoccupied burrows.

Haug and Oliphant (1990) found that a male burrowing owl's home range in the prairie region of Saskatchewan may extend an average of 2.41 km^2 away from the nest burrow. Their study was conducted on burrowing owls nesting in burrows excavated by badgers. We assumed their data were applicable to burrowing owls living in prairie dog towns in Colorado because their study area was in similar grassland habitat. These data suggest that owls may be foraging on habitat patches adjacent to prairie dog towns if towns were <2.41 km^2. The only other home-range data on burrowing owls are in Grant (1965) and Butts (1973), and these studies only report diurnal movements. The Haug and Oliphant (1990) study includes nocturnal movements, and therefore, we assumed this to be a more accurate assessment of home-range movements of burrowing owls than those studies reporting only diurnal data.

Assuming owls forage in habitats adjacent to their nest sites, we hypothesized that conversion of homogeneous shortgrass prairie to heterogeneous agricultural mosaics in landscapes surrounding prairie dog towns may affect nest-site selection by burrowing owls by decreasing the availability of preferred foraging habitat (shortgrass). To our knowledge this question has not been previously investigated.

The aim of this study is to investigate the influence of land-use patterns and fragmentation surrounding prairie dog towns on nest-site selection by burrowing owls. We predicted that patches of rangeland and native prairie grasslands (herein combined and referred to as "shortgrass patches") would occur at a higher total percentage of landscape surrounding active prairie dog towns in which burrowing owls nest when compared with active prairie dog towns in which no owls nest. Our second prediction was that shortgrass patches in the landscape would be located at a closer proximity to the prairie dog town than other patch types. We also predicted that landscapes surrounding owl-occupied prairie dog towns would be more homogeneous, thus less fragmented and reminiscent of the natural shortgrass prairie, than the landscape surrounding owl-unoccupied prairie dog towns. We tested these predictions using a landscape analysis of habitat patches surrounding owl-occupied and owl-unoccupied prairie dog towns in northeastern Colorado.

Methods

Study area

Our study population included prairie dog towns located within the Great Plains shortgrass prairie region in northeastern Colorado. Our study area was Logan County. Historically, this 4709-km^2 tract of land at 1190 m average elevation was a homogeneous shortgrass prairie, but today it is a heterogeneous agricultural mosaic.

Much of the northern end of the county is under dry-land cultivation. Dry-land crops include winter wheat (*Triticum aestivum*), corn (*Zea mays*), sunflowers (*Helianthus annuus*), millet (*Panicum miliaceum*), oats (*Avena* sp.), and barley (*Hordeum* sp.) (J. Weiss, Agricultural Stabilization and Conservation Service, personal communication). In the southern portion of the country, near the South Platte River, land-use patterns are varied. The landscape is a mix-

Table 1. Status of owl-unoccupied and owl-occupied prairie dog towns in Logan County, Colorado, during the 1991, 1992, 1994, and 1995 breeding seasons.

Prairie dog town sites	1991[a]	1992[b]	1994[c]	1995[c]
Owl-unoccupied				
C2	No owls	Not surveyed	Town gone	Town gone
C3	No owls	Not surveyed	Town inactive	Town inactive
C7	No owls	Not surveyed	Town inactive	No owls
C9	No owls	Not surveyed	Town inactive	No owls
C10	No owls	Not surveyed	Town gone	Town gone
C12	No owls	Not surveyed	No owls	No owls
C14	No owls	Not surveyed	Town inactive	Town inactive
Owl-occupied				
T2	Owls present	Owls present	Owls present	No owls
T3	Owls present	Owls present	Owls present	No owls
T5	Owls present	Owls present	Owls present	No owls
T6	Owls present	Owls present	Owls present	No owls
T7	Owls present	Not surveyed	Owls present	No owls
T8	Owls present	Not surveyed	Town gone	Town gone
T9	Owls present	Not surveyed	Town gone	Town gone
T10	Owls present	Not surveyed	Town inactive	Town inactive
T11	Owls present	Not surveyed	Town inactive	Town inactive
T12	Owls present	Not surveyed	Owls present	Town inactive
T13	Owls present	Owls present	Owls present	Town inactive
T14	Owls present	Not surveyed	Town inactive	Owls present
T15	Owls present	Not surveyed	Town inactive	Town inactive
T18	Owls present	Not surveyed	Town inactive	Town inactive
T19	Owls present	Not surveyed	Town gone	Town gone

Note: "Owls present" describes a town that had prairie dogs and owls. "No owls" describes a town that had prairie dogs but no owls. "Not surveyed" describes a town that was not surveyed during that year. "Town gone" describes a town that was not relocated. "Town inactive" describes a town where burrows were located but the area had neither prairie dogs nor owls.

[a]Results of USFWS survey of black-footed ferrets (unpublished data).

[b]Data from Hughes (1993).

[c]This study.

ture of irrigated croplands interspersed with livestock pastures, hay meadows, and shortgrass prairie. Dominant grass species on the remaining natural prairie include blue gramma (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), with non-native species predominating on pastureland (Hughes 1993).

Data collection

In 1991, the United States Fish and Wildlife Service (USFWS, unpublished data) conducted an extensive survey of black-footed ferrets (*Mustela nigripes*) in 100% of the prairie dog towns known to exist in Logan County that year. We obtained data sheets and maps from this survey, which included information on location and acreage of active prairie dog towns. The USFWS made incidental notation of those towns with nesting burrowing owls and those towns in which no owls were observed. We used this information to determine which prairie dog towns were occupied by burrowing owls in 1991 and initially to assign owl-unoccupied and owl-occupied sites.

The 1991 data were used to conduct the landscape analysis. However, we thought it was important to corroborate the 1991 data. To confirm presence or absence of burrowing owls on the prairie dog towns, we compiled data from (*i*) the USFWS 1991 study, (*ii*) a study on burrowing owls conducted in this area in 1992 (Hughes 1993), and (*iii*) our field observations from 1994 and 1995 (Table 1). Hughes also used a portion of the USFWS survey to locate towns in which owls were nesting. However, she did not survey the owl-unoccupied towns. In 1994 and 1995, we attempted to survey all of the 1991 towns reported as active by the USFWS (N = 33) in Logan County. Our field observations were obtained from roadside surveys where we determined presence or absence of owls by scanning the entire town with binoculars. Our field observations began 3 June and ended 1 July in 1994. In 1995, field observations began 26 May and ended 25 June. Each town was surveyed a minimum of two times for owl presence or absence during both the 1994 and 1995 field seasons.

Initially, 14 towns were selected as potentially unoccupied sites. Seven of these towns were excluded from the sample because (*i*) the habitat areas we analyzed overlapped adjacent towns, thereby causing the data to be non-independent (for a discussion of buffer zones see the Spatial analysis section of this manuscript), and (*ii*) habitat areas crossed into adjacent counties and we only had land-use data for Logan County. Of the seven remaining 1991 unoccupied sites, we could not relocate two of them during 1994 or 1995 (Table 1). We assumed they disappeared because of prairie dog control efforts or land conversion and not because of errors in the 1991 data set.

Nineteen potentially occupied sites were originally selected from the 1991 data set. Four of these sites were eliminated from the sample for the same reasons we eliminated the potentially unoccupied towns. Of the 15 remaining occupied sites, we were unable to relocate three of them in 1994 or 1995 (Table 1). In 1994, six towns that were active in 1991 had become inactive (Table 1). In 1995, one of these six towns (T14) had been recolonized and two towns (T12 and T13) that were active in 1994 had become inactive.

We designated an owl-unoccupied town as an active prairie dog town where no burrowing owls were observed during the 1991, 1992, 1994, and 1995 breeding seasons. Towns that were only observed during 1991 and were either not relocated in future years or not occupied by owls in 1991 were included as owl-unoccupied sites. Owl-occupied towns were towns where at least one burrowing owl was observed at least once during the 4 years. Our final sample size was 7 for owl-unoccupied towns and 15 for owl-occupied prairie dog towns.

Protocol was more stringent for assignment of unoccupied towns because determining owl absence is more difficult than determining owl presence. We assumed that if an owl was sighted on a prairie dog town it was nesting in that town. An owl may be nesting in a town but may not be sighted because it is either in its burrow or foraging off-site. Burrowing owls also spend a portion of their time on the ground and their coloration may conceal their presence. Additionally, raptor territories typically have less than 100% occupancy annually (Haug and Oliphant 1990; Kennedy et al. 1995; Kennedy 1997, 1998).

Information on land-use types and patterns in Logan County was obtained from the Colorado State University Long Term Ecological Research (LTER) project. We used an existing database of land-use patterns of Logan County (I. Burke and W. Lauenroth, unpublished data) created from Soil Conservation Service data (United States Department of Agriculture, Soil Conservation Service, 1985 Colorado County Map Series, Landuse and Natural Plant Communities, Colorado, 1 : 126 720). The LTER staff updated this database in 1991 with current information obtained from Soil Conservation Service offices in Logan County.

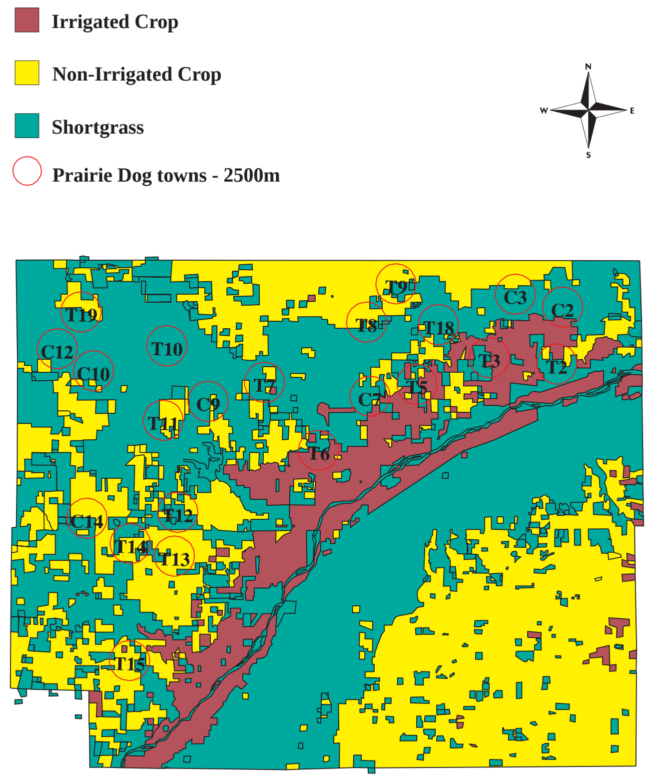
Spatial analysis

We created a map of owl-unoccupied and owl-occupied prairie dog towns in Logan County using ARC/INFO (Environmental Systems Research Institute, Inc. 1993), a vector-based, geographic information system (GIS) software package. For ease of analysis, each town was plotted as a circle with acreage equaling the acreage of the town on the ground estimated by the USFWS in 1991. We then incorporated this map into the aforementioned land-use database (Fig. 1) using ARC/INFO. All landscape patches were classified into four types: prairie dog town, irrigated crops, non-irrigated crops, and shortgrass.

Circles with radii of 1000 and 2500 m were centered on each town. The area within each circle was the area in which landscape structure was analyzed and their size was independent of the size of the prairie dog town. The circle sizes were chosen to determine if our results would be consistent at different spatial scales (Wiens 1989). The 2500-m circle was selected because it approximates the size of an average home range of male burrowing owls (Haug and Oliphant 1990). The 1000-m circle was chosen because we have regularly observed owls foraging in habitat patches immediately adjacent to the prairie dog town in which they were nesting. In addition, Haug and Oliphant (1990) reported that in one study year 95% of all owl locations were within 600 m of nest burrows, so the 1000-m buffer is another potential representation of an owl's foraging area.

Landscape structure surrounding the prairie dog town was quantified using the spatial analysis program FRAGSTATS[3]. We chose four metrics a priori to be the most appropriate test of our predictions: (1) percentage of landscape, (2) number of patches, (3) proximity index, and (4) nearest neighbor distance. Percentage of landscape is the total landscape area divided by the total area of the patch type. Percentage of landscape was chosen to address the prediction that the percentage of shortgrass around owl-occupied towns would be higher than around owl-unoccupied towns. The percentage of landscape variable was derived from the FRAGSTAT

Fig. 1. Examples of landuse database created in ARC/INFO. Prairie dog towns in Logan County, Colorado, are circled and coded alphanumerically; C, owl-unoccupied, N = 7; T, owl-occupied, N = 15.



variable, the landscape similarity index. Landscape similarity index equals the total area of a particular patch type divided by the total landscape area then multiplied by 100 to convert to a percentage. Because we were interested in the landscape surrounding the prairie dog town, the area for the prairie dog town was removed from the measure and the equation adjusted to reflect only the landscape within the analysis area.

Number of patches is simply the number of patches of the corresponding patch type. The number of patches variable was chosen to test the prediction that fragmentation of shortgrass areas would be greater within the buffer zones surrounding owl-unoccupied towns.

Proximity index is defined as

$$l_i = \sum_{j=1}^{n} \frac{a_j}{d_j^2}$$

where l_i is the degree of interaction of patch i (prairie dog town) with n neighboring patches of patch type j; a_j is the area of any neighboring patch j; and d_j is the distance between the edges of the prairie dog town and any patch of patch type j. Proximity index increases as patches of the same type increasingly occupy the analysis area and those patches are closer to the specified focal patch (prairie dog town). Proximity is used to evaluate the prediction that shortgrass patches would be in closer proximity to the prairie dog town and to other shortgrass patches than other patch types.

Nearest neighbor distance is the distance (m) of a patch to the nearest patch of the same type. This metric can be used to evaluate the prediction that patches of shortgrass would be closer to other

[3] K. McGarigal and B.J. Marks. 1993. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Unpublished software, Department of Forest Science, Oregon State University, Corvallis.

Table 2. Selected landscape features of 1000 m radius circles surrounding owl-occupied and owl-unoccupied prairie dog towns in northeastern Colorado.

	Owl-unoccupied		Owl-occupied	
Habitat/landscape metric[a]	Median	10–90th percentile	Median	10–90th percentile
Non-irrigated cropland				
Percentage of landscape	0.0	0.0–0.0	0.0	0.0–45.8
Number of patches	0.0	0.0–0.0	0.0	0.0–1.0
Proximity index	0.0	0.0–0.0	0.0	0.0–0.0
Nearest neighbor distance	0.0	0.0–0.0	0.0	0.0–0.0
Irrigated cropland				
Percentage of landscape	7.4	0.0–34.0	23.4	2.0–90.9
Number of patches	1.0	0.0–1.0	1.0	0.0–2.0
Proximity index	0.0	0.0–0.0	0.0	0.0–0.4
Nearest neighbor distance	0.0	0.0–0.0	0.0	0.0–540.0
Shortgrass prairie				
Percentage of landscape	92.6[b]	66.0–100.0	48.9[b]	9.1–97.4
Number of patches	1.0	1.0–1.4	1.0	0.0–2.0
Proximity index	0.0	0.0–2.6	0.0	0.0–16.6
Nearest neighbor distance	0.0	0.0–168.0	0.0	0.0–330.3

[a]Landscape metrics (percentage of landscape, number of patches, proximity index, and nearest neighbor distance) are defined in the text.
[b]Medians are significantly different between owl-occupied and owl-unoccupied prairie dog towns (two-sample Wilcoxon's test, $P < 0.05$).

shortgrass patches (increasing homogeneity) within the analysis area surrounding owl-occupied prairie dog towns as compared with the same area surrounding owl-unoccupied towns.

Statistical analyses

Desmond and Savidge (1996) reported that town size was positively correlated with burrowing owl densities in Nebraska. We tested the hypothesis that unoccupied towns were smaller than occupied towns using a one-tailed *t* test assuming equal variances (Excel 2000; unoccupied towns: s^2 = 2488.3 ha, N = 7; occupied towns: s^2 = 2744.8 ha, N = 15).

Tests for normality (PROC UNIVARIATE; SAS Institute Inc. 1990) were conducted on the four landscape metrics and the data were determined to be non-normal (see Table 3 in Biddle 1996 for details on the results of the normality tests). At both spatial scales, percentage of landscape, number of patches, proximity index, and nearest neighbor distance variables were compared between owl-unoccupied and owl-occupied areas using a two-sample Wilcoxon's test (PROC NPAR1WAY; SAS Institute Inc. 1989) for both the 1000- and 2500-m analysis areas. The α level used in all hypothesis tests was $P < 0.05$. No statistical comparisons were made between the 1000- and 2500-m landscapes because the 1000-m area could be considered a repeated measure of the 2500-m buffer.

We used logistic regression (PROC LOGISTIC; SAS Institute Inc. 1989) to determine which of the significant variables in the pairwise comparisons were the best predictors of detecting burrowing owls in a prairie dog town. The α level of $P < 0.05$ was used as the criterion for inclusion of a variable in the model. This analysis was only conducted on the 2500-m buffered area because only one variable was significant in the two-sample Wilcoxon's tests of the 1000-m area.

Results

Prairie dog town size

The size of unoccupied towns ($\bar{x}$ = 45.7 ha) was not significantly different (t = –0.11, P = 0.46) from the size of occupied towns ($\bar{x}$ = 48.5 ha). So, occupancy was probably not influenced by town size in our study area.

Landscape matrix

The only patch type that was significantly different between unoccupied and occupied towns was shortgrass (Tables 2, 3). At the 2500-m scale (Table 3), all four variables (percentage of landscape ($|z|$ = 0.0345, $P < 0.05$), number of patches ($|z|$ = 0.0135, $P < 0.05$), proximity index ($|z|$ = 0.0318, $P < 0.05$), and nearest neighbor distance ($|z|$ = 0.0349, $P < 0.05$)) were significantly different for shortgrass patches between owl-unoccupied and owl-occupied towns. However, at the 1000-m scale (Table 2) only percentage of landscape in shortgrass ($|z|$ = 0.0233, $P < 0.05$) was significant and it was lower at owl-occupied sites.

The results of the logistic regression indicated that only one variable, number of patches (χ^2 = 6.34, df = 1, P = 0.034), could be used to predict the presence of burrowing owls in the prairie dog towns in our study area. The probability of detecting an owl increased as number of shortgrass patches increased (Fig. 2).

Discussion

Our results suggest that burrowing owls in Logan County during 1991 (the date of the land-use database used in this study) may have been selecting nest sites in prairie dog towns where the landscape was more fragmented than the landscape surrounding unoccupied prairie dog towns (Fig. 3). There is no evidence that occupied nest sites were in the least fragmented areas of shortgrass, which is contrary to our predictions. Nor were the unoccupied towns smaller in size than the occupied towns. These results support the results of other recent studies that suggest burrowing owls are more

Table 3. Selected landscape features of 2500 m radius circles surrounding owl-occupied and owl-unoccupied prairie dog towns in northeastern Colorado.

Habitat/landscape metric[a]	Owl-unoccupied Median	Owl-unoccupied 10–90th percentile	Owl-occupied Median	Owl-occupied 10–90th percentile
Non-irrigated cropland				
Percentage of landscape	0.0	0.0–14.4	0.0	0.0–57.4
Number of patches	0.0	0.0–1.8	0.0	0.0–3.6
Proximity index	0.0	0.0–6.4	0.0	0.0–85.5
Nearest neighbor distance	0.0	0.0–268.0	0.0	0.0–814.8
Irrigated cropland				
Percentage of landscape	10.3	2.8–42.7	36.2	4.0–70.7
Number of patches	2.0	1.0–3.4	2.0	0.4–3.6
Proximity index	2.0	0.0–6.6	0.4	0.0–282.3
Nearest neighbor distance	630.0	0.0–907.9	30.0	0.0–927.8
Shortgrass prairie				
Percentage of landscape	85.5[b]	57.0–93.2	48.1[b]	25.7–84.5
Number of patches	1.0[b]	0.6–1.4	3.0[b]	1.0–3.0
Proximity index	0.0[b]	0.0–21.2	9.1[b]	0.0–239.8
Nearest neighbor distance	0.0[b]	0.0–144.5	328.0[b]	0.0–799.2

[a]Landscape metrics (percentage of landscape, number of patches, proximity index, and nearest neighbor distance) are defined in the text.
[b]Medians are significantly different between owl-occupied and owl-unoccupied prairie dog towns (two-sample Wilcoxon's test, $P < 0.05$).

Fig. 2. Probability of detecting a burrowing owl as a function of number of shortgrass patches in a landscape within a 2500 m radius circle surrounding a prairie dog town. Predicted values (■), as well as the upper (◆) and lower (✶) 95% confidence intervals, are presented.

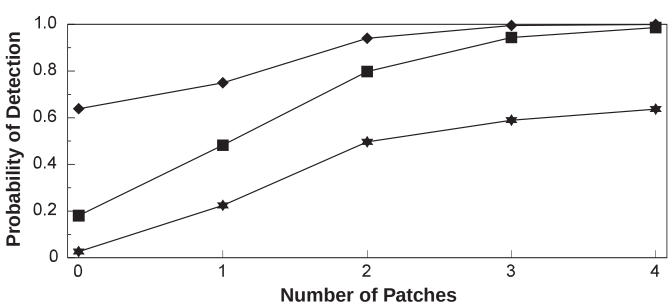
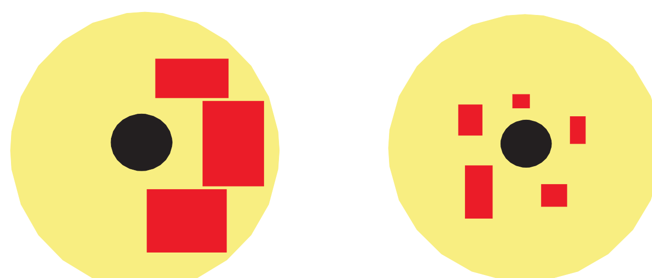


Fig. 3. Schematic diagram of the expected layout of shortgrass patches within a 2500 m radius circle surrounding owl-unoccupied and owl-occupied prairie dog towns based on results from two-sample Wilcoxon's tests.



successful in areas with moderate levels of disturbance and (or) fragmentation.

When the disturbance is urbanization, several studies indicate that burrowing owls nesting in human-altered areas have higher productivity than in proximate undeveloped areas (Botelho and Arrowood 1996; Millsap and Bear 2000). Gehlbach (1994) reported similar findings for a population of eastern screech-owls (*Otus asio*) in north-central Texas. The authors suggest that moderate levels of urbanization provide more prey and protection from predators than nearby undeveloped areas. However, at high levels of development this high prey base maybe offset by other factors, e.g., higher mortality from human-caused agents.

In a rural western agricultural setting similar to our study area, J.R. Belthoff and R.A. King (unpublished data) found burrowing owl productivity to be negatively correlated with distance to irrigated agriculture. According to J.R. Belthoff and R.A. King, associations with irrigated agriculture maybe important for burrowing owls in this arid environment (southern Idaho) because farmland provides increased access to montane voles (*Microtus montanus*), an important prey item. Alternatively, they proposed that nesting near agriculture decreases nest predation, perhaps related to higher densities of nesting owls in these areas and the resulting increased vigilance. Rich (1986) also concluded that the proximity of prey to nest burrows explained some preferential habitat selection by the owls he observed in Idaho.

During the data collection phase of our study, we noted that a majority of occupied owl nests were located along the perimeter of the prairie dog towns near edges of the patch (P. Orth, unpublished data). This suggests that owls in Logan County may be selecting towns in highly fragmented habitat because of the increased amount of edge associated with these landscapes. Arthropod abundance is often higher on the borders of fields within a mosaic landscape of small-sized crop fields and semi-natural habitats (Webb and Hopkins 1984; Duelli 1990). Arthropods are a major food item of burrowing owls in Colorado (Marti 1974; Thompson and

Anderson 1988) and the increased abundance of this prey may explain why nest sites of burrowing owls in our study occur in prairie dog towns surrounded by a fragmented landscape. We cannot, however, fully evaluate this hypothesis on food availability because data on arthropod and small-mammal availability were not collected.

The results of this study may also be influenced by the fact that the shortgrass prairie in Colorado is relatively unfragmented. Of the three prairie types in North America, the shortgrass remains the least disturbed type of prairie, with 30–70% remaining unplowed (Central Shortgrass Prairie Ecoregional Planning Team 1998). Howard et al. (2001) did a GIS analysis of our study area and the surrounding counties and found that only 38% of the cover types is not shortgrass. For the small number of patches (0–4) observed around towns in this study, the probability of detecting an owl increased as fragmentation increased (Fig. 2). Perhaps this effect would stabilize at some threshold level at some intermediate level of fragmentation and then decrease as fragmentation increased. The effects of fragmentation on nest-site selection by burrowing owls are probably a complex function of local habitat structure, landscape structure, and prey and predator availability making it difficult to generalize about the effects of fragmentation on this species (Tewksbury et al. 1998).

Alternatively, landscapes with more shortgrass may support more livestock than the adjacent cropland. Prairie dog colonies in areas of livestock grazing maybe subjected to more control programs. These control programs effectively reduce prairie dog densities, and prairie dog densities have been positively correlated with numbers of nesting pairs of owls in Nebraska (Desmond et al. 2000).

Although the landscape analyses conducted at both scales suggest that occupied towns are in more fragmented landscapes than unoccupied towns, the 1000-m scale had fewer significant variables than did the 2500-m scale. These differences could have occurred for two reasons: (*i*) there were fewer significant landscape variables at the 1000-m scale or (*ii*) the 1000-m scale was too small to include a variety of patch types. We speculate that the 1000-m scale was too small to evaluate the landscape metrics we used in this study. It would be interesting to compare our results with similar data collected at a scale larger than 2500 m. In our initial study design we had included a 5000-m scale because it approximated the maximum size of the home range reported for burrowing owls (Haug and Oliphant 1990). However, at this scale approximately 90% of the 5000-m circles overlapped with comparable analysis areas of adjacent towns. For statistical reasons, we eliminated the 5000-m scale because we were concerned about data independence. Perhaps future studies could explore ways to analyze the landscapes surrounding the nests of burrowing owls at larger spatial scales.

We also suggest that future research evaluate the landscape matrix surrounding nest sites of burrowing owls in landscapes with a wide range of fragmentation to determine if burrowing owls prefer nest sites in intermediate levels of fragmentation. Future studies on this topic should also measure small-mammal and arthropod availability in the various patch types surrounding owl nest. This would allow researchers to evaluate if moderate levels of fragmentation can enhance prey availability for burrowing owls.

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