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Research Article

Multiscale Habitat Selection by Burrowing Owls in Black-Tailed Prairie Dog Colonies

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ABSTRACT Some populations of western burrowing owls (*Athene cunicularia hypugaea*) have declined in recent decades. To design and implement effective recovery efforts, we need a better understanding of how distribution and demographic traits are influenced by habitat quality. To this end, we measured spatial patterns of burrowing owl breeding habitat selection within black-tailed prairie dog (*Cynomys ludovicianus*) colonies in northeastern Wyoming, USA. We compared burrow-, site-, colony-, and landscape-scale habitat parameters between burrowing owl nest burrows ($n = 105$) and unoccupied burrows ($n = 85$). We sampled 4 types of prairie dog colonies: 1) owl-occupied, active with prairie dogs ($n = 16$); 2) owl-occupied, inactive ($n = 13$); 3) owl-unoccupied, active ($n = 14$); and 4) owl-unoccupied, inactive ($n = 14$). We used an information-theoretic approach to examine a set of candidate models of burrowing owl nest-site selection. The model with the most support included variables at all 4 spatial scales, and results were consistent among the 4 types of prairie dog colonies. Nest burrows had longer tunnels, more available burrows within 30 m, and less shrub cover within 30 m, more prairie dog activity within 100 m, and were closer to water than unoccupied burrows. The model correctly classified 76% of cases, all model coefficients were stable, and the model had high predictive ability. Based on our results, we recommend actions to ensure persistence of the remaining prairie dog colonies as an important management strategy for burrowing owl conservation in the Great Plains of North America. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2664–2672; 2007)

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KEY WORDS *Athene cunicularia*, black-tailed prairie dog, burrowing owl, *Cynomys ludovicianus*, Great Plains, habitat selection model, information-theoretic, logistic regression, model accuracy, Wyoming.

Studies of wildlife–habitat relationships often seek to identify the proximate cues that trigger an animal to settle (Hutto 1985, Morrison 2001). Results of such studies depend on the spatial scale at which variables were measured, and reliable inference about the cues animals use to select habitat requires that the spatial scale be made explicit (Morrison 2002). Migratory birds are thought to select their nest sites through a hierarchy of choices at increasingly smaller scales, where the availability of and proximity to required resources are at levels and distances that optimize reproductive success (Rosenzweig 1981, Hutto 1985, Morrison 2002). As such, wildlife managers should not only strive to identify the proximate cues migratory birds use to select breeding habitat, but also to understand the spatial scale at which those cues elicit selection.

The western burrowing owl (*Athene cunicularia hypugaea*) is a Neotropical migratory bird that breeds throughout western North America. Range contraction and local population declines have prompted conservation action for burrowing owls in the United States (Bird of National Conservation Concern), Canada (Endangered), and Mexico (Klute et al. 2003). Habitat degradation has been implicated in population declines along the northern and eastern peripheries of their breeding range since the 1970s (Wellicome and Holroyd 2001, Klute et al. 2003). Consequently, a common recommendation in burrowing owl conservation plans is to quantify habitat selection at sites throughout their range (Holroyd et al. 2001, Klute et al. 2003, McDonald et al. 2004).

Burrowing owls typically nest in relatively flat, sparsely vegetated, open areas that harbor burrowing mammals to dig potential nest burrows (Haug et al. 1993). But beyond these common features, few vegetation or structural characteristics represent ubiquitous components of burrowing owl breeding habitat across their range (Haug et al. 1993, Klute et al. 2003). Thus, we need to quantify patterns of burrowing owl habitat selection throughout their distribution to ensure appropriate management actions in each region. When we increase resolution from a range-wide scale down to a regional scale, patterns of burrowing owl habitat selection are more readily apparent. In the Great Plains region, for example, breeding burrowing owls are strongly associated with black-tailed prairie dogs (*Cynomys ludovicianus*; Butts and Lewis 1982, MacCracken et al. 1985, Plumpton and Lutz 1993, Desmond et al. 2000, Sidle et al. 2001). As a result, most of the previous burrowing owl habitat selection studies in the Great Plains examined nest-site use within black-tailed prairie dog colonies (Table 1).

Conclusions about what constitutes optimal burrowing owl habitat have come primarily from univariate comparisons between nests and unoccupied burrows (see MacCracken et al. 1985, Desmond et al. 2000, Ronan 2002 for

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Table 1. Features that influenced burrowing owl habitat selection within black-tailed prairie dog colonies in the Great Plains, USA, 1982–2001.

Scale	Habitat feature	Location[a]						
		OK[b]	SD[c]	Northeastern CO	Southeastern CO	Central CO	NE	MT
Burrow	Soil coarseness	X	↑[d] $P < 0.14$					
	Tunnel length	X				↑ $P = 0.13$		
	Entrance width	X	↑ $P < 0.05$		↑ $P = 0.30$			
	Entrance ht	X			↑ $P = 0.02$			
	Orientation					$P > 0.05$[c]		
Nest-site	Vegetation ht	↓	↓ $P < 0.10$			↓ $P = 0.02$		
	% forb cover		↑ $P < 0.10$			↓ $P = 0.1$		
	% bare ground		↑ $P < 0.10$			↑ $P < 0.01$		
	Burrow density			↑ $P = 0.30$	↑ $P = 0.04$	↑ $P < 0.01$	↑ $P < 0.01$	↑ $P = 0.47$
	% canopy cover		↓ $P < 0.10$					
	Distance to active burrow							↓ $P = 0.08$
	Distance to inactive burrow				↓ $P < 0.01$			↓ $P = 0.50$
Prairie dog colony	Distance to colony edge	X			↓ $P < 0.01$			↑ $P = 0.40$
	Colony size			↑ $P < 0.01$	↑ $P < 0.01$	↓ $P = 0.16$	↑ $P < 0.01$	↑ $P = 0.22$
	Prairie dog activity[e]	↑		↑ $P < 0.01$	↑ $P = 0.03$		↑ $P < 0.01$	
	Colony soil coarseness				↑ $P = 0.21$			
Landscape	Slope	X						↑ $P = 0.79$
	Elevation	X						↓ $P = 0.88$
	Distance to road					↑ $P > 0.05$		↓ $P = 0.21$
	Distance to perch					↑ $P = 0.04$		
	Distance to conspecific							↓ $P = 0.21$

[a] OK (Butts and Lewis 1982), SD (MacCracken et al. 1985), ne CO (Hughes 1993), se CO (Toombs 1997), central CO (Plumpton and Lutz 1993), NE (Desmond 1991, Desmond and Savidge 1996, Desmond et al. 2000), MT (Restani et al. 2001).

[b] Authors of OK study did not conduct statistical tests. X denotes habitat features deemed insignificant by the authors.

[c] Authors did not report actual *P*-values.

[d] Arrows indicate features that were positively (↑) or negatively (↓) correlated with use by burrowing owls.

[e] All studies (except OK) measured prairie dog activity using belt-transect methods adapted from Biggins et al. (1993), where % activity was a ratio of active vs. total prairie dog burrows. The OK study qualitatively measured prairie dog activity on the colony scale, as either yes (active) or no (inactive).

exceptions). Univariate comparisons can be insightful ways to differentiate nests and unoccupied burrows. However, univariate comparisons may be misleading if the probability of selection is influenced by the simultaneous effect of multiple habitat features at multiple scales, or if habitat features at multiple scales are correlated. Furthermore, the few studies that developed multivariate habitat models did not assess the predictive ability or stability of their models (e.g., MacCracken et al. 1985, Green and Anthony 1989, Desmond et al. 2000, Belthoff and King 2002, Ronan 2002).

In light of these considerations, we examined patterns of breeding habitat selection by burrowing owls in northeastern Wyoming, USA. We developed presence–absence, logistic regression models comparing burrow-, site-, colony-, and landscape-scale parameters surrounding nest burrows and randomly selected, unoccupied burrows. We included comparisons between prairie dog colonies (both active and inactive) occupied by nesting owls and prairie dog colonies not occupied by nesting owls. We evaluated the predictive performance of our model by examining several metrics related to model accuracy and stability.

STUDY AREA

We examined burrowing owl habitat selection in the Thunder Basin National Grassland (TBNG), near the towns of Wright (43°44′N, 105°28′W), Newcastle (43°51′N, 104°12′W), and Douglas (42°45′N, 105°22′W) in northeastern Wyoming. Thunder Basin National Grassland encompassed 2,300 km^2 of the southern Powder River Basin between the Bighorn Mountains and the Black Hills, within Campbell, Weston, and Converse counties. Topography within TBNG included valleys, rough breaks and badlands, steep coniferous mesas, and low riparian bottomlands, with elevation ranging from 1,090 m to 1,580 m. Annual precipitation varied from 15 cm to 40 cm, annual temperatures varied from −10° C to 41° C (Western Regional Climate Center 2004). The study area was located within the Great Plains–Palouse Dry Steppe Province (Bailey 1995), and dominant vegetation included grasses (*Agropyron smithii*, *Buchloe dactyloides*, *Bouteloua gracilis*), sedges (*Carex* spp.), and shrubs (*Artemesia tridentata*, *Artemesia cana*, *Sarcobatus vermiculatus*). Under the jurisdiction of the United States Forest Service, lands were managed privately (ranchers, coal companies) and publicly (U.S. Forest Service, Bureau of Land Management, and State Trust of Wyoming). Primary land uses included cattle and sheep grazing and mineral extraction. Thunder Basin National Grassland contained the largest land coverage of black-tailed prairie dog colonies (7,381 ha) of any United States Forest Service Great Plains National Grassland (Luce 2003). Given the association between burrowing owls and black-tailed prairie dog colonies in the Great Plains, we restricted our sampling efforts to black-tailed prairie dog colonies.

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Table 2. Variable descriptions, means, and 95% confidence intervals for habitat features measured at burrowing owl nest burrows and unoccupied burrows, and at burrows within active and inactive prairie dog colonies, in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

		Nest burrows		Unoccupied burrows		Active colonies		Inactive colonies			
Abbreviation	Habitat variable	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	$\bar{x}$	CI	t[a]	P
Burrow scale											
T	Tunnel length (m)	3.0	2.8–3.3	1.7	1.5–2.0	2.5	2.3–2.8	2.1	1.7–2.5	−2.0	0.045
Nest-site scale (within 30 m)											
B	Burrows (no.)	29	27–31	20	17–23	27	25–29	21	17–24	−3.4	<0.001
S	Shrub cover (%)	6	4.3–7.4	14	9.9–17.8	9	7–12	9	6–12	−0.1	0.971
G	Ground cover (%)	20	17.5–23.3	18	14.5–21.5	21	18–24	15	12–19	−2.4	0.017
Prairie dog colony scale (within 100 m)											
A	Prairie dog activity (%)	44	40.2–48.6	34	28.4–39.2						
Landscape scale (within 2 km)											
P	Nearest perch (m)	99	79–119	77	50–104	86	69–103	96	58–133	0.6	0.581
W	Nearest water (m)	762	652–871	926	781–1071	845	735–956	820	667–973	−0.3	0.798
D	Nearest drainage (m)	128	96–160	196	142–250	152	119–184	169	103–234	0.5	0.601

[a] t-values and P-values correspond to t-test comparisons of habitat features within active colonies vs. inactive colonies.

METHODS

Nest Burrows

We located our sample of nests by conducting call-broadcast surveys along dirt roads within prairie dog colonies (Conway and Simon 2003). We surveyed 73 prairie dog colonies in 2003 and 2004 between 4 April and 27 July, including all known colonies on state, federal, and private lands within the study area (except for 7 colonies where access had not been granted). Upon completion of a survey route, we revisited areas where we had detected burrowing owls and conducted thorough ground searches to look for signs of nesting (shredded cow or horse manure, prey remains, whitewash, and regurgitated castings; Haug et al. 1993). We monitored nest sites weekly to confirm nest status, and we visited nests from the date of discovery through the date of failure, or until the last juvenile fledged (44 d of age). Determining whether an occupied burrow is indeed a nest is difficult for burrowing owls because the clutch is typically located ≥3 m below the ground surface. We only included burrows as nests if we detected 2 adult owls at the burrow entrance on ≥2 of our weekly nest visits.

Unoccupied Burrows

Because we wanted to account for the fact that burrowing owls might prefer to nest in prairie dog colonies with high prairie dog activity (Toombs 1997, Desmond et al. 2000, Restani et al. 2001), we stratified our sample of unoccupied burrows among 4 types of black-tailed prairie dog colonies: 1) owl-occupied, with visible prairie dog activity, 2) owl-occupied, with little or no prairie dog activity detected, 3) owl-unoccupied, with visible prairie dog activity, and 4) owl-unoccupied with little or no prairie dog activity detected. We classified a colony as having visible prairie dog activity if we observed ≥10 prairie dogs on ≥2 consecutive survey points during the initial burrowing owl survey(s). To select a random sample of unoccupied burrows, we overlaid a grid onto a map of all 73 surveyed prairie dog colonies within TBNG. We randomly selected grid points within each prairie dog colony, and then we randomly selected an unoccupied, usable burrow within 50 m of the grid point. We considered a burrow usable if the tunnel entrance diameter measured ≥5 cm and no obstructions blocked the tunnel passage to ≥10 cm deep. We confirmed that the burrow was not occupied by burrowing owls using an infrared videoscope (Peeper Video Probe; Sandpiper Technologies, Manteca, CA), as well as the lack of nesting sign. We ensured that all unoccupied burrows included in our sample were ≥150 m from any known nest burrow.

Habitat Variables

We selected 8 habitat variables as potential covariates to include in the modeling effort (Table 2). We classified habitat variables at 4 concentric spatial scales of resolution, radiating out from the focal burrow: 1) burrow scale, 2) nest-site scale, 3) prairie dog colony scale, and 4) landscape scale. We defined the nest-site scale as 30 m from the focal burrow, prairie dog colony scale as 100 m from the focal burrow, and landscape scale as 2 km from the focal burrow.

At the burrow scale, we measured the length (m) of the main tunnel from burrow entrance to the nest chamber (or end of the burrow) using an infrared videoscope. The shape and length of burrow tunnels were highly variable; some bent at angles too sharp for the videoscope to navigate, and some were longer than the length of the videoscope (4.5 m). We assigned burrow tunnels that were >4.5 m long ($n = 17$ for nests, $n = 3$ for unoccupied burrows) as length = 5 m. If we could not reach the end of the tunnel because of sharp bends ($n = 21$ for nests, $n = 15$ for unoccupied burrows), we assigned that tunnel the mean length of all nests and unoccupied burrows (1.9 m). To ensure these designations did not lead to spurious conclusions, we also repeated our analyses after excluding the 56 burrows with uncertain length. Direction and strength of model coefficients, and model ranking did not change substantially when we excluded burrows with uncertain lengths, so we report results from the analysis with all burrows included.

To measure selection at the nest-site scale, we counted the

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number of usable burrows within 30 m of the focal burrow. We estimated percent shrub- and bare-ground cover within 30 m of the focal burrow by visually partitioning all ground cover types (grass, forb, shrub, litter, bare ground) into a percentage summing to 100%. At the scale of the prairie dog colony, we used an index of prairie dog activity (%) within 100 m of the focal burrow, based on Biggins et al. (1993). We bisected the focal burrow with 2 200-m belt transects that were each 4 m wide, and counted the number of active burrows and total burrows in each of the 2 belt transects. We considered a burrow to be active when we detected fresh prairie dog digging, or by a combination of fresh prairie dog scat and a lack of cobwebs in the burrow entrance. We calculated an index of prairie dog activity for each transect as (no. of active burrows/total no. of burrows) $\times$ 100. We averaged the index of prairie dog activity across the 2 transects at each focal burrow.

At the landscape scale, we measured distance (m) from the focal burrow to the nearest perch (any structure $\geq$0.5 m tall that could potentially support a 150-g bird), distance (m) to the nearest permanent water, and distance (m) to the nearest drainage. We defined drainage as any linear depression capable of draining water through a prairie dog colony and supporting higher densities of vegetation relative to the prairie dog colony. Burrowing owls often use linear landscape features with tall vegetation as hunting flyways (e.g., roadsides and rights-of-way) because these areas often have higher prey densities relative to adjacent uplands (Haug and Oliphant 1990). We measured distance from the focal burrow to each of these landscape features using a Global Positioning System (GPS) receiver. If we did not find a permanent water source within 2 km of the focal burrow, we recorded 2 km as the distance to water for that burrow.

To test for multi-collinearity among habitat variables, we regressed each explanatory variable against all the others and examined the variance inflation factor (VIF), $\text{VIF}(X_i) = 1/(1 - R_i^2)$, where X_i is the explanatory variable (Chatterjee and Price 1991). A VIF that strongly deviated from 1 (VIF closer to 0.1 or 10) indicated a departure from independence and a tendency toward collinearity (Chatterjee and Price 1991).

Model Selection

Seeking a model that best approximated the reality of burrowing owl nest-site selection, we employed both information-theoretic and frequentist methods (Burnham and Anderson 2002, Stephens et al. 2005). With a presence–absence response variable and a suite of continuous explanatory variables, we chose binary logistic regression to model the probability of burrow use (Hosmer and Lemeshow 2000). We developed 20 candidate models that isolated potential effects: prairie dog activity, distance to hunting sites, burrow availability, vegetation structure, and combined effects of prairie dog activity and resource availability (Table 3).

We ran all 20 nest-selection models in SAS PROC LOGISTIC, pooling data from 2003 and 2004 (SAS Institute 2000). To avoid pseudo-replication, we only included nest burrows from 2003 that were not reoccupied in 2004 (i.e., nest burrows occupied in both 2003 and 2004 were not included as 2 entries in the data file). Running models with year as a covariate did not improve the performance of the model and the direction, strength, and significance of all estimated coefficients were similar between years. Hence, we report the models without a year effect, as we were interested in a simple, yet robust model. In addition, we ran the full model with interactions between prairie dog activity and burrow availability, shrub cover, and bare ground. Interaction terms were not significant and their inclusion did not improve model fit; therefore, we left interaction terms out of the models to maintain parsimony.

We ranked candidate models with Akaike's Information Criterion (AIC; Burnham and Anderson 2002). To avoid problems associated with a small sample-to-parameter ratio, we applied a small-sample bias adjustment to the AIC value associated with each candidate model (AIC_c; Burnham and Anderson 2002). We ranked models with ascending AIC_c values. Based on this ranking, we included Akaike weights (w_i) and deviance as relative measures of support for each model (Burnham and Anderson 2002). We also judged the stability of the top model by the prevalence of the selected variables in the other top-ranking models. If the same set of variables consistently appeared within the top set of candidate models ($\text{AIC}_c < 0.5$; $w_i > 0.01$), we assigned greater confidence to the top model.

As an additional model selection diagnostic, we report classification accuracy as the Area Under the Curve (AUC) from the Receiver Operating Characteristic (ROC) plot of each model (Hosmer and Lemeshow 2000). For each ROC curve, we plotted sensitivity (probability a model will correctly classify nests, or true positives) versus 1-specificity (probability a model will incorrectly classify unoccupied burrows, or false positives) over a range of probability thresholds from 0 to 1 (Hosmer and Lemeshow 2000). The AUC value for each ROC plot estimated the model's ability to correctly distinguish between a nest and an unoccupied burrow. If a model performed no better than chance, then AUC $\approx$ 0.50. An AUC substantially >0.50 indicated a high rate of model sensitivity to nest burrows (Fielding and Bell 1997).

Correlation between binary responses, or variation between response probabilities, is typically referred to as overdispersion (SAS Institute 2000). Numerous potential model inadequacies can cause overdispersion: failure to include important interaction terms, nonlinear relationships between explanatory variables and response variables, presence of outliers, inadequate sub-sample size, or inappropriate transformation of variables. If data are overdispersed, the variance of parameter estimates is underestimated. We calculated a dispersion parameter for the top model by dividing the deviance chi-square statistic (χ^2_D) by the degrees of freedom (from SAS PROC LOGISTIC). If the dispersion parameter approximated 1.0, we assumed no overdispersion within the best model.

We elucidated differences between nests and unoccupied

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Table 3. Model-ranking results for burrowing owl nest-selection models developed in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Model[a]	q[b]	AIC_c	ΔAIC_c	w_i[c]	Deviance[d]	AUC[e]
T B S A W	5	188.9	0.00	0.29	176.6	0.87
T B S G A W	6	189.3	0.39	0.24	174.8	0.87
		---------- *natural break* AIC_c ----------				
T B S G A	5	191.0	2.09	0.10	178.7	0.86
T B S G A P W D (full model)	8	191.3	2.38	0.09	172.5	0.87
T B S G P W	6	192.1	3.14	0.06	177.6	0.87
T B S A D	5	192.1	3.14	0.06	179.7	0.86
T B S G A D	6	192.4	3.45	0.05	177.9	0.86
T B A	3	193.0	4.09	0.04	184.9	0.86
		---------- *natural break* AIC_c ----------				
T B S G P	5	194.7	5.79	0.02	182.4	0.86
T B	2	195.1	6.14	0.01	189.0	0.85
T B G P W	5	196.3	7.39	0.01	184.0	0.86
T B W D	4	196.5	7.58	0.01	186.3	0.85
T B P W D	5	196.6	7.72	0.01	184.3	0.86
		---------- *natural break* AIC_c ----------				
T A	2	199.7	10.77	0.00	193.6	0.83
T	1	203.8	14.92	0.00	199.8	0.81
P W D	3	205.5	16.57	0.00	195.4	0.83
B A	2	238.3	49.40	0.00	232.3	0.72
B	1	241.2	52.32	0.00	237.2	0.71
G S	2	250.0	61.04	0.00	243.9	0.63
A	1	256.0	67.10	0.00	252.0	0.63

[a] We ranked 20 models by ascending ΔAkaike's Information Criteria adjusted for small sample size (ΔAIC_c). T = tunnel length (m), B = no. of burrows, S = % shrub cover, A = % prairie dog activity, W = distance to water, G = % ground cover, D = distance to drainage, and P = distance to perch.
[b] q is the no. of model parameters.
[c] w_i is the model wt of evidence.
[d] Deviance is $-2\{\log_e[L(\theta)]-2\log_e[L_s(\theta)]\}$, where θ is a max. likelihood estimate evaluated for the model in question [$L(\theta)$] and for the full model [$L_s(\theta)$].
[e] AUC is the Area Under Curve for a Receiver Operating Characteristic graph, plotting sensitivity (true positives) vs. (1 − specificity [false positives]).

burrows with the strength and direction of coefficients (α-level of 0.05) from the best model. To illustrate the effect of each habitat variable on probability of selection by burrowing owls, we modeled the probability of use for each variable and compared variable means between nests and unoccupied burrows.

Colony Comparisons

Because we stratified our sampling regime to include active and inactive prairie dog colonies, as well as owl-occupied and owl-unoccupied colonies, we explored how results might change when we restricted our analyses to only certain types of colonies. We used *t*-tests to compare burrows in active and inactive prairie dog colonies in terms of burrow tunnel length, number of burrows within 30 m, percent shrub cover, percent bare ground, distance to nearest water, and distance to nearest drainage. To test for burrowing owl nest-site preferences within owl-occupied colonies only, we used our top-ranking logistic regression model to measure the probability of burrow use only within owl-occupied prairie dog colonies.

Model Evaluation

Including several different metrics to evaluate the predictive ability of a presence–absence model provides more confidence in the reliability and applicability of the model over space and time (Fielding and Bell 1997, Manel et al. 2001). Ideally, predictive performance is evaluated with data from another location. When external data are lacking, available data can be partitioned into independent sets of training (model-building) and testing data (Fielding and Bell 1997, Manel et al. 1999). We built sets of training and testing cases using a $k = 2$ data partition, and based those partitions (k) on a heuristic ratio of $[1 + (q - 1)^{1/2}]^{-1}$, where q is the number of predictors (Fielding and Bell 1997). Our 2-fold data partitioning broke 70% ($n = 133$) of data into training sets, and 30% ($n = 57$) into testing sets. We randomly generated 10 subsets of our data for training (model-building) and ensured that these subsets had an equal ratio of nests and unoccupied burrows. We calculated predictive accuracy for all training and testing data sets based on the top model selected by AIC_c. We averaged correct classification rates for the 10 training data sets and 10 testing data sets as a simplified bootstrap approach (Manel et al. 1999, Boyce et al. 2002).

We assessed model performance based on both training and testing data in several ways: the kappa statistic, predictive accuracy, and ROC plots and their AUC. The kappa statistic measured the proportion of nests and unoccupied burrows predicted correctly after accounting for chance (Fielding and Bell 1997, Manel et al. 2001). Because predictive accuracy and kappa require identification of a probability threshold, usually identified at the probability cutoff point at which the best model has its highest correct-classification rate, we measured predictive

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Table 4. Estimated coefficients ($\hat{\beta}$), standard errors, odds ratios [Exp ($\hat{\beta}$)], 95% confidence intervals of odds ratios, and associated *P*-values for all variables within the top-ranking model to predict burrowing owl nest-site selection in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Habitat feature[a]	$\hat{\beta}$	SE	Exp ($\hat{\beta}$)	95% CI	*P*	P_{use}[a]
T	0.88	0.18	2.43	1.71–3.44	<0.001	↑
B	0.05	0.02	1.05	1.02–1.08	0.004	↑
S	−0.04	0.02	0.97	0.94–1.00	0.028	↓
A	0.02	0.01	1.02	1.00–1.03	0.047	↑
W	−0.0007	−0.0003	0.99	0.99–1.00	0.059	↓

[a] T = tunnel length (m), B = no. of burrows, S = % shrub cover, A = % prairie dog activity, and W = distance to water.
[b] Arrows represent the positive or negative effect of each variable on probability of use (P_{use}).

accuracy (i.e., sensitivity, specificity, predictive power) at a probability cutoff of 0.5. We interpreted kappa proportions using the rule from Fielding and Bell (1997), where kappa <0.4 indicated poor model performance, 0.4 < kappa < 0.75 indicated good model performance, and kappa >0.75 indicated excellent model performance. In contrast, we did not evaluate ROC plots and their AUC at a probability cutoff, as they are threshold-independent measures of performance. Instead, we evaluated ROC plots over a range of probabilities, and an AUC >0.5 indicated an improvement over chance model performance.

RESULTS

We measured habitat characteristics of 105 burrowing owl nests and of 85 unoccupied burrows at 73 prairie dog colonies in TBNG. Of the 73 colonies surveyed, 47% were active with prairie dogs and 53% were inactive colonies. Of the 105 burrowing owl nests we located, 81% were within active prairie dog colonies, and 19% were within inactive prairie dog colonies. Unoccupied burrows were distributed evenly among the 4 types of prairie dog colonies: 21 in owl-occupied, active colonies; 20 in owl-occupied, inactive colonies; 23 in owl-unoccupied, active colonies; and 21 in owl-unoccupied, inactive colonies. American badger (*Taxidea taxus*), coyote (*Canis latrans*), and thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) burrows were also present within sampled colonies, but all sampled burrows were excavated by prairie dogs. Because all VIF values from correlation tests were between 1.0 and 1.2, we assumed little multicollinearity among habitat variables.

The best approximating models included variables related to both prairie dog activity and distance to resources (Table 3). Seven other competing models had relatively small ΔAIC_c (<5), but the top-ranking model (TBSAW) was the most parsimonious model ($q = 5$), with the lowest AIC-score, and had competitive deviance and AUC values (Table 3). All of the top 5 models included tunnel length, burrow availability, and percent shrub cover, and 4 of the 5 top models included percent bare ground, prairie dog activity, and distance to water. Model TBSAW correctly classified 76% of cases, with 79% sensitivity (true positives) and 73% specificity (false positives = 27%). The dispersion parameter for TBSAW was 0.960, close enough to 1 that over- or under-dispersion was not a concern.

Odds of burrow occupancy increased for every unit-increase in burrow tunnel length (143%/m), number of usable burrows within 30 m (5%/burrow), and percent prairie dog activity within 100 m (2%/%; Table 4). Conversely, odds of use decreased for every unit-increase in percent shrub cover within 30 m (−3%/%) and distance to permanent water (−1%/m; Table 4). Nest burrows had longer tunnels, more available burrows within 30 m, less shrub cover within 30 m, more prairie dog activity within 100 m, and shorter distances to nearest water than unoccupied burrows (Table 4, Fig. 1). Results did not change appreciably when we restricted our sample of unoccupied burrows to only those within owl-occupied prairie dog colonies. Burrows within active colonies had longer tunnels, more available burrows, and a higher percentage of bare ground within 30 m than burrows in inactive colonies (Table 2).

Correct classification (probability cutoff = 0.5) averaged 80% (range 74–83%) in the 10 training data sets and 75% (range 67–89%) in the 10 testing data sets (Table 5). The ROC plots of overall sensitivity versus overall 1-specificity were similar for training and testing data. Area Under the Curve for these ROC plots was 0.84 for training data and 0.83 for testing data. Predictive power was similar between training and testing data sets. Overall kappa statistics indicated good model performance when fitted with training (0.589) and testing (0.488) data (Table 5).

DISCUSSION

Five of the 8 habitat features influenced burrowing owl nest-site selection in northeastern Wyoming, including features at all 4 spatial scales considered: the structure of the burrow itself (burrows with longer tunnels), the area surrounding the nest burrow (high burrow density and low shrub cover), characteristics of the prairie dog colony (colonies with more prairie dog activity), and features within the surrounding landscape (sites close to water). Main tunnel length within the focal burrow was the most influential variable. Several previous studies recognized the importance of burrow tunnel length (Butts and Lewis 1982, Plumpton and Lutz 1993, Belthoff and King 2002). However, hypotheses about why burrowing owls select longer burrow tunnels remain to be tested.

In addition to tunnel length, our results suggested that features in the area immediately surrounding the burrow affected the probability of use. Average shrub cover was significantly lower at occupied burrows, and the odds of use decreased as shrub cover increased. The effect of shrub cover

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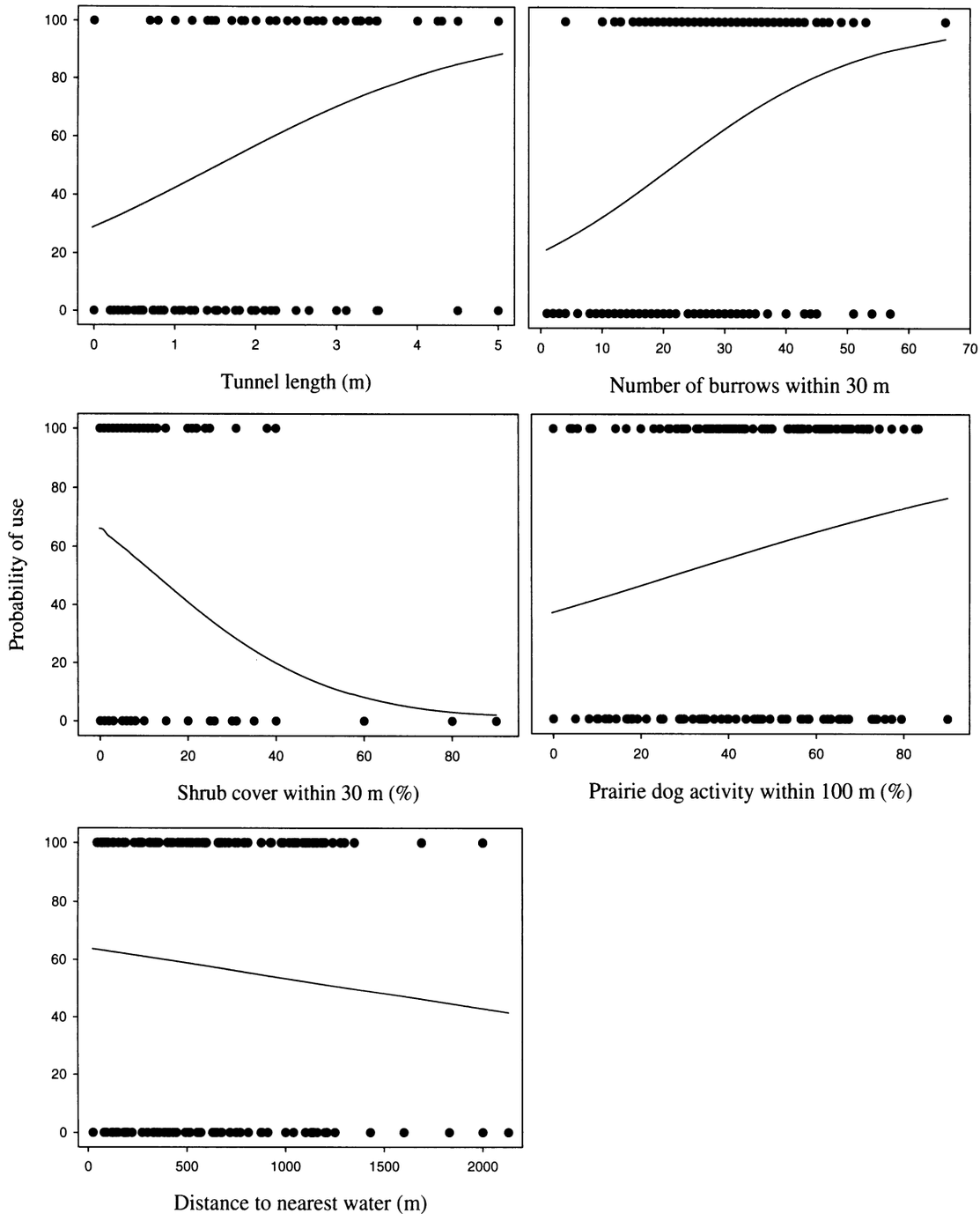

Figure 1. Modeled probabilities of burrow use by nesting burrowing owls for the 5 habitat variables. We collected data in 2003–2004 at nests in Thunder Basin National Grassland, northeastern Wyoming, USA.

on burrow selection was not simply an artifact of differences in shrub cover between active and inactive prairie dog colonies (which did not differ in % shrub cover). Similarly, vegetation was shorter at nest sites relative to unoccupied sites in South Dakota and Colorado (MacCracken et al. 1985, Plumpton and Lutz 1993). Because adult and juvenile owls spend much of their time outside the nest burrow, visibility from the nest burrow may be important for foraging and anti-predator efficiency (MacCracken et al. 1985, Plumpton and Lutz 1993, Ronan 2002). The other habitat features that we associated with foraging efficiency (distance to nearest perch and distance to nearest drainage) did not differentiate nests from unoccupied burrows. The number of usable burrows was higher near nests compared to unoccupied burrows, and higher in active prairie dog colonies compared to inactive colonies. Burrowing owls have

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Table 5. Performance of our burrowing owl nest-site selection model based on 10 training data sets (70% of original data) and 10 testing data sets (30% of original data) in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Measure	Data	
	Training	Testing
Correct classification (%)	80	75
Sensitivity	0.803	0.777
Specificity	0.788	0.716
Positive predictive power	0.212	0.284
Negative predictive power	0.197	0.223
Kappa	0.589	0.488

also been found in areas of high burrow density in other studies (Plumpton and Lutz 1993, Toombs 1997, Desmond and Savidge 1999, Restani et al. 2001, Ronan 2002). When shrub cover and grass height are low, burrowing owls may seek cover in nearby satellite burrows (Haug et al. 1993, Desmond and Savidge 1999, Ronan 2002). Satellite burrows are the primary cover for roosting, caching prey, and refugia for adult and juvenile owls (Desmond and Savidge 1999, Ronan 2002).

At the colony scale, prairie dog activity was higher in colonies with burrowing owl nests compared to colonies with randomly selected, unoccupied burrows. This pattern is consistent with past studies in Oklahoma, South Dakota, Colorado, Nebraska, and Montana (Table 1). Because owls in the Great Plains do not dig their own burrows, prairie dogs provide the structural maintenance of potential nest burrows. In the absence of prairie dogs, unkempt burrows often collapse within 3 years after abandonment by prairie dogs (Butts and Lewis 1982, MacCracken et al. 1985). Indeed, we found more available burrows and increased bare ground within active prairie dog colonies.

At the landscape scale, nest burrows were closer to permanent water sources (<1 km) than unoccupied burrows. Water sources in our study area were primarily windmill-powered cattle tanks. Although we did not observe burrowing owls foraging or drinking from tanks, we did retrieve 2 drowned juvenile burrowing owls from cattle tanks. Remote cameras in Arizona documented that burrowing owls do visit water catchments to drink and bathe (Rosenstock et al. 2004). Water catchments also attract an abundance of small vertebrates (passerines, bats, rodents, reptiles, and amphibians; Rosenstock et al. 2004), and may be attractive hunting sites for breeding owls. Features that influenced burrowing owl habitat use in our study were markedly similar to results from past studies in the Great Plains (Table 1). However, the habitat features influencing burrow use in areas where colonial mammals are largely absent (e.g., coastal scrub or monoculture farmland) may be very different from those observed in the Great Plains.

TBSAW Model Assessment

We used an AIC, weight-of-evidence approach to identify features associated with nest-site selection (Burnham and Anderson 2002, Stephens et al. 2005). One drawback with the information-theoretic approach is that researchers select the best model from a candidate set of models. Although the set of candidate models should be biologically informed, the best model is only better than the models tested (Stephens et al. 2005). One way to alleviate this concern is to include many candidate models (we included 20), and include classification accuracy with other model-selection metrics (Boyce et al. 2002). We did this by examining ROC plots for each candidate model. Percent correct classification, sensitivity, and kappa all suggested that our model performed well. The best model offered a large improvement in predictive ability over chance performance. Moreover, 2-fold cross-validation results demonstrated that the model performed well with partitioned, independent data. Our model performed well in overall and cross-validation settings, for multiple model-assessment criteria, and over a range of probability thresholds. Hence, we have great confidence in the value of our model for predicting habitat selection in burrowing owls.

MANAGEMENT IMPLICATIONS

Our results suggest that most elements of burrowing owl nesting habitat could be managed at the scale of the prairie dog colony. Hence, management of prairie dog colonies to maintain prairie dog activity, burrow availability, and low vegetative cover will be important for burrowing owl conservation and management in Wyoming and throughout the Great Plains (Byer 2001, Klute et al. 2003, McDonald et al. 2004). Our nest-selection model has the potential to be effective for prediction-based management applications, and could be used to evaluate other areas based on their potential to support burrowing owls. In this way, managers could begin to plan management strategies for protecting and enhancing burrowing owl habitat in the Great Plains.

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