NESTING ECOLOGY AND HABITAT SELECTION OF WESTERN BURROWING OWLS (*ATHENE CUNICULARIA HYPUGAEA*) IN THE THUNDER BASIN NATIONAL GRASSLAND, NORTHEASTERN WYOMING

by
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A thesis submitted to the Department of Zoology and Physiology
and The Graduate School of the University of Wyoming
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE
in
ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming
May, 2005

Lantz, Sarah J., Nesting Ecology and Habitat Selection of Western Burrowing Owls (*Athene cunicularia hypugaea*) in the Thunder Basin National Grassland, Northeastern Wyoming, M.S., Department of Zoology and Physiology, May, 2005.

Local populations of western burrowing owls (*Athene cunicularia*) have been reportedly declining since the late 1970s. To prevent further declines, and to design and implement effective recovery efforts, we need a better understanding of how distribution and demographic trends are influenced by habitat quality. To this end, I measured spatial patterns of nest-site selection as well as the influence of habitat, and non-habitat (e.g. time within season), features on daily nest survival for a population of burrowing owls in the Thunder Basin National Grassland, in northeastern Wyoming. I examined spatially explicit patterns of burrowing owl nest-site selection within black-tailed prairie dog (*Cynomys ludovicanus*) colonies. In 2003 and 2004, I compared burrow-, site-, colony-, and landscape-scale habitat parameters between nest burrows (n = 105) and unused burrows (n = 85). Burrowing owls selected nests at four spatial scales. Nest sites had longer burrow tunnels (burrow-scale), more available burrows and less shrub cover in within 30 m (nest-site scale), more prairie dog activity in within 100 m (colony scale), and were closer to water (landscape scale) than unoccupied burrows. My results demonstrate the importance of maintaining and expanding prairie dog colonies for burrowing owl conservation.

I measured reproductive parameters for the same population of burrowing owls during the 2003 (n = 65) and 2004 (n = 71) breeding seasons. I modeled daily nest survival using the logistic-exposure approach, and compared the overall probability of nest success from the model to the empirical estimates of apparent-, and Mayfield nest success. Daily nest survival rates were lower, but annual fecundity was higher in 2003 compared to 2004. Empirical estimates of burrowing owl nest success were similar among methods (70.2% logistic-exposure, 71.4% apparent, 70.5% Mayfield). However, the model-based approach allowed for daily nest survival rates to vary with time, temperature, and habitat features, and I found a clear upward trend in the probability of nest survival over time within the breeding season. Daily survival of burrowing owl nests varied between years, differed among nest stages, and was influenced by ambient temperature. My results suggest that burrowing owls can have high daily nest survival but low fecundity within the same year, and emphasize the importance of multiple years of study when measuring demographic trends.

ACKNOWLEDGEMENTS

This study would not have been possible without cooperation from private landowners in the Thunder Basin National Grassland. I give kind thanks to those individuals and families for permission to access their lands, for sharing historical and biological information, and for their patience. I also thank the cooperating agencies (Wyoming Bureau of Land Management – Casper Field Office, Wyoming Game and Fish Department, and US Forest Service – Douglas Ranger District) for their financial and logistical support, and for their interest in burrowing owl conservation within Wyoming. Deepest gratitude to all of the research technicians who kept my spirits high: Stephen LeFaiver, Andy Ostrander, Matthew Meyer, Sara Garreau, Bill Wesselink, Kevin Bronson, Bethany Hontz, Kris Lightner, Patrick Keys, Timothy Donner, and Jeff Jewell.

Warm thanks to my committee members for their mentorship and direction. In particular, I thank Dr. Courtney Conway for the opportunity to work on burrowing owls in Wyoming. Trailing a mountain of emails and long-distance phone calls, I learned so much from your guidance and I am proud of our collaborative work. To Dr. Richard Anderson-Sprecher, I am sincerely grateful for your statistical tutelage and your patience. To Dr. David McDonald, for the opportunity to work collaboratively on a burrowing owl conservation assessment. And to Dr. Stanley Anderson, my major advisor and stress manager, thank you for always reminding me to enjoy graduate school and to explore Wyoming. And thanks to the administrative staff of the Wyoming Cooperative Fish and Wildlife Research Unit, in particular Laurie Kempert, Linda Ohler, and Mandi Barry; thanks for all of your help and friendship.

I also extend loving, heartfelt thanks to my parents and family for their support and pride in everything that I do. To all of my pals in the Laramie community, thanks for all of the good times on the trails, on the rocks, in the classroom, and in the pints; thanks for keeping me sane in grad school, I will never forget this time in my life. And to Brian, my co-conspirator throughout this adventure, thanks for the inspiration and everything yet to come.

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PREFACE

Local populations of western burrowing owls have been reportedly declining since the late 1970s. Burrowing owls are listed as endangered in Canada, and are a species of special concern in 9 U.S. states. To prevent further declines, and to design and implement effective recovery efforts, we need a better understanding of how distribution and demographic trends are influenced by habitat quality. To this end, I measured spatial patterns of nest site selection and the impact of intrinsic and extrinsic factors on daily nest survival for a population of burrowing owls in the Thunder Basin National Grassland, in northeastern Wyoming. Herein, I present these findings in two chapters.

In Chapter One, the primary objective was to describe patterns of burrowing owl nest-site selection within black-tailed prairie dog colonies in Wyoming. I incorporated habitat variables at several scales into models of burrowing owl nest use within prairie dog colonies, drawing comparisons between owl-occupied, owl-unoccupied, active, and inactive colonies. I evaluated the predictive performance of the top nest-site selection model to test for accuracy and stability, and provided a robust model that could be applied in predictive or comparative studies.

In Chapter Two, I measured 6 reproductive parameters for burrowing owls in Wyoming: clutch size, brood size, fledgling success, annual fecundity, annual nest survival, and daily nest survival. The first objective was to verify breeding, estimate nest initiation dates, and measure fecundity at burrowing owl nests. The second objective was to identify an appropriate, model-based estimator of nest survival given the unique limitations associated with monitoring burrowing owl nests. The third objective was to assess habitat quality for breeding burrowing owls in Wyoming. I measured the effects of habitat features, year, time within season, and temperature on daily nest survival (DSR).

CHAPTER ONE

Spatial Patterns of Burrowing Owl Nest Selection in Black-tailed Prairie Dog Colonies in Wyoming

ABSTRACT

I used a comparative approach to examine spatial patterns of burrowing owl (*Athene cunicularia*) nest-site selection within black-tailed prairie dog (*Cynomys ludovicanus*) colonies in northeastern Wyoming. In 2003 and 2004, I compared burrow-, site-, colony-, and landscape-scale habitat parameters between burrowing owl nest burrows (*n* = 105) and unused burrows (*n* = 85). I sampled 4 prairie dog colony types: owl-occupied, active (*n* = 16), owl-occupied, inactive (*n* = 13), owl-unoccupied, active (*n* = 14), and owl-unoccupied, inactive (*n* = 14). I used an information-theoretic approach to examine models of burrowing owl nest selection, and evaluated the predictive performance, accuracy, and stability of the best model. The best model of burrowing owl nest selection included variables at all 4 spatial scales, and patterns were consistent among the 4 prairie dog colony types. Nest sites had longer burrow tunnels (burrow-scale), more available burrows and less shrub cover within 30m (nest-site scale), more prairie dog activity within 100m (colony scale), and were closer to water (landscape scale) than unoccupied burrows. The best model correctly classified 76.3% of cases, and all metrics of model performance indicated stability of model coefficients and accurate predictive power. I suggest maintenance and expansion of existing prairie dog colony area as an important management strategy for burrowing owl conservation, and I provide a nest-site selection model for prediction-based management applications.

INTRODUCTION

Efforts to conserve rare and threatened wildlife often begin with resource selection studies to explain variation in animal distribution, abundance, and demographic trend. Descriptive studies of wildlife-habitat relationships work to identify the proximate cues that trigger selection by the searching animal (Hutto 1985, Morrison 2001, Manly et al. 2002). This depends on spatial scale, and reliable inference about the mechanisms that drive habitat selection requires that the spatial scale be made explicit (Morrison 2002). Migratory birds are thought to select breeding habitats over a large, hierarchical set of choices at increasingly smaller spatial scales (Johnson 1980, Cody 1981, Hutto 1985, Orians and Wittenberger 1991, Morrison 2002). At each spatial scale, birds may select nests where the availability of and proximity to required resources are at levels and distances that optimize reproductive success (Cody 1974, Rosenzweig 1981). At the continental scale, a migratory bird's choice of where to settle is constrained by geographic and evolutionary (genetic) influences (Hutto 1985). Regionally, migratory birds may select breeding habitats based on physiography, vegetation type, climate, predators, and the presence of inter- and intraspecific competitors (Weins 1985, Orians and Wittenberger 1991). These broad-scale cues may be necessary but insufficient without proximate cues at the microhabitat level (Hutto 1985). At the microhabitat scale, birds settle into nest-sites where the intrinsic (within-habitat) requirements are met. Biologists often study microhabitat selection, because avian response to proximate cues in their immediate environment may resemble the ultimate factors that determine reproductive success and therefore species persistence (Klopfer 1967, Hutto 1985, Klopfer and Ganzhorn 1985).

Scalar patterns of habitat selection may be most clearly illustrated in a multivariate setting. Multivariate models can be powerful tools to illustrate the complex interaction of spatial habitat features and their influence on the probability of selection. This becomes critical when managing rare or threatened species. Modeling selection at multiple scales facilitates recognition of spatially variable resources that may be critical to regionally imperiled populations. For the purpose of this study, I examined habitat selection for a declining migratory bird, the burrowing owl (*Athene cunicularia*), to see if selection did occur at multiple scales, and if those patterns were measurable in a modeled environment.

The burrowing owl is a Neotropical migrant breeding throughout much of western North America. Though distributed across most of western North America, range contraction and local population declines have prompted conservation action for burrowing owls in the United States (National Bird of Conservation Concern), Canada (Endangered), and Mexico (*see* Klute et al. 2003 *for full legal status*). Habitat degradation has been implicated in losses of local breeding populations of burrowing owls along the periphery of their range since the 1970s (from southern Canada, Minnesota, and Iowa south to northern Texas; and from western California to Washington; Wellicome and Holroyd 2001, Klute et al. 2003). Consequently, primary recommendations for conservation have been to define burrowing owl habitat across their range, to identify threats to their habitat, and to pro-actively conserve areas of stability (Holroyd et al. 2001, Klute et al. 2003, McDonald et al. 2004).

Burrowing owls occupy a wide array of landscapes. From shrub-steppe to mixed- and short-grass prairie, coastal to desert scrub, and agricultural to sub-urban lands, few vegetal and structural characteristics unify the definition of burrowing owl habitat (Haug et al. 1993, Klute et al. 2003). They typically nest in relatively flat, sparsely vegetated, open areas, with burrowing mammals that dig potential nest burrows (Haug et al.1993). But beyond these basic features, burrowing owl habitat appears structurally different between regions. Because of this spatial heterogeneity, and because proximate cues may differ regionally, much of the burrowing owl research to date has focused on quantifying selection patterns at several points throughout their distribution.

Narrowing the focus from the continental- to the regional level, a pattern in burrowing owl habitat preference begins to emerge. In the Great Plains, burrowing owls are strongly associated with colonial, burrowing mammals, particularly the black-tailed prairie dog (*Cynomys ludovicanus*) (Butts and Lewis 1982, Desmond et al. 2000, Sidle et al. 2001). Surveys in western Oklahoma found owls nesting in 66% of the black-tailed prairie dog colonies surveyed where colony land coverage was 0.16% of the surveyed area (Butts and Lewis 1982). Similarly, surveys in the Nebraska panhandle showed higher nest densities within black-tailed prairie dog colonies relative to the surrounding landscape (Desmond 1991, Desmond and Savidge 1996). And, surveys in eastern Colorado identified 423 burrowing owl locations within short- and mixed-grass prairie, 80% of which were located within black-tailed prairie dog colonies (VerCauteren et al. 2001). As a result, most of the studies in the Great Plains have chosen to examine burrowing owl nest-site use within black-tailed prairie dog colonies, including those in northeastern Colorado (Hughes 1993), Comanche National Grassland in southeastern Colorado (Toombs 1997), Rocky Mountain Arsenal National Wildlife Refuge in east-central Colorado (Plumpton and Lutz 1993), the panhandle of Nebraska (Desmond and Savidge 1996 and 1999, Desmond et al. 2000), southeastern Montana (Restani et al. 2001), and Buffalo Gap National Grassland in southwestern South Dakota (MacCracken et al. 1985) (Table 1.1).

With few exceptions, conclusions about burrowing owl-habitat relationships have been drawn from multiple, univariate comparisons of used and unused burrows (*see* MacCracken et al. 1985, Desmond et al. 2000, Ronan 2002, *as exceptions*). Univariate comparisons can be insightful ways to differentiate used and unused sites, even at multiple scales. However, if the probability of selection by burrowing owls varies depending on the combination of habitat variables at multiple scales, then univariate comparisons may be inadequate.

In light of these considerations, I examined patterns of nest-site selection for a population of burrowing owls in northeastern Wyoming, USA. I developed presence/absence, logistic regression models comparing burrow-, site-, colony-, and landscape-scale habitat parameters between nest burrows and randomly selected, unused burrows. The primary objective was to describe patterns of burrowing owl nest-site selection within black-tailed prairie dog colonies in Wyoming. I incorporated habitat variables at several scales into models of burrowing owl nest use within prairie dog colonies, drawing comparisons between owl-occupied, owl-unoccupied, active, and inactive colonies. The secondary objective was to evaluate the predictive performance of my top nest-site selection model. I evaluated the model to test for accuracy and stability, and to produce a model that could be applied in comparative habitat studies among populations of burrowing owls.

STUDY AREA

I conducted my study in the Thunder Basin National Grassland (TBNG), near Wright (43º 44'N, 105º28'W), Newcastle (43º 51'N, 104º 12'W), and Douglas (42º 45'N, 105º22'W), Wyoming. TBNG encompasses 2,300 km^2 of the southern Powder River Basin, between the Bighorn Mountains and the Black Hills. Topography within TBNG includes valleys, rough breaks and badlands, steep coniferous mesas, and low riparian bottomlands, with elevation ranging 1,090 – 1,580 m. Annual precipitation varies from 15 - 40 cm. Located within the Great Plains-Palouse Dry Steppe Province (Bailey 1995), vegetation is dominated by grasses (*Agropyron smithii, Buchloe dactyloides, Bouteloua gracilis*), sedges (*Carex* spp.), and shrubs

(*Artemesia tridentata, Artemesia cana, Sarcobatus vermiculatus*). Under the jurisdiction of the US Department of Agriculture Forest Service, lands are managed privately (ranchers, coal companies), and publicly (Forest Service, US Department of Interior Bureau of Land Management, and State Trust of Wyoming). Primary land uses include cattle and sheep grazing, and mineral extraction.

TBNG contains the largest land coverage of black-tailed prairie dog colonies (7,381 ha) of any US Forest Service Great Plains National Grassland (Luce 2003). Given the well-documented association between burrowing owls and black-tailed prairie dog colonies in the Great Plains (*see introduction*), I restricted my sampling efforts solely to black-tailed prairie dog colonies within the study area.

METHODS

I collected data on burrowing owls in TBNG during the 2003 - 2004 breeding seasons. I chose a *Design I* study regime (Manly et al. 2002): I made comparisons at the population level by sampling burrowing owl nest burrows and random, unused burrows from the entire study area. I was not monitoring selection by marked individuals.

Nest Burrows

I located my sample of used burrows (nests) by conducting call-broadcast surveys along dirt roads within prairie dog colonies (Conway and Simon 2003). I surveyed 73 prairie dog colonies in 2003 and 2004, 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, I revisited areas where I had detected burrowing owls and conducted thorough ground searches to look for signs of nesting (shredded cow/horse manure, prey remains, whitewash, and regurgitated castings; Haug et al. 1993, Smith 2004). These sites were monitored weekly to confirm nest status and monitor fate (nest survival results presented in Chapter 2). For a burrow to be included as a nest, I had to detect both the male and the female at the burrow on at least two visits.

Unused burrow selection

Unused burrows were randomly sampled within each surveyed prairie dog colony in TBNG. I evenly sampled prairie dog colony attributes within each of the following categories: 1) owl-occupied, active with prairie dogs, 2) owl-occupied, inactive (no prairie dogs), 3) owl-unoccupied, active, and 4) owl-unoccupied, inactive. A colony was classified active if ≥ 10 prairie dogs were present on ≥ 2 spatially consecutive survey points during the initial burrowing owl survey(s). I overlaid a point-grid system onto a map of all surveyed prairie dog colonies within TBNG. Grid points were chosen randomly, and each point corresponded to a set of UTM coordinates. In the field, I established a 50-m x 50-m quadrat in the 4 cardinal directions from the random point, and placed randomly numbered pin flags at each usable burrow within the quadrat. A burrow was usable if the tunnel entrance diameter was ≥ 5 cm and no obstructions blocked the tunnel passage to at least 10 cm deep. I randomly chose a flagged burrow within the 50-m quadrat and confirmed owl-absence using an infrared, burrow videoscope as well as the lack of nesting sign. If the burrow was unoccupied by burrowing owls, and was at least 150 m from any known nest burrow, then it qualified as a sampling unit within the unused sample.

Variable selection and measurement

Based on results from previous studies (Table 1.1) and preliminary observations during the 2002 breeding season in TBNG, I selected 8 habitat variables as potential covariates to include in the modeling effort (Table 1.2). I parameterized the models at a localized scale of burrowing owl habitat selection by restricting measurements to within 2 km of the focal burrow.

Habitat variables were classified at 4 concentric scales of resolution, radiating out from the focal burrow: 1) the burrow scale, 2) the nest-site scale, 3) the prairie dog colony scale, and 4) the landscape scale.

At the burrow scale, I measured the length (m) of the main tunnel from burrow entrance to the nest chamber (or end of the burrow) using an infrared burrow videoscope. The shape and length of burrow tunnels were highly variable; some bent at angles too sharp for a flexible camera scope to navigate, and some were longer than the length of the scope (4.5 m). While tunnel length was a continuous variable, I assigned burrows with tortuous (unavailable) tunnels the mean length of all used and unused burrows (length = 1.90 m; $n = 13$ for nests, $n = 23$ for unused burrows). I assigned burrows > 4.5 m as length = 5 m ($n = 5$ for nests, $n = 23$ for unoccupied burrows). To be sure these designations did not lead to spurious conclusions, I also ran analyses excluding burrows for which length was uncertain. Direction and strength of model coefficients, and model ranking, did not change substantially when I excluded burrows with uncertain lengths. Hence, I reported results from the analysis with all burrows included.

To measure selection at the nest-site scale, I counted the number of usable burrows within 30 m. I also estimated percent ground cover by shrubs, and percent bare ground within 30 m of the focal burrow. Because I was only interested in relative bare ground and shrub cover, I was satisfied with visual estimates from trained observers.

At the scale of the prairie dog colony, I formed an index of prairie dog activity within 100 m of the focal burrow, roughly based on methods by Biggins et al. (1993). I bisected the focal burrow with two 200-m belt transects of 4-m width, and counted the number of active burrows and total burrows in each belt transect. Indices for both transects were averaged for an overall percentage of prairie dog activity within 100 m of the focal burrow.

At the landscape scale, I measured distance from the focal burrow to the nearest perch (any structure ≥ 0.5 m that could support a 160-g bird), distance to nearest permanent water, and distance to nearest drainage. A drainage was any linear depression capable of draining water through a prairie dog colony, 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), as these tend to support higher prey densities relative to the uplands (Haug and Oliphant 1990). I measured distances from the focal burrow to these landscape features within a 2-km radius using a Global Positioning System (GPS). If I did not find any of these features within 2 km of the focal burrow, I assigned them a value of 2 km.

To test for multicollinearity among habitat variables, I regressed each explanatory variable against all the others and examined the variance inflation factor, $\text{VIF}(X_i) = 1 / (1 - R_i^2)$, where X_i is the explanatory variable (Chatterjee and Price 1991). A VIF that strongly deviated from 1 ($0.1 < \text{VIF} < 10$) 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, I 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, I chose binary logistic regression to model the probability of burrow use by nesting burrowing owls (Hosmer and Lemeshow 2000). I developed 20 candidate models of varying combinations of the 8 potential explanatory variables (Table 1.3). By varying covariate combinations, I isolated models of potential effects: prairie dog activity, distance to hunting sites, habitat structure, vegetation structure, and combined effects of prairie dog activity and resource availability (Table 1.3).

I ran all 20 nest-site selection models in SAS PROC LOGISTIC, pooling data from 2003 and 2004 (SAS Institute 2000). 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. Hence, I report the models without a year effect, as I was interested in a simple, yet robust model. In addition, I 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 I left interaction terms out of the models to maintain parsimony.

I ranked candidate models with Akaike's Information Criterion (AIC), where the best model most closely resembled the mechanism behind the observed patterns (Burnham and Anderson 2002). To avoid problems associated with a small sample-to-parameter ratio, I applied a small-sample bias adjustment to the AIC value associated with each candidate model (AIC_c; Burnham and Anderson 2002). Models were ranked with ascending AIC_c values. Based on this ranking, I included Akaike weights (w_i) and deviance as relative measures of support for each model (Burnham and Anderson 2002). I also judged the top model by the prevalence of the selected variables in the other top-ranking models. If variables consistently appeared within the top set of candidate models ($AIC_c < 0.5$, $w_i > 0.01$), I assigned greater confidence to the top model.

As an additional model selection diagnostic, I 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, I plotted sensitivity (probability a model will correctly classify positive cases; 'true positives') versus *1 –specificity* (probability a model will incorrectly classify negative cases; '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 two cases. If a model performed no better than chance, then AUC $\approx$ 0.50. An AUC substantially > 0.05 indicated a high rate of model sensitivity to presence cases (Fielding and Bell 1997, Poirazidis et al. 2004).

Correlation between binary responses, or variation between response probabilities, is typically referred to as overdispersion (SAS institute 2000, Menard 2001). Overdispersion results from any number of potential model inadequacies: failure to include important interaction terms, nonlinear relationships between explanatory variables and response variables, the presence of outliers, inadequate sub-sample size, or inappropriate transformation of variables. If data are overdispersed, the variance of parameter estimates is underestimated. I calculated a dispersion parameter for the top model by dividing the Deviance Chi-square Statistic, χ^2_D, by degrees of freedom (given in SAS logistic procedure output). If the dispersion parameter approximated 1.0, I assumed no overdispersion within the best model (Menard 2001).

I elucidated differences between used and unused burrows with the strength and direction of coefficients (α-level of 0.05) from the best model. To illustrate variable effect on presence/absence, I plotted log-odds for each parameter, modeled the probability of use, and compared variable means between used and unused burrows.

Colony comparisons

Because I stratified my sampling regime to include active and inactive prairie dog colonies, as well as owl-occupied and owl-unoccupied colonies, I was interested in how results might change when those classifications were tested separately. I ran univariate tests for site differences between active and inactive prairie dog colonies. I compared burrow tunnel lengths, and burrow availability, shrub and ground cover, as well as perch distance between active and inactive prairie dog colonies, grouping used and unused burrows for the comparison. To test for within-colony variation, I restricted my comparisons to used burrows and unused burrows within owl-occupied colonies only. I modeled the probability of burrow use within owl-occupied prairie dog colonies using the best approximating model.

Model evaluation

The value of a predictive model is unknown if its reliability is not proven. The more metrics used to evaluate the predictive ability of a presence/absence model, the more confidence we have in the reliability and applicability of the model over space and time (Fielding and Bell 1997, Guisan and Zimmermann 2000, Manel et al. 2001). Ideally, predictive performance is evaluated with external data. 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). I built sets of training and testing cases using a $k = 2$ data partition, in which partitions (k) were based on a heuristic ratio of $[1 + (p - 1)^{1/2}]^{-1}$, where p is the number of predictors (Fielding and Bell 1997). Randomly generating 10 sets of training/testing cases of equal presence/absence ratios, I compared predictive accuracy between training/testing sets using the top model selected in the AIC comparison. I averaged correct classification rates for the 10 training data sets and 10 testing data sets as a simplified bootstrap approach (Efron and Tibshirani 1993, Manel et al. 1999, Boyce et al. 2002).

I assessed performance of the training and testing data with several measures: predictive accuracy, ROC plots, AUC, and the kappa statistic (K), which measures the proportion of presence and absence cases that are predicted correctly after accounting for chance (Fielding and

Bell 1997, Manel et al. 2001). Predictive accuracy and kappa require identification of probability threshold, usually identified at the probability cutoff point at which the best model has its highest classification rate. Hence, I measure predictive accuracy (i.e., sensitivity, specificity, positive/negative predictive power, and kappa) at a probability cutoff of 0.5. I interpreted kappa proportions using the rule of thumb from Fielding and Bell (1997), where $K < 0.4$ indicates poor model performance, $0.4 < K < 0.75$ indicates good model performance, and $K > 0.75$ indicates excellent model performance. ROC plots and AUC are not evaluated at a probability cutoff, as they are threshold-independent measures of performance (Menard 2001). Instead, ROC plots are evaluated over a range of probabilities, where an AUC > 0.5 indicates an improvement over chance model performance.

RESULTS

In 2003 and 2004, I sampled habitat characteristics at 105 burrowing owl nests and 85 unoccupied burrows from 73 prairie dog colonies in TBNG. Of the 73 colonies surveyed, 47% were active with prairie dogs and 53% were inactive colonies. I located 81% of burrowing owl nests within active prairie dog colonies, and 19% of nests within inactive prairie dog colonies. Unused burrows came from a relatively even composition of prairie dog colony types: 16 owl-occupied, active colonies, 13 owl-occupied, inactive colonies, 14 owl-unoccupied, active colonies, and 14 owl-unoccupied, inactive colonies. Badger (*Taxidea taxus*), coyote (*Canis latrans*), and ground squirrel (*Spermophilus* spp.) 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, I assumed no multicollinearity among habitat variables.

The best approximating models were those that included variables related to both prairie dog activity and distance to resources (Table 1.4). Hereafter, I refer to the best model by its variable code, MBSDOGW. Four other competing models had relatively small ΔAIC_c (< 5), but MBSDOGW was the most parsimonious model (*k* = 5), with the lowest AIC-score, and had competitive deviance and AUC values (Table 1.4). Of the top 5 models, all 5 included M, B, and S, and 4 of the 5 top models included G, DOG, and W. MBSDOGW correctly classified 76.3% of cases, with 78.8% sensitivity (true positives) and 73.3% specificity (false positives = 26.7%). The dispersion parameter for MBSDOGW was 0.9597, 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 (142% per m), number of usable burrows within 30m (5% per burrow), and % prairie dog activity within 100m (2% per percent) (Table 1.5). Conversely, odds of use decreased for every unit-increase in % shrub cover in 30m (- 4% per percent), and distance to permanent water (1% per m) (Table 1.5, Figure 1.1). These results are supported by differences in variable means and associated 95% confidence intervals (Table 1.6). Nest burrows had longer tunnels, more available burrows within 30m, less shrub cover within 30m, more prairie dog activity within 100m, and shorter distance to nearest water than unused burrows (Table 1.6, Figure 1.2).

In univariate site comparisons of active and inactive prairie dog colonies, burrows in active colonies had longer tunnels, more available burrows within 30m, and a higher percentage of bare ground within 30m than burrows in inactive colonies (Table 1.7). Shrub cover and perch distance did not differ between burrows located in active and inactive prairie dog colonies. When the unused sample was restricted to those burrows within owl-occupied prairie dog colonies in the MBSDOGW model, the influence of shrub cover and distance to water decreased

(Table 1.8). Yet, the odds of nesting use still increased with increasing burrow tunnel length (152% per m), increasing availability of burrows (8% per burrow), and increasing prairie dog activity (2% per percent).

In the accuracy assessment, the 2-fold data partitioning broke 70% (*n* = 133) of data into training sets, and 30% (*n* = 57) into testing sets. Correct classification (probability cutoff = 0.5) in the training sets ranged from 73.9 – 83.3%, for an average of 79.6% (matching the classification rate of the full data set). Correct classification rates using the testing data were more variable, ranging from 67.3 - 88.5%, for an overall rate of 75.2% (Table 1.9). ROC plots of overall sensitivity vs. overall *1-specificity* were markedly similar for training and testing data (Figure 1.3). AUC's for these ROC plots were 0.84 training and 0.83 testing, a large improvement over chance (chance AUC = 0.50). Overall kappa statistics indicated good model performance when fitted with training (0.589) and testing data (0.488) (Table 1.9).

DISCUSSION

In the following discussion, I clarify patterns of selection for burrowing owls in TBNG, compare results from other studies, and discuss the implications. I provide a simple, yet robust model to predict the probability of burrow use by nesting burrowing owls within prairie dog colonies, discuss the predictive power and limitations of the model, and suggest application within research and management. The statistical rigor of my results help to refine our understanding of the influence of habitat on burrowing owl distribution in 2 ways: 1) sample sizes herein were larger compared to previous studies of burrowing owl habitat selection, and 2) I employed model assessment techniques that increased confidence and reliability of observed effects.

Habitat characteristics in TBNG

Burrowing owls in TBNG are selecting nest sites at 4 scales of perception: inside the burrow (burrows with longer tunnels), at the nest site (high burrow density and low shrub cover), among prairie dog colonies (colonies with more prairie dog activity), and within the landscape (sites close to water). According to the MBSDOGW model, main tunnel length within the focal burrow was the most influential variable in the MBSDOGW model (142% increase in the odds of use for every 1-m increase in tunnel length). Potential reasons for observed patterns may relate to nest-chamber microclimate and predator avoidance, but these possibilities have yet to be assessed. Few studies measure and recognize the importance of burrow tunnel length (*but see* Plumpton and Lutz 1993, Belthoff and King 2002). Barring human excavation, tunnel measurements are admittedly difficult to obtain in the absence of an underground, scoping camera. Yet, considering its influence on observed patterns in TBNG, the importance of tunnel dimensions should not be overlooked elsewhere. However, burrowing owls will modify burrow tunnels to create nest chambers, potentially increasing tunnel length. This could confound the results found in this study. To properly address the issue, future studies might consider an experimental approach, whereby known nest burrows from previous years are blocked at specified tunnel lengths, and the effect on selection measured during migratory arrival.

Scaling outward from the burrow, the MBSDOGW model illustrated burrowing owl preference patterns at the nest site. Adult and juvenile owls spend much of their time outside the nest burrow, where visibility from the ground may be important for foraging and anti-predator efficiency (MacCracken et al. 1985, Plumpton and Lutz 1993, Ronan 2002). Average shrub cover in TBNG was significantly lower at occupied burrows, and the odds of use decreased as shrub cover increased. Similarly, studies in South Dakota and Colorado found shorter vegetation at nest sites relative to unoccupied sites (MacCracken et al. 1985, Plumpton and Lutz 1993). But while burrowing owls may prefer low vegetal structure, percent bare ground near nests did not differ from unoccupied burrows in TBNG. Since grazing behavior of black-tailed prairie dogs maintains lots of bare ground throughout colonies, the effects of bare-ground and prairie dog activity may have explained a similar portion of the variation. Nevertheless, I did not detect statistical redundancy; the estimated coefficient for % bare ground did not change appreciatively when I removed prairie dog activity from the model. Percent bare ground was higher, however, at used and unused burrows in active prairie dog colonies compared to used and unused burrows in inactive prairie dog colonies.

When shrub cover and grass height are low, burrowing owls may seek thermal- and anti-predator cover in nearby 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). Burrowing owls are consistently found in areas of high burrow density (Haug et al. 1993, Plumpton and Lutz 1993, Toombs 1997, Desmond 1991, Desmond and Savidge 1999, Restani et al. 2001, Ronan 2002). Results from TBNG were no exception: the number of usable burrows was significantly higher near nests compared to unoccupied burrows, and significantly higher in active prairie dog colonies.

At the colony scale, prairie dog activity was higher at burrowing owl nests in TBNG; consistent with studies in Oklahoma, South Dakota, Colorado, Nebraska, and Montana; (Butts and Lewis 1982, MacCracken et al. 1985, Toombs 1997, Plumpton and Lutz 1993, Desmond et al. 2000, Restani et al. 2001). In the absence of prairie dogs, unkempt burrows quickly grow over with tall forbs that obstruct visibility for owls, and prairie dog burrows often collapse within 3 years of abandonment (Butts and Lewis 1982, MacCracken et al. 1985). Because owls in the

Great Plains do not dig their own burrows, prairie dogs provide the structural maintenance of potential nest burrows. Indeed, colony comparisons in TBNG indicated more available burrows and increased visibility (bare ground) within active prairie dog colonies. Prairie dogs may also be conferring behavioral benefits to burrowing owls. They may prefer active colonies because prairie dogs create a dilution effect, whereby an abundance of alternative prey (prairie dogs) dilutes the possibility of owl-detection by their predators (Desmond et al. 2000). They may also respond to and benefit from the complex alarm vocalizations elicited by adult prairie dogs as an early warning of approaching predators, however this possibility has not been tested.

At the landscape scale, nest burrows in TBNG were closer to permanent water sources (< 1 km) than unused burrows. Water sources were primarily windmill-powered cattle tanks in TBNG, and while I did not document active use, I retrieved drowned juvenile burrowing owls from cattle tanks on two occasions. Remote camera observations in Arizona documented burrowing owls visiting water catchments to drink and bathe (Rosenstock et al. 2004). Water catchments also attract an abundance of small vertebrates commonly eaten by burrowing owls (passerines, bats, rodents, reptiles, and amphibians; Rosenstock et al. 2004), and may be attractive hunting sites for breeding owls. Thus, burrowing owls may prefer nest burrows near water tanks in TBNG to facilitate short travel time from the nest burrow to rewarding hunt sites.

Other hunting-related effects such as distance to nearest perch and drainage did not differentiate occupied and unoccupied sites. In prairie dog colonies where vegetation height is monotypically low, burrowing owls may avoid perches as a defense tactic against raptorial predators (Plumpton and Lutz 1993). Conversely, burrowing owls may hunt from perches to increase their ability to locate prey (Rich 1986, Green and Anthony 1989, Haug et al. 1993). Adult owls frequently hunted and roosted from perches near nest burrows in TBNG, yet average distance to a perch was greater for nests compared to unoccupied burrows. This contradiction may be because I considered the nearest perch as any structure ≥ 0.5 m that could support an owl. This definition included shrubs, yet owls avoided areas with high shrub density. Except for one male owl that repeatedly perched on greasewood (*Sarcobatus vermiculatus*), all perch observations involved wooden and metal fence posts. By including shrubs as perches, preference or avoidance of perches may have gone undetected. Future studies might consider measuring distance to different types of potential perches (i.e., fence or utility posts, shrubs, etc.).

When I compared habitat features between used and unused burrows in owl-occupied prairie dog colonies, the observed patterns were similar to those from the full data set where unused burrows were sampled from both owl-occupied and owl-unoccupied colonies. In the owl-occupied colony analysis, nest burrows had more prairie dog activity, more available burrows, and longer burrow tunnels than unoccupied burrows within those same colonies. Thus, the effect of prairie dog activity on burrowing owl nest selection may be visible at both inter- and intra-colony scales.

Imposing the 4 spatial scales identified by the MBSDOGW model onto the combined results from previous studies (Table 1.1), the patterns of burrowing owl habitat use in TBNG are markedly similar in terms of colony- and nest-site requirements. It is noteworthy, however, that the generality of these patterns is likely restricted to landscapes engineered by prairie dogs. The mechanisms and limiting factors in other regions where colonial mammals are largely absent (e.g., coastal scrub or monoculture farmland) may be different enough from those observed in the Great Plains that such comparisons may not prove useful.

MBSDOGW Model Assessment

I used an AIC, weight-of-evidence approach to choose a biologically informative, multivariate model that was free of the bias and variance-estimation issues associated with null-hypothesis testing (Burnham and Anderson 2002, Stephens et al. 2005). One potential problem with the information-theoretic approach is that researchers select the best model from a candidate set of models generated from intuition and experience. While researcher hypotheses should be biologically informed, the best model is only better than the suite of candidate models (Stephens et al. 2005). One way to alleviate this concern is to include classification accuracy with other model-selection metrics (Chatfield 1995, Boyce et al. 2002). Reported herein as AUC, correct classification was high for all models (range 0.62 - 0.84), suggesting reasonable accuracy among the candidate set.

Because I was interested not only in description, but whether my model had predictive ability, I tested accuracy, applicability, and generality of the MBSDOGW model. In terms of correct classification, sensitivity, and kappa, the model performed well. The best model offered a large improvement in predictive ability over chance performance. Moreover, 2-fold cross-validation results showed the MBSDOGW model performed well when rigorously tested with partitioned, independent data. The MBSDOGW model performed well in overall and cross-validation settings, for multiple model-assessment criteria, over a range of probability thresholds.

Partitioning the data is not the same as collecting new data, and the predictive ability of models should ultimately be evaluated with new data (Chatfield 1995). However, certain situations preclude external validation. For example, in the absence of time, funding, or opportunity, holdout samples from original data sets are adequate surrogates (Manel et al. 1999). Additionally, spatially explicit models that assume homogeneous availability of resources among animals may not be applicable in other regions (Manly et al. 2002, McGrath et al. 2003). These are used primarily for adaptive management of the area for which the model was built; hence the model cannot be validated with external data (McGrath et al. 2003).

I did not have the opportunity to collect new data for testing the MBSDOGW model within the scope of this study. Therefore, cross-validation was a useful first step to assess predictive performance and applicability. Sample sizes were substantial enough to split data into training and testing data sets, and any one of the iterative tests ran with holdout samples could have been representative of a real attempt with new data (Manel et al. 1999). In k-fold cross-validation, variability within the data will force variation in model coefficients estimated from training/testing data sets. If the model can still accurately predict presence/absence within independent data, regardless of the variability in coefficient estimates in models built with training data, then we can assign greater confidence to the observed effects.

Model assessment, or model validation, is a useful pre-cursor to comparative studies of habitat selection. Once model validation proves the reliability of the modeled effects for a given population in a given geographic area, the model may facilitate comparisons of habitat selection by other populations of burrowing owls in a standardized, meaningful manner. For example, all 5 explanatory variables in the MBSDOGW model had significant effects on the probability of burrow use in my study area, and the reliability of those effects were tested and proven. If I tested the MBSDOGW model on other populations of burrowing owls nesting in prairie dog colonies of different National Grasslands, I might find differences in the strength and direction of estimated coefficients. Those differences could be informative measures of the variation in habitat selection among populations, whereby physical factors important for nesting burrowing owls in one area are less or more important for nesting burrowing owls in other areas.

MANAGEMENT IMPLICATIONS

A consistent pattern among populations in the Great Plains, burrowing owls in TBNG are strongly associated with active, black-tailed prairie dog colonies. However, North American land coverage by prairie dog colonies is conservatively estimated to have declined by as much as 98% since the early 1900s (Miller et al. 1994). These losses are largely due to eradication programs aimed at reducing competition for foraging livestock, and more recently, to large-scale, sylvatic plague (*Yersinia pestis*) epizootics (Miller et al. 1994, Antolin et al. 2002). From 1991-1997, burrowing owls in the Nebraska panhandle declined by 63%, and declines were strongly correlated with widespread loss of prairie dog activity (Desmond et al. 2000). The US Forest Service reports active prairie dog colony area in TBNG has declined by 89% since they first documented sylvatic plague in 1999 (Byer 2001). Burrowing owl nest occurrence in TBNG was disproportionately higher within active prairie dog colonies compared to inactive prairie dog colonies, and the effects of prairie dog activity increased the probability of burrow use. Thus, burrowing owls in TBNG are selecting for an apparently declining resource, and the population may be experiencing an ongoing decline in preferred habitat. Given the potential threat of habitat loss, my findings suggest maintenance and expansion of existing prairie dog colony area as an important management strategy for burrowing owl conservation (Klute et al. 2003, McDonald et al. 2004).

An effective resource model enables managers to reliably predict distribution and occurrence of wildlife species, and to assess impacts of local and regional land management practices (McGrath et al. 2003). The MBSDOGW model has the potential to be effective for prediction-based management applications. This model could be used to evaluate areas based on their potential to support burrowing owls. In this way, we can continue to refine our conceptual understanding of how burrowing owls respond to varying habitat conditions, and begin to direct management strategies for protecting and enhancing burrowing owl habitat in the Great Plains.

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Table 1.1. Habitat variables measured in previous burrowing owl nest-site selection studies within black-tailed prairie dog colonies. For comparison, I categorized variables into 4 spatial scales: landscape, colony, nest site, and burrow. (*) indicates variables that were listed as meaningful by previous authors.

Region	Authors	Habitat Measurements			
		Landscape	Prairie Dog Colony	Nest site	Burrow
Oklahoma	Butts and Lewis 1982	Topography	Presence prairie dogs* Distance to colony edge	Species Vegetation height*	Burrow type Soil type Tunnel length
South Dakota	MacCracken et al. 1985	None	None	Canopy cover* % Bare ground* Vegetation height*	Soil type* Tunnel width*
Colorado, northeast	Hughes 1993	None	Colony area* Prairie dog activity*	None	None
Colorado, southeast	Toombs 1997	None	Soil type Colony area Prairie dog activity* Distance to colony edge*	Burrow density*	Soil type
Colorado, central	Plumpton and Lutz 1993	Nearest road Nearest perch* Slope	Colony area	Canopy cover % Bare ground Vegetation height* Burrow density*	Orientation Tunnel length
Nebraska	Desmond 1991 Desmond and Savidge 1996, 1999 Desmond et al. 2000	Owl group size Nearest neighbor*	Colony area* Active burrow density* Badger predation density	Burrow density*	None
Montana	Restani et al. 2001	Nearest road Slope Elevation Nearest neighbor	Colony area Prairie dog activity Distance to colony edge	Nearest active burrow*	None

Table 1.2. Habitat variables, and their abbreviations, used in burrowing owl nest-site selection models, Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004. All habitat variables were measured at nest burrows and at randomly selected, unused burrows within black-tailed prairie dog colonies.

Abbreviation	Variable Description
Burrow scale	
M	Length of main tunnel (m)
Nest-site scale	
B	Number of usable burrows
S	Ground cover by shrubs (%)
G	Bare ground (%)
Prairie dog colony scale	
DOG	Index of prairie dog activity (%)
Landscape scale	
P	Distance to perch (m)
W	Distance to permanent water (m)
D	Distance to drainage (m)

Table 1.3. Twenty candidate models of burrow selection based on nesting burrowing owls during the 2003-2004 breeding seasons, Thunder Basin National Grassland, northeastern Wyoming, USA. Models are grouped by their potential effects: prairie dog activity, distance to hunting sites, habitat structure, vegetation structure, and the combined effects of prairie dog activity and resource availability. Variable abbreviations are given in
Table 1.2.

Model Effects
Terms
Full Model
1) M B S G DOG P W D
Effect of prairie dog activity
2) M
3) B
4) DOG
5) M B
6) M DOG
7) B DOG
8) M B DOG
9) M B S G DOG
Distance to hunting sites
10) P W D
Distance to hunting sites and available cover
11) M B W D
12) M B P W D
Habitat structure
13) M B S G P
Vegetation structure
14) S G
Prairie dog activity and distance to resources
15) M B G P W
16) M B S DOG W
17) M B S DOG D
18) M B S G P W
19) M B S G DOG D
20) M B S G DOG W

Table 1.4. Model-ranking results for burrowing owl nest-selection models developed in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004. Models were ranked by ascending ΔAIC_c; w_i is the model weight, and K is the number of parameters. Deviance is $-2[\log_e(L(\theta))-2\log_e(L_s(\theta))]$, where θ is a maximum likelihood estimate evaluated for the model in question L(θ) and for the saturated model $L_s(\theta)$. AUC is the Area Under Curve for an ROC graph, plotting sensitivity (true positives) vs. (1-specificity) (false positives).

Model	K	AIC_c	ΔAIC_c	w_i	Deviance	AUC
M B S DOG W	5	188.91	0.00	0.2959	176.59	0.870
M B S G DOG W	6	189.30	0.39	0.2438	174.84	0.869
M B S G DOG	5	191.01	2.09	0.1039	178.68	0.863
M B S G DOG P W D	8	191.29	2.38	0.0901	172.50	0.874
M B S G P W	6	192.05	3.14	0.0617	177.59	0.866
M B S DOG D	5	192.05	3.14	0.0617	179.73	0.860
M B S G DOG D	6	192.37	3.45	0.0527	177.91	0.861
M B DOG	3	193.00	4.09	0.0383	184.87	0.856
M B S G P	5	194.70	5.79	0.0164	182.38	0.859
M B	2	195.05	6.14	0.0137	188.99	0.851
M B G P W	5	196.31	7.39	0.0073	183.98	0.859
M B W D	4	196.50	7.58	0.0067	186.28	0.850
M B P W D	5	196.64	7.72	0.0062	184.31	0.856
M DOG	2	199.68	10.77	0.0014	193.62	0.833
M	1	203.84	14.92	0.0002	199.82	0.814
P W D	3	205.49	16.57	0.0001	195.36	0.825
B DOG	2	238.31	49.40	0.0000	232.25	0.723
B	2	241.23	52.32	0.0000	237.17	0.710
G S	2	249.96	61.04	0.0000	243.89	0.633
DOG	1	256.01	67.10	0.0000	251.99	0.626

Table 1.5. Estimated coefficients ($\hat{\beta}$), errors (SE), odds ratios (Exp ($\hat{\beta}$)), 95% confidence intervals (CI) of odds ratios, and associated *p*-values for all parameters within the MBSDOGW model of burrowing owl nest selection in Thunder Basin National Grassland, northeastern Wyoming, USA. Arrows represent the effect of each variable on probability of use (P_{use}).

Variable	$\hat{\beta}$	SE	Exp ($\hat{\beta}$)	CI	*p*	P_{use}
M	0.886	0.178	2.425	1.711, 3.437	< 0.001	↑
B	0.046	0.016	1.047	1.015, 1.080	0.004	↑
S	-0.035	0.016	0.965	0.935, 0.996	0.028	↓
DOG	0.016	0.008	1.016	1.000, 1.031	0.047	↑
W	-0.001	0.000	0.999	0.999, 1.000	0.059	↓

Table 1.6. Means and 95% confidence intervals (CI) for habitat variables measured at Burrowing Owl nest burrows and at randomly selected, unused burrows in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004.

	Nest burrows		Unused burrows	
Variable	Mean	CI	Mean	CI
Burrow scale				
M (m)	3.0	2.8, 3.3	1.7	1.5, 2.0
Nest-site scale				
B (#)	29	27.2, 31.3	20	17.5, 23.4
S (%)	5.8	4.3, 7.4	13.9	9.9, 17.8
G (%)	20.4	17.5, 23.3	17.9	14.5, 21.5
Prairie dog colony scale				
DOG (%)	44.4	40.2, 48.6	33.8	28.4, 39.2
Landscape scale				
P (m)	98.9	78.7, 119.2	76.7	49.8, 103.6
W (m)	761.7	652.3, 871.2	925.6	780.5, 1070.7
D (m)	128.0	96.0, 160.0	195.9	141.9, 249.8

Table 1.7. Comparison of means ($\bar{x}$) and 95% confidence intervals (CI) of habitat features within active and inactive black-tailed prairie dog colonies in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004. Features were measured at burrowing owl nest burrows as well as randomly selected, unused burrows. Nest burrows and unused burrows were grouped for these comparisons.

	Active colonies		Inactive colonies			
Variable	Mean	CI	Mean	CI	*t*	*p*
M (m)	2.5 *	2.3, 2.8	2.1	1.7, 2.5	-2.02	0.045
B (#)	27 **	25, 29	21	17, 24	-3.38	< 0.001
S (%)	9.5	6.8, 12.1	9.4	6.4, 12.4	-0.04	0.971
G (%)	21.2 *	18.4, 24.0	15.4	11.9, 18.9	-2.41	0.017
P (m)	85.7	68.8, 102.7	95.7	58.0, 133.3	0.55	0.581

Table 1.8. Estimated coefficients ($\hat{\beta}$), errors (SE), odds ratios (Exp ($\hat{\beta}$)), 95% confidence intervals (CI), and associated *p*-values for all parameters within the MBSDOGW model of burrowing owl selection, Thunder Basin National Grassland, northeastern Wyoming, USA. Arrows represent the effect of each variable on probability of use (P_{use}). Here, the unused sample was restricted to burrows within owl-occupied prairie dog colonies.

Variable	$\hat{\beta}$	SE	Exp ($\hat{\beta}$)	CI	*p*	P_{use}
M	0.928	0.244	2.529	1.569, 4.077	< 0.001	↑
B	0.082	0.023	1.086	1.037, 1.137	< 0.001	↑
S	- 0.033	0.021	0.968	0.928, 1.008	0.118	-----
DOG	0.023	0.001	1.023	1.004, 1.043	0.019	↑
W	- 0.001	0.000	0.999	0.999, 1.000	0.104	-----

Table 1.9. Comparison of burrowing owl nest-selection model, MBSDOGW, performance using training (70% of original data) and testing (30%) data in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004.

	Data	
Measure	Training	Testing
Prevalence	0.560	0.598
Correct Classification Rate	0.796	0.752
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	0.828	0.803

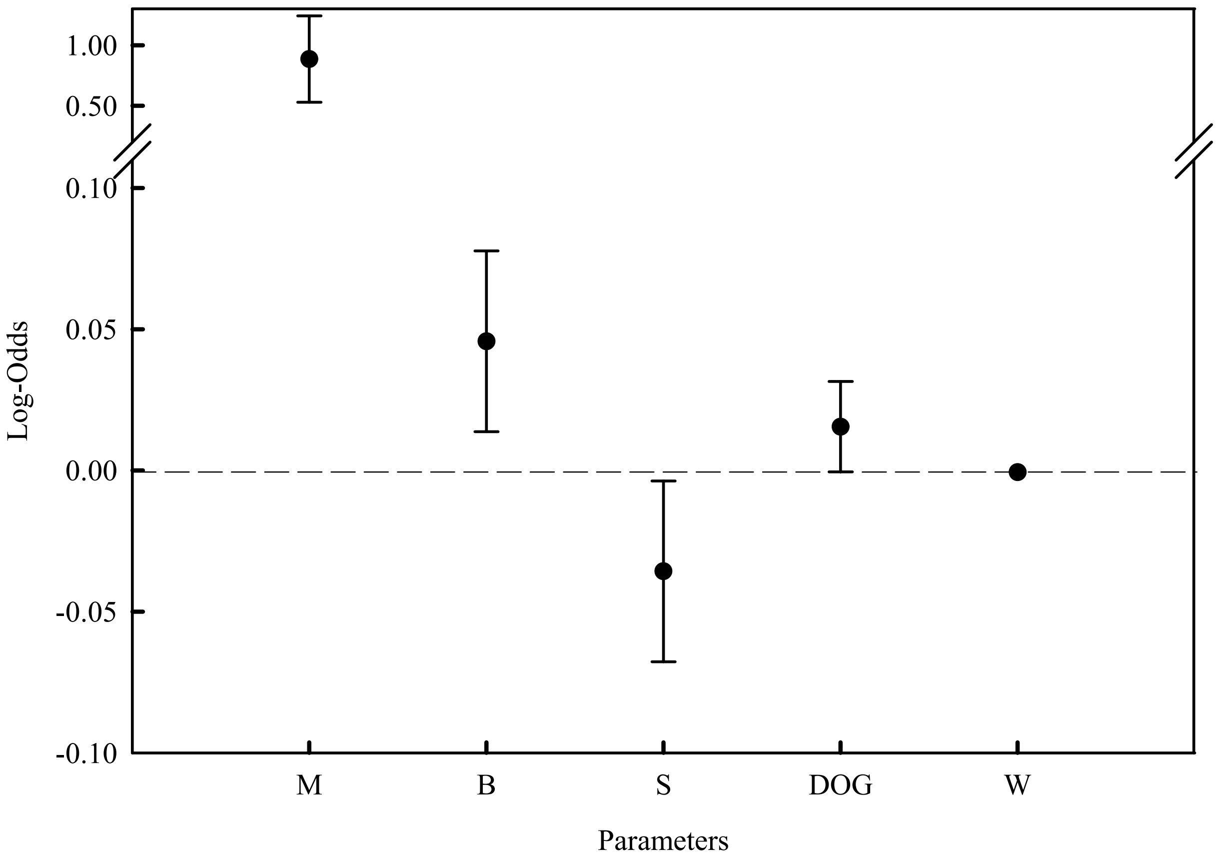

Figure 1.1. Log-odds of habitat parameter estimates from the best approximating nest-selection model (MBSDOGW) for burrowing owls in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004. Variables were: M = main tunnel length in burrow, B = burrow availability in 30m, S = shrub cover in 30m, DOG = prairie dog activity in 100m, and W = distance to nearest permanent water source.

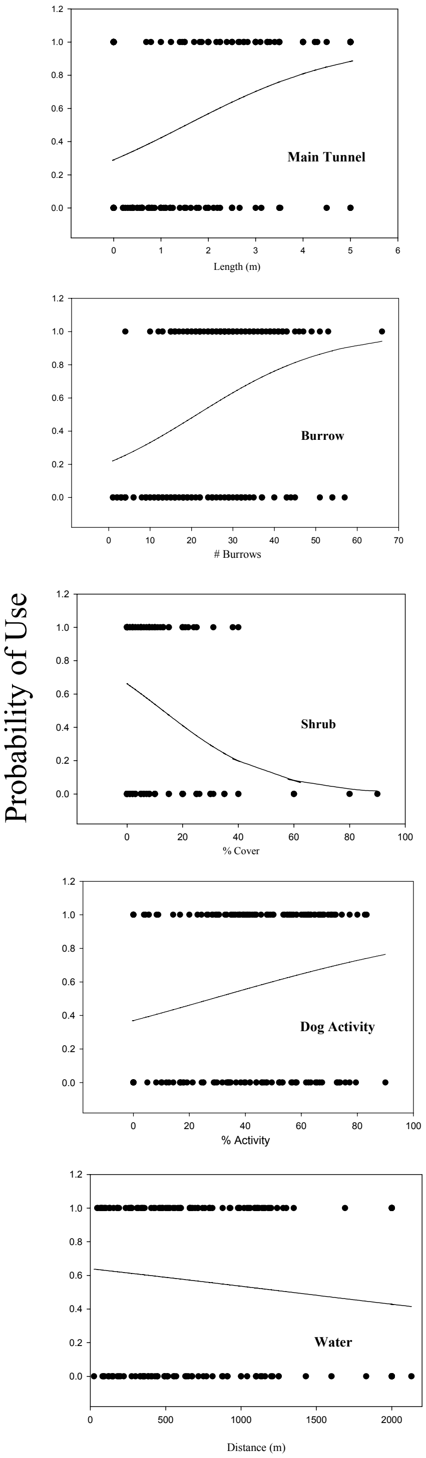

Figure 1.2. Relationship between the probability of burrow use and the five habitat parameters from the MBSDOGW nest-selection model for burrowing owls in Thunder Basin National Grassland, northeastern Wyoming USA.

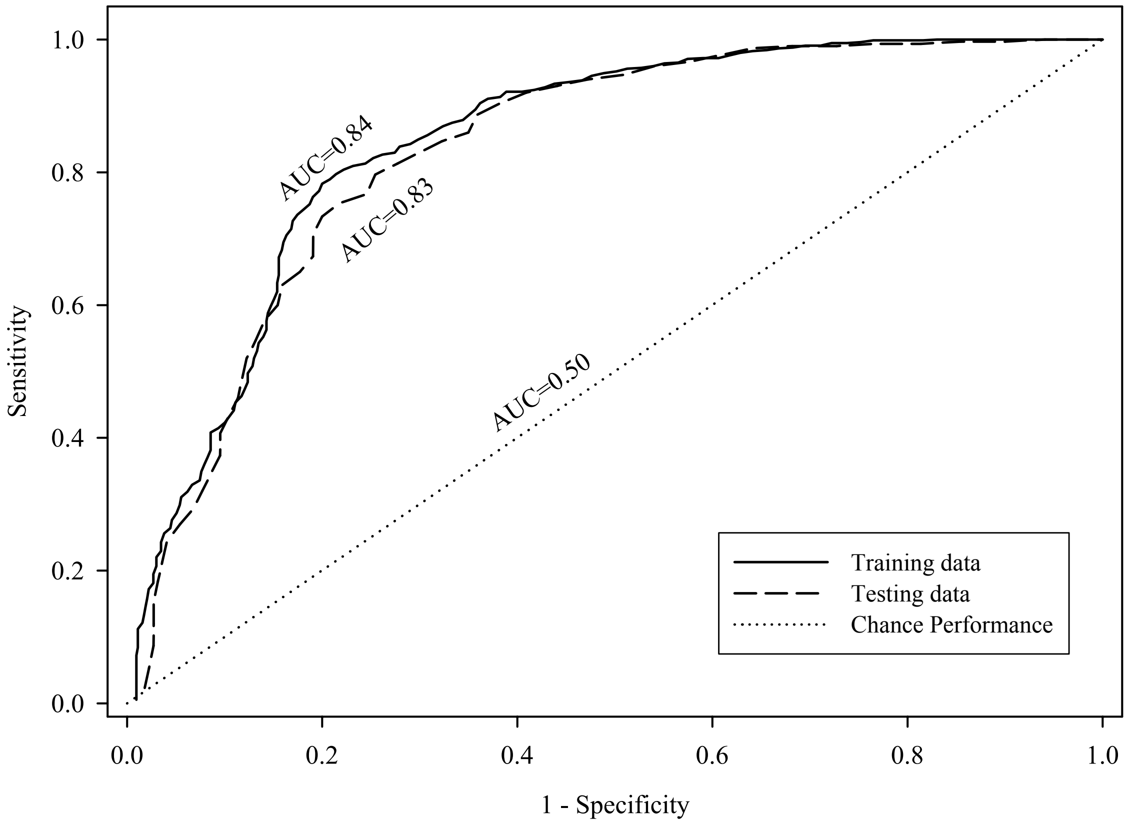

Figure 1.3. ROC plots of MBSDOGW nest-selection model performance in 2-fold cross-validation. Training and testing data are from nesting burrowing owls in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004. AUC represents the Area Under the Curve, where an AUC > 0.5 indicates an improvement over chance performance.

CHAPTER TWO

Burrowing Owl Nest Survival within Black-tailed Prairie Dog Colonies

ABSTRACT

Prior estimates of burrowing owl (*Athene cunicularia*) nest success have been simple calculations of the fraction of observed nesting attempts that were successful (referred to as apparent nest success). Previous nest success estimates may have been positively biased because failures in early nest stages are often underrepresented. This bias can be exacerbated by the inaccessibility of the burrowing owl's subterranean nest chamber. I measured six reproductive parameters for a migratory population of burrowing owls nesting within black-tailed prairie dog (*Cynomys ludovicanus*) colonies in northeastern Wyoming. I measured clutch size, brood size, fledge success, annual fecundity, daily nest survival, and annual nest survival for burrowing owl nests during the 2003 (n = 65) and 2004 (n = 71) breeding seasons. I determined nest- and hatch initiation dates for both years. Fledge success and annual fecundity were significantly lower in 2004 compared to 2003, and nest initiation dates were significantly later in 2004 compared to 2003. I modeled daily nest survival for burrowing owls using the logistic-exposure approach, and compared the overall probability of nest success from the model to the empirical estimates of apparent-, and Mayfield nest success. Apparent nest success was positively biased by 5% compared to the logistic-exposure estimate (57.5% logistic-exposure, 62.5% apparent, 60.1% Mayfield). Unlike the apparent- and Mayfield methods, the model-based, logistic-exposure approach allowed for daily nest survival rates to vary with time, temperature, and habitat features, and I found a clear upward trend in the probability of nest survival over time within the breeding season. Daily survival of burrowing owl nests varied between years, increased as the season progressed, decreased as nest stage progressed, and was influenced by temperature.

INTRODUCTION

Many populations of Neotropical migrant birds are declining (Sauer and Droege 1992, Donovan et al. 2002). During their peregrinations, Neotropical migrants may encounter qualitatively different breeding, non-breeding, and stopover habitats. Quality of these habitats can influence individual performance in terms of nest survival, reproductive success, and overwinter survival (Martin 1992). Large-scale monitoring efforts seek to identify declining Neotropical species, and conservation priority is going to their critical habitats (Donovan et al. 2002). Most studies have tried to correlate species presence or breeding density with habitat quality (Martin 1992, Donovan et al. 2002). However, density-quality relationships are often confounded by the existence of source and sink habitats, where species presence may not translate into species persistence (Pulliam 1988), and because site tenacity can reflect past rather than current habitat quality (Van Horne 1983). Instead, studies relating trends in reproductive parameters to habitat quality are more effective for managing Neotropical migrants (Martin 1992, Christoferson and Morrison 2001, Donovan et al. 2002).

For the purpose of this study, I measured 6 reproductive parameters for a Neotropical migrant, the burrowing owl (*Athene cunicularia*). These reproductive parameters were clutch size, brood size, fledglings per nest (= fledge success), annual fecundity, annual nest survival, and daily nest survival. I defined annual fecundity as the number of fledglings produced per nest per year. I defined annual nest survival as the probability a nesting attempt will survive from initiation to fledge, within a given year (Dinsmore et al. 2002). And, I defined daily nest survival as the probability a nesting attempt will survive a single day within the nesting period (Dinsmore et al. 2002).

The burrowing owl is a migratory bird for which local populations have declined along the periphery of their breeding range since the 1970s (James and Ethier 1989, James and Espie 1997, Wellicome and Holroyd 2001, Klute et al. 2003). Data from the North American Breeding Bird Survey suggest a negative trend in burrowing owl detections from 1966 - 2003 (trend = -1.2 breeding birds detected per year, 95% CI = -6.1 - 3.7, $p = 0.63$) (Sauer et al. 2004). Population losses have been attributed to degradation and loss of native prairie, and therefore loss of burrowing owl habitat (Knopf 1994, Vickery et al. 1999, Klute et al. 2003). An open-prairie specialist, the Burrowing Owl typically breeds in desert, grassland, and shrub-steppe landscapes. Burrowing Owls prefer areas where digging activity by fossorial sciurids, canids, and mustelids promotes high burrow availability for nesting. Nest burrows are typically surrounded by low, sparse vegetation to facilitate cursorial activity (Butts and Lewis 1982, Green and Anthony 1989, Haug et al. 1993, Plumpton and Lutz 1993, Desmond and Savidge 1999, Desmond et al. 2000, Ronan 2002).

Despite a general consensus that diminishing habitat drives population loss (Klute et al. 2003), little work has been done to quantify how habitat features affect trends in burrowing owl reproduction (*but see* Plumpton 1992, Ronan 2002). Studies of burrowing owl nesting ecology commonly report mean brood size (Plumpton 1992, Green and Anthony 1989, Wellicome et al. 1997, Botelho and Arrowood 1998, Millsap and Bear 2000, Desmond et al. 2000, Restani et al. 2001, Ronan 2002, Gorman et al. 2003, Holmes et al. 2003, Rosenberg and Haley 2004). However, Gorman et al. (2003) point out that many studies likely underestimate actual brood size because juvenile burrowing owls often retreat into burrows during researcher observation. To facilitate comparison among populations, Gorman et al. (2003) recommend reporting brood size as the maximum number of juveniles observed during multiple nest visits throughout the nesting season.

Reproductive parameters such as brood size and fecundity are essential for estimating population growth (Thompson et al. 2001, Gorman et al. 2003). But, annual nest survival may be a more sensitive measure of the effects of habitat and non-habitat (e.g. time within season) variables on the probability of a successful nesting attempt (Martin 1992, Jehle et al. 2004). Without exception, prior estimates of burrowing owl nest survival have been simple calculations of the fraction of observed nesting attempts that were successful (hereafter, apparent nest survival) (Green and Anthony 1989, Plumpton 1992, Botelho and Arrowood 1998, Millsap and Bear 2000, Holmes et al. 2003). However, apparent nest survival can be positively biased (Mayfield 1961). Unless all nests are found at the time of initiation, unsuccessful nesting attempts survive only briefly and are less likely to be detected compared to successful nesting attempts. Thus, failures in early nest stages are often underrepresented. A widely accepted alternative is the Mayfield estimator (Mayfield 1961, 1975, Hensler and Nichols 1981). Mayfield's estimator incorporates exposure days (number of days the nest is under observation and 'at risk') into a daily survival rate (DSR), such that

$$DSR = 1 - \frac{\text{number of failed nests}}{\text{number of exposure days}}.$$

Overall nest survival (e.g., from egg laying to fledging) is then DSR^d, where d is the average number of days in the nesting period. Mayfield's estimator assumes DSR is constant over the defined nesting period, and optimal use of the estimator assumes the date of nest events (e.g., hatch, fledge, failure, or stage transition) is known exactly. Hence, nest fate information should be collected daily; else observers must arbitrarily decide date of failure or fledge (Johnson 1979, Manolis et al. 2000). Most research avoids daily nest visits for logistical reasons and to minimize disturbance to adult nest attendance, and nests are usually visited at irregular intervals that may vary in length (Bart and Robson 1982, Dinsmore et al. 2002, Shaffer 2004).

As a cavity-nesting bird, there are some unique limitations to monitoring burrowing owls relative to open-nesting birds. For example, observers tend to spend more time observing burrowing owl nests for reliable juvenile counts than would be necessary at an open nest. Extended observations at each nest then preclude daily nest visits when sample sizes are large. Also, nest contents cannot be directly accessed without excavation, and underground refugia may preclude accurate ageing of juveniles. While rigorous methods should be used to determine nest stage and fate, exact dates are rarely known. Given these limitations, a method that allows for varying nest visit intervals and unknown nest event dates may be more appropriate for burrowing owls.

Variation in the overall probability of nest survival can be measured in terms of habitat features and annual variation in climate, densities of potential predators, or abundance of food. Daily nest survival, however, may be influenced by time and weather; elements that change daily instead of annually. Nest stage can affect daily nest survival, with mortality risks decreasing as juveniles approach independence (Dinsmore et al. 2002, Jehle et al. 2004, Peak et al. 2004). Daily nest survival may also vary seasonally, such that the risk of mortality is higher early in the season, or vice versa (Hazler 2004).

I measured reproductive parameters for a migratory population of burrowing owls breeding in black-tailed prairie dog (*Cynomys ludovicanus*) colonies in Thunder Basin National Grasslands, northeastern Wyoming, USA. The first objective was to verify breeding, estimate nest initiation dates, clutch sizes, hatch dates, brood sizes, fledge dates, and number of fledglings at burrowing owl nests. The second objective was to identify an appropriate, model-based estimator of nest survival given the unique limitations to monitoring burrowing owl nests. To assess performance of this method, I compared overall nest survival estimates from the model-based approach to apparent and Mayfield estimates. The third objective was to assess habitat quality for breeding burrowing owls in Wyoming. To assess habitat quality, I measured the effects of habitat features, year, time within season, and temperature on daily nest survival (DSR).

STUDY AREA

I conducted my study in the Thunder Basin National Grassland (TBNG), near Wright (43º 44’N, 105º28’W), Newcastle (43º 51’N, 104º 12’W), and Douglas (42º 45’N, 105º22’W), Wyoming. TBNG encompasses 2300 km^2 of the southern Powder River Basin, between the Bighorn Mountains and the Black Hills, in Cambell, Weston, and Converse counties. Topography within TBNG includes valleys, rough breaks and badlands, steep coniferous mesas, and low riparian bottomlands, with elevation ranging 1090 – 1580 m. Annual precipitation varies from 15 – 40 cm. Located within the Great Plains-Palouse Dry Steppe Province (Bailey 1995), vegetation is dominated by grasses (*Agropyron smithii, Buchloe dactyloides, Bouteloua gracilis*), sedges (*Carex* spp.), and shrubs (*Artemesia tridentata, Artemesia cana, Sarcobatus vermiculatus*). While TBNG is under the jurisdiction of the US Department of Agriculture Forest Service, lands are managed privately (ranchers, coal companies), and publicly (Forest Service, US Department of Interior Bureau of Land Management, and State Trust of Wyoming). Primary land uses include cattle and sheep grazing, coal mining, as well as oil, natural gas, and coal-bed methane extraction.

In the Great Plains, burrowing owls are strongly associated with colonial mammals, particularly the black-tailed prairie dog (Butts and Lewis 1982, Desmond et al. 2000). Studies in

Oklahoma (Butts and Lewis 1982), Nebraska (Desmond and Savidge 1996), and Colorado (VerCauteren et al. 2001) found higher burrowing owl nest densities within black-tailed prairie dog colonies relative to the surrounding landscape. Burrowing owls likely select black-tailed prairie dog colonies in response to proximate cues indirectly supplied by prairie dog activity: burrow availability, burrow density, and short or sparse vegetation (MacCracken et al. 1985, Plumpton and Lutz 1993, Toombs 1997, Desmond and Savidge 1999, Restani et al. 2001). TBNG contains the largest land coverage by black-tailed prairie dogs (7,381 ha) of any US Forest Service Great Plains National Grassland (Luce 2003). Given the well-documented association between burrowing owls and black-tailed prairie dog colonies in the Great Plains, I restricted my sampling efforts solely to black-tailed prairie dog colonies within the study area. All nest burrows were excavated by prairie dogs. Coyotes (*Canis latrans*), badgers (*Taxidea taxus*), Ferruginous Hawks (*Buteo regalis*), Golden Eagles (*Aquila chryseatos*), bullsnakes (*Pituophis catenifer sayi*), and prairie rattlesnakes (*Crotalus viridis viridis*) were common in owl-occupied prairie dog colonies.

METHODS

Nest searches

I located burrowing owl nests in three ways: standardized surveys, visits to historical nest burrows, and continual visitation to owl-occupied black-tailed prairie dog colonies. First, I located owl nests using call-broadcast surveys on dirt roads within black-tailed prairie dog colonies (Conway and Simon 2003). I surveyed 73 prairie dog colonies in 2003 and 2004, 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, I revisited areas where burrowing owls had been detected and conducted thorough ground searches near the pre-flushing location of all adult owls. Nesting sign included the presence of shredded cow/horse manure, and/or prey remains, owl feces, and regurgitated castings at burrow entrances (Haug et al. 1993, Smith 2004). I examined the contents of all potential nest burrows using an underground, infrared, burrow videoscope within 1 - 4 days after discovery. A burrow qualified as a nest if I detected the male and female at least once during the nesting period, and by the eventual confirmation of eggs or juveniles. Without visual confirmation of eggs or juveniles, burrows were not included in the sample of nests even if sign and adult territorial behavior indicated nesting activity.

Additionally, I visited all known burrowing owl nest territories from previous years. Male and female burrowing owls are partially philopatric and frequently return to former nest territories (Lutz and Plumpton 1999). If resident owls did not occupy a nest burrow, former nest burrows or territories were frequently re-settled by new owls. Location information was available for former burrowing owl nest burrows in TBNG due to an ongoing demography study (C.J. Conway, unpublished data). I monitored occupancy at former nest burrows every 3 - 4 days at the beginning of each breeding season, attenuating the frequency of nest visits at unoccupied burrows as the season progressed. Confirmation of nesting activity at these historical burrows followed the protocol described above.

Burrowing owls are semi-colonial, and nests are particularly clustered within black-tailed prairie dog colonies (Haug et al. 1993, Desmond et al. 1996). Because I visited active nest burrows frequently, I was able to conduct repeated visual scan surveys for additional nesting pairs in owl-occupied prairie dog colonies. Additional nesting pairs were easily detected because they tended to occupy burrows near (< 400 m) known nests. Clusters of burrowing owl nests were common in the prairie dog colonies in TBNG, and incidental nest detections contributed substantially to my final sample size. Repeated visitation to nest clusters also facilitated detection of nests at their time of initiation or in early nesting stages. However, I did not include nest burrows detected in the cluster that failed prior to time of discovery, or those nests detected after the last known hatch date in TBNG.

Nest monitoring

I visited nest burrows every 3 - 7 days throughout the breeding season (barring unforeseen delays such as muddy roads or temporary ranch closures). I observed nests at 125 – 300 m distances depending on owl tolerance, with spotting scopes and binoculars. I approached the nest burrow every other visit (approximately once a week) to confirm nest stage and record burrow condition. On the approach, flush distances and burrow retreat behaviors by the adult owls were used as clues to the presence of eggs or juveniles in the nest burrow. On each visit, I recorded the number of juveniles, and approximated juvenile age (day) using feather emergence, satellite burrow use, as well as hopping, wing flapping, and flight behaviors (C. J. Conway and V. Garcia, University of Arizona, unpublished document). I recorded flush/retreat behaviors and flight performance (short, wobbly, or long) for the oldest and youngest owlets to refine age estimates. Signs of depredation at the nest included burrow excavation, and/or the presence of dirty eggs or owl carcasses outside the nest entrance (including feather piles, dismembered wings or feet, decapitated bodies, or plucked breast bones). On visits when I approached the nest burrow, I also examined nest chamber contents using an infrared burrow videoscope. I recorded the presence and sex of adult owls (based on size and plumage), clutch size, maximum number of hatched owlets seen, and aged each owlet based on morphological development, percent of down feathers, and percent of flight feather emergence (C. J. Conway and V. Garcia, University of Arizona, unpublished document).

Nest timelines

Using a combination of these above- and belowground observations, I assigned an observed nesting stage (laying, incubation, and nestling) to each nest visit. Burrowing owl eggs could not be directly accessed to determine nest age and therefore, nest stage. Exact dates of initiation and stage transition were not absolutely necessary, but approximate dates were essential to assign each nest visit to an appropriate nest stage. To keep subjectivity to a minimum, I used a standardized protocol to determine nest stage (C.J. Conway and V. Garcia, unpublished document). If burrow tortuosity precluded accurate brood counts, I assumed a population mean of 8 eggs for nest stage determination. Nests initiated with the first egg laid, and I used partial clutch counts to determine the length of egg-laying and incubation stages. For example, a suspected nest was discovered on day 1 during pair formation. On day 4, 2 eggs and the adult female were present in the nest chamber. I assumed egg 2 was laid the morning of day 4, and then backdated to a nest initiation date using a laying pattern of egg 1, egg 2, skip a day, egg 3, egg 4, skip a day, etc. This asynchronous laying pattern approximates known burrowing owl egg laying rates of 1 egg per 1.5 days (Wellicome 2005). Thus, I assumed the example nest above initiated on day 3.

In general, burrowing owl clutch sizes range from 6 to 12 eggs, females lay eggs for 8 - 17 days, and incubation begins at the midpoint of clutch completion (Wellicome 2005). Hence, I estimated the egg-laying stage from first egg to the midpoint of laying (i.e., day 5 for a clutch of 8 eggs). For example, nest visit data may indicate that 2 eggs were observed in the nest chamber on day 4, 6 eggs on day 11, and 8 eggs on day 18. Using the described laying pattern, I assumed the first egg was laid on day 3, the last egg was laid on day 13, and incubation began at the midpoint of laying on day 8. The incubation stage (median = 26 days) was from the laying midpoint to first hatch. Nestling stage began with first hatch and ended with the first juvenile to reach 44 days, which I assumed an appropriate fledge age for my study population. I included nests discovered post hatch, but only if they were discovered prior to the last known hatch date for TBNG, and only if juveniles could be accurately aged in the nest chamber.

I recorded nest stage and fate for each observation interval. For suspected nests located prior to the first egg, the first observation interval began on the day the first egg was laid. For nests found in later stages, the first observation interval began on the day of discovery. If a nest had at least 1 surviving egg or juvenile, the nest survived the observation interval. For successful nests, the end of the last observation interval was the estimated date in which at least one juvenile had reached 44 days. The last day of the observation interval for failed nests was the first nest visit in which failure was confirmed. While fledge dates could be reliably estimated using juvenile age data from previous nest visits, I could not reliably estimate a failure date without making an arbitrary decision about nest fate. Many researchers assign failure to the midpoint of the last observation interval (Manolis et al. 2000), and such decisions may be appropriate when all nests are visited at even interval lengths (Shaffer 2004a). But when nest survival is only assumed to be constant within a given observation interval, and nest visit intervals vary across nests, I would argue that my assumption that failure did not occur until the last day of the last observation interval was just as appropriate as a midpoint assumption.

Clutch, brood, and fledge counts

I reported mean clutch size for all nests where observers were 100% confident in their egg count. Consequently, I calculated egg success (number of young fledged per number of eggs per nest) for only those nests with accurate egg counts. I reported brood size as the mean number of young observed for all nests surviving incubation. I reported fledge counts for successful nests only. For annual fecundity, as described above, I used the total number of nests in the calculation.

Habitat, season, and weather covariates

I considered 4 site features as potentially influencing burrowing owl nest survival, including tunnel length of the nest burrow, burrow availability within 30m, percent shrub cover within 30m, and prairie dog activity within 100m. I measured the length of the main tunnel (m) from burrow entrance to the nest chamber using an infrared burrow videoscope. The shape and length of burrow tunnels were highly variable; some bent at angles too sharp for a flexible camera scope to navigate, and some were longer than the length of the scope (4.5m). While tunnel length was a continuous variable, I assigned burrows with tortuous (unavailable) tunnels the mean length of all used and unused burrows (length = 3.43 m; $n = 0$ for failed nests, $n = 9$ for successful nests). I assigned burrows > 4.5 m as length = 5 m ($n = 0$ for failed nests, $n = 5$ for successful nests). To be sure these designations did not lead to spurious conclusions, I also ran analyses excluding burrows for which length was uncertain. Direction and strength of model coefficients, and model ranking, did not change substantially when I excluded burrows with uncertain lengths. Hence, I reported results from the analysis with all burrows included.

To measure burrow availability, I counted the number of usable burrows within 30 m. Because I was only interested in relative shrub cover, I was satisfied with visual percent estimates from trained observers. As a measure of prairie dog activity, I developed an activity index within 100 m of the nest burrow, roughly based on methods developed by Biggins et al. (1993). I bisected the nest burrow with two, 200-m belt transects of 4 m width, and counted number of active burrows and total burrows in each belt transect. I averaged indices for both transects for an overall percentage of prairie dog activity within 100 m of the nest burrow.

I measured temporal effects on burrowing owl nest survival in terms of year, nest stage (*see Nest timelines*) and season. Year and nest stage were categorical variables. To measure seasonal variation, I used the midpoint between the first and last observation day at each nest as a proxy for early-, mid-, and late- season nests (Hazler 2004). Testing for possible effects of ambient temperature on burrowing owl daily nest survival, I determined the average weekly temperature (maximum °C) for each observation interval, for each nest. I used temperature data collected at the Dull Center 1 SE weather station, Wyoming, centrally located within the study area (Western Region Climate Center, http://www.wrcc.dri.edu/inventory/sodwy.html).

To test for multicollinearity among habitat variables, I regressed each explanatory variable against all the others and examined the variance inflation factor and its reciprocal, tolerance (Chatterjee and Price 1991, PROC REG in SAS Institute 2000). A VIF that strongly deviated from 1.0 ($0.1 < \mathrm{VIF} < 10$), and a tolerance value approaching zero indicated a departure from independence and a tendency toward collinearity (Chatterjee and Price 1991).

Nest survival

I modeled the effects of habitat features, year, time within season, and temperature on daily survival of burrowing owl nests using the logistic-exposure approach (Shaffer 2004). The logistic-exposure method is a generalized-linear-model with a binomial response distribution (where interval nest fate = 1 if successful and 0 if failed), a logistic equation, and a modification of the logit link function ($\log_e[p/(1-p)]$, where p is the probability of a success) (McCullagh and Nelder 1989). The probability that a nest survives an observation interval is $\theta = [\,s(x)\,]^t$, where s is a daily survival rate that depends on an independent variable x, and t is the number of days in the observation interval. Daily survival s is estimated with a logistic function, such that

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}.$$

The link function is modified (Shaffer 2004) to account for varied observation interval lengths, such that

$$g(\theta) = \log_e\left(\frac{\theta^{1/t}}{1-\theta^{1/t}}\right).$$

This modification converts survival probabilities for observation intervals into daily probabilities. Underlying assumptions are that nest fates are independent, daily survival probabilities are constant within an observation interval, and survival probabilities are homogeneous among nest-days with the same values of the explanatory variables (Shaffer 2004, Rotella et al. 2004).

I developed 28 logistic-exposure models based on 10 explanatory variables related to the effects of habitat features, time, and temperature on burrowing owl nest survival (Table 2.1). I evaluated sets of models representing temporal, weather, and habitat effects, and models of combined effects. I included squared terms for observation midpoint and temperature into some models to test for optimal ranges of survival. The Hosmer and Lemeshow goodness-of-fit test suggested adequate fit of the global model: $\chi^2 = 9.2$, df = 8, $p = 0.326$ (Hosmer and Lemeshow 2000). To look for outliers or necessary variable transformations, I visually inspected standardized residual plots for all explanatory variables and found no large residual values ($-3 <$ acceptance < 3). To measure support for alternative models, I used an information-theoretic approach (Burnham and Anderson 2002). I used Akaike's Information Criterion (AIC) to rank candidate models (Burnham and Anderson 2002). To avoid problems associated with a small sample-to-parameter ratio, I applied a small-sample bias adjustment to the AIC value associated with each candidate model (AIC_c; Burnham and Anderson 2002). I ranked models by ascending

AIC_c values. Based on this ranking, I reported ΔAIC_c, Akaike weights, w_i, and deviance for each model as relative measures of support (Burnham and Anderson 2002).

To elucidate differences between failed and successful nests, I reported coefficients from the most-supported model as odds ratios with 95% confidence intervals (CI). I compared means of influential variables between failed and successful nests. To assess model-selection uncertainty, I calculated model-averaged coefficients from all 28 candidate models, and averaged the 95% CI based on unconditional standard errors (Burnham and Anderson 2002). I calculated model averages as the sum of model coefficients multiplied by their Akaike weights, w_i, and used $\beta = 0$ for a coefficient when a model did not contain an explanatory variable. I reported model-averaged coefficients as odds ratios with 95% CI. I also judged competing models by the prevalence of the selected variables in the other top-ranking models. If variables consistently appeared within the top set of candidate models ($\Delta AIC_c < 7.0$ and $w_i > 0.001$), I assigned greater confidence to the top model.

I performed the logistic-exposure analysis using PROC GENMOD in SAS (SAS Institute 2000). Model ranking and model averaging procedures were also performed in SAS, using macros developed by T. Shaffer (Shaffer 2004b, Rotella et al. 2004).

I estimated the overall probability of burrowing owl nest survival using the model-based estimates from the null model and the most-supported model. I then compared the survival probabilities from the logistic-exposure method to those derived from apparent nest success and the Mayfield estimator. Active nest burrows that were known from previous years were typically detected at their time of initiation or in early nest stages. Because historical information may not always be available in burrowing owl studies, I wanted to accurately compare methods of estimating nest survival for burrowing owls, and assess their potential biases. Hence, I restricted comparisons to a subset of nests, including only newly discovered nests from each year and excluding known nests from previous years.

Sample sizes

Sample sizes varied within my results. I reported the number of nesting attempts, brood counts, and fecundity for all nests confirmed in the study area. Burrowing owl nest chambers were difficult to access even with a burrow videoscope, therefore I determined initiation date, clutch size, and egg success from reduced samples where estimates could be generated with confidence. For the same reason, I restricted survival estimates to nests with reliable stage information. Because I modeled nest survival using an information-theoretic approach, I excluded nests with missing data for any of the covariates to ensure equal sample sizes among competing models. When I compared methods, I further restricted the sample sizes to facilitate comparison between empirical and model-based estimates of nest survival. All reported nest survival estimates are from this restricted subset used in method comparison.

RESULTS

Initiation dates and reproductive parameters

I located 136 burrowing owl nest burrows in black-tailed prairie dog colonies of TBNG during the 2003 (n = 65) and 2004 (n = 71) breeding seasons. Nest initiation dates were between 14 April and 30 May in 2003 and between 26 April and 2 June in 2004 (Table 2.2). Nest initiation dates were significantly later in 2004 (t = 2.09, df = 74, p = 0.040). Average clutch size was 6.9 eggs per nest in 2003, and 7.4 eggs per nest in 2004. Clutch sizes did not differ significantly between years (t = -1.10, df = 74, p = 0.322). Hatch initiation occurred between 18 May and 28 June in 2003, and between 29 May and 29 June in 2004. Hatch initiation dates did not differ significantly between years (t = - 1.83, df = 56, p = 0.073). The maximum number of young observed at successful and failed nests in 2003 ranged from 0 to 8 juveniles, and from 0 to 11 juveniles in 2004. Brood sizes (per total nest) did not differ significantly between years (t = -0.31, df = 133, p = 0.754). Egg success was similar in both years (t = -0.18, df = 32, p = 0.862), at an average 56% of eggs hatching per brood. Mean fledge success (44 days) was 3.9 fledglings per nest in 2003 and 2.7 juveniles in 2004. Fledge success was significantly lower in 2004 (t = 3.58, df = 94, p = 0.001). Annual fecundity was 3.02 juveniles fledged per nest in 2003, and 1.92 juveniles fledged per nest in 2004. The average nesting period for successful nests was 75 days (SE = 0.29, range 70 to 79 days).

Habitat, season, and weather covariates

Site features were very similar between failed and successful burrowing owl nests in TBNG (Table 2.3). The continuous temporal covariate, observation midpoint, was earlier (31 May) for nests in 2003 compared to nests in 2004 (15 June), with non-overlapping 95% CI. I did not detect multicollinearity among any of the continuous or categorical variables (tolerance > 0.65; 1.1 < VIF < 1.5).

Nest survival

Of the 65 burrowing owl nests in 2003, 52 were successful in rearing at least one juvenile to fledge age. Of the 71 nests in 2004, 54 were successful. Sources of nest failure were largely unknown (52%). Sixteen percent of nest failures were suspected mammalian depredations, 4% were suspected avian depredations, and 7% of nest failures were suspected depredations of unknown cause. I suspected nest abandonment in 21% of nest failures.

Of the 65 nests located in 2003, 13 were newly discovered (not known from a previous year of study). Nineteen of the 71 nests located in 2004 were not previously known. Hence, I compared nest success estimates from a restricted subset of nesting attempts (n = 32). With survival held constant over the 75-day nesting period, the null logistic-exposure model estimated DSR = 0.9930, and an overall probability of nest survival of $\theta = 57.5\%$. The logistic-exposure nest survival estimate was 5% lower than the apparent estimate (62.5%), and 2.6% lower than the Mayfield estimate (DSR = 0.9932, $\theta = 60.1\%$). Nest survival was lower in 2003 compared to 2004. The null logistic-exposure model for 2003 estimated DSR = 0.9890 and $\theta = 43.3\%$ (apparent success: 46.2%, Mayfield estimate: DSR = 0.9887, $\theta = 42.6\%$). The null model for 2004 estimated DSR = 0.9950 and $\theta = 67.1\%$ (apparent success: 73.6%, Mayfield estimate: DSR = 0.9956, $\theta = 72.2\%$).

According to the most-supported model, daily nest survival varied seasonally and yearly, and differed among nest stages and with temperature (Table 2.4). Weight of evidence for the most-supported model, hereafter the MSYT model, was $w_i = 0.184$. Among the top 7 competing models with $w_i \geq 0.06$, 6 were permutations of the MSYT model, indicating that date of nest initiation and weather had the most prevalent effects on burrowing owl nest survival. Of the 28 candidate models, I reported results for only the top 13 competing models where $\Delta AIC_c < 7.0$ and $w_i > 0.001$ (Table 2.4).

The odds of DSR were higher during egg laying relative to the nestling stage (Table 2.5). However, large variability was present in the odds ratio estimate for the egg laying stage (95% CI: (0.32, 34.96). The large variability was likely due to the relatively minor contribution of egg laying observations to the overall sample (9%, as opposed to 36% from incubation and 55% from nestling). Odds of DSR were also higher during the incubation stage relative to the nestling stage, but the 95% CI included 1.0. While recognizing the prevalence of nest stage in 8 of 13 competing models, I did not further examine the effects of nest stage on DSR because the 95% CI for their odds ratio overlapped with 1.0. Similarly, the MSYT model indicated the odds of

DSR decreased with increasing temperature, but the 95% CI included 1.0. Temperature (and its quadratic) appeared in 6 of the 13 competing models, but because the 95% CI of the odds ratio overlapped with 1.0 I did not further examine the effect of temperature on on DSR.

The MSYT model indicated seasonal and annual variation had the greatest influence on burrowing owl daily nest survival. Odds of DSR increased 12% for every 1-day increase in observation midpoint (Table 2.5). Hence, the odds ratio for observation midpoint can be interpreted such that the odds of daily survival were higher for late season nests (Figure 2.1). Concordantly, the daily mortality risk, calculated as 1-DSR, decreased with increasing observation midpoint (Figure 2.2). Daily survival was lower in 2003 than in 2004 (Figure 2.3). Odds of DSR for burrowing owl nests were 64% lower in 2003 relative to 2004 (Table 2.5).

Habitat effects were present in 4 of the top 13 models for which $w_i > 0.01$. Burrow availability was the only habitat variable present in all 4 of the top habitat models. However, habitat variables did not appear in the top model, and 1 of 4 of the habitat models had $w_i > 0.05$. Because habitat variables were not prevalent among competing models, I found little support for models containing habitat effects.

An advantage of the logistic-exposure modeling approach is that the probability of nest success can be evaluated over a continuous range of values for influential explanatory variables. Apparent and Mayfield estimators assumed constant daily survival, resulting in a single nest survival probability (62.5% and 60.1% for burrowing owls in TBNG, respectively). Based on the MSYT model, I evaluated the probability of nesting attempt success over a range of observation midpoints, and found an increasing trend in the probability of nesting attempt success over time within season (Figure 2.4). Survival probabilities, estimated with DSRs from the MSYT model, ranged from 0.175 to 0.978 with increasing observation midpoint.

Despite patterns observed in the MSYT model, there was uncertainty in model selection. Odds ratios of the model-averaged coefficients all had 95% CI overlapping 1.0 (Table 2.6).

DISCUSSION

Clutch, brood, and fledge counts in TBNG were comparable to reported parameters for other burrowing owl populations. Clutch sizes remained stable between years (6.9 in 2003; 7.4 in 2004), and were within reported ranges (6 - 12 eggs per nest) (Haug et al. 1993, Wellicome 2005). The maximum number of young observed (brood count) was higher at nests in the black-tailed prairie dog colonies of TBNG (4.5 juveniles per total nests) than reported in the white-tailed prairie dog (*C. leucurus*) colonies of southern Wyoming (2.7; Martin 1983). Black-tailed colonies typically contain higher densities of prairie dogs than white-tailed colonies (Cully and Williams 2001), and burrowing owls may prefer the higher burrow density and lower vegetation height of the black-tailed colonies. However, differential preference for black-tailed or white-tailed prairie dog colonies has not been assessed. Brood counts were also higher at nests in TBNG than those reported for populations in an agroecosystem in California (2.5; Rosenberg and Haley 2004) and a university campus in New Mexico (2.2; Botelho and Arrowood 1998).

Restricting comparisons to studies that report the number of juveniles that reached 40 days, TBNG fledge success (2.4 juveniles per total nests) was similar to other reports. In the panhandle of Nebraska, burrowing owl fledge success in black-tailed prairie dog colonies was 1.9 juveniles per nest (Desmond et al. 2000). In southeastern Montana, burrowing owl nests in black-tailed prairie dog colonies fledged an average of 2.6 juveniles (Restani et al. 2001). Fledge success in an urban landscape in Florida was also similar to the Great Plains (2.9 juveniles per nest; Millsap and Bear 2000).

Daily survival of burrowing owl nests varied between years, increased as the season progressed, and was influenced by nest stage and temperature. Year had the greatest effect on daily nest survival in TBNG. Indeed, nest initiation dates were significantly later in 2004. The overall probability of nest survival was higher for the population in 2004 ($\theta = 67.1\%$) than in 2003 ($\theta = 43.3\%$). This effectively large annual variation in the overall probability of nest survival is a good example of the importance of multi-year studies of reproductive trend. Had I measured nest survival probabilities in 2003 but not 2004, I would have presented a relatively low probability of burrowing owl nest survival.

Daily survival was higher for burrowing owl nesting attempts that initiated later in the breeding season, and DSR was higher during the laying- and incubation stages relative to the nestling stage. For comparison, mountain plover (*Charadrius montanus*) nests in Montana had higher DSR for late-season nests but DSR increased as nest stage progressed (Dinsmore et al. 2002). In Colorado, daily survival of lark bunting (*Calamospiza melanocorys*) nests declined with both time within season and nest age (Jehle et al. 2004). My results differ from most studies where avian nest survival increased with increasing nest stage (Martin 1992, Dinsmore et al. 2002, Stephens 2003, Peak et al. 2004, Traylor et al. 2004). Studies for which nest survival decreased with increasing nest stage typically cite increased predation rates on nests where juveniles are available compared to nests with only eggs (Burhans et al. 2002, Jehle et al. 2004), but starvation may also have been an important cause of nest failure for burrowing owl nests in TBNG.

Owl nest survival often depends on predator densities as well as prey availability (Korpimaki and Norrdahl 1991, Desmond et al. 2000, Ronan 2002). The observed annual and seasonal variation of burrowing owl DSR in TBNG may have been a function of annual and seasonal changes in predator densities and prey availability. However, functional responses of raptors to prey densities usually manifest in reproductive trends (Korpimaki and Norrdahl 1991, Wellicome et al. 1997). As such, one would have expected higher clutch-, brood-, and fledge counts in the year with higher daily nest survival. Paradoxically, fecundity was significantly lower in the year of higher daily nest survival. This somewhat surprising result corroborates arguments by Thompson et al. (2001), that nest survival estimates should not replace fecundity as a measure of demographic performance. The relationships between burrowing owl nest survival, reproductive success, and predator/prey densities deserve further investigation.

Models including habitat effects were not well supported. This is consistent with other studies of burrowing owl nesting ecology, where site characteristics had little effect on reproductive parameters (Plumpton 1992, Ronan 2002). Because nest-site selection in other birds is usually related to concealment from predators (Martin 1992), I selected habitat variables that related to cover as well as visibility of predators. However, site features did not differ between successful and failed nests, although I suspected nest depredation in 27% of nest failures. The relationship between burrowing owl nest survival and habitat quality may have been operating at a larger spatial scale than what I measured. For example, I may not have incorporated important habitat effects operating at the landscape scale. Important site characteristics may be homogeneous within a prairie dog colony. Important habitat features may have been more evident if I had compared daily survival rates between burrowing owl nests on and off prairie dog colonies.

Modeling burrowing owl nest survival involved a series of assumptions. To make reliable inferences from my modeling effort, I evaluated these assumptions and recognized confounded effects (Dinsmore et al. 2002). For example, frequent visitation can disturb nests and affect daily survival. Failure to recognize observer effects can lead to biased estimates of daily nest survival (Rotella et al. 2000). While suspected abandonment of burrowing owl nests may have been the result of observer disturbance of breeding adults, I chose not to include observer effects to maintain model simplicity (Rotella et al. 2000). In addition, because I used an information-theoretic approach, the MYST model was only better than the suite of candidate models from which it was ranked (Stephens et al. 2005). The effects modeled in the candidate set were based on biologically informed hypotheses, but researcher-selected models inevitably suffered from subjectivity (Burnham and Anderson 2002). If the MSYT model were clearly the best model, predicted coefficients for those variables would not differ markedly among models (Burnham and Anderson 2002). Averaging the coefficients of all 28 models reduced the apparent influence of season, year, nest stage and temperature on daily nest survival. Thus the influence of those variables may have been situational, lacking generality. I argue, however, that the prevalence of temporal and weather effects in all of the top 13 models (registering weight of evidence > 0.001) lends support to the conclusion that those variables influenced daily nest survival.

Estimates of apparent nest success in TBNG (62.5%) were comparable to previous studies that reported nest success as the number of nests that fledged at least one juvenile to 40 days. Studies in Colorado and Montana reported burrowing owl nest success within black-tailed prairie dog colonies at 85% and 92%, respectively (Plumpton 1992, Restani et al. 2001). In the shrub-steppe zone of north-central Oregon, 53 – 57% nests were successful (Green and Anthony 1989, Holmes et al. 2003), and in urban Florida, 69% of burrowing owl nests were successful (Millsap and Bear 2000).

Comparisons of apparent, Mayfield, and model-based probabilities of nest success typically show a decreasing bias in estimates, respectively (Hensler and Nichols 1981, Rotella et al. 2004, Shaffer 2004, Traylor et al. 2004). Constant-survival models from the logistic-exposure approach have typically produced estimates similar to, if not slightly less than, Mayfield estimates (Peak et al. 2004, Shaffer 2004). Of the 3 methods I compared, the logistic-exposure method gave the most conservative estimate of nest success. This conservative estimator may be more appropriate than apparent and Mayfield methods, particularly when: 1) observations are limited by the inaccessibility of nest contents, 2) nests are found at both early- and late nest stages, and 3) when observation intervals vary in length.

However, the 5% potential bias (apparent vs. logistic-exposure) I identified in my comparisons is still lower than the biases identified by other studies that compared methods of estimating nest success. Hensler and Nichols (1981) used Monte Carlo simulations to illustrate a 9 – 27% positive bias in apparent estimates compared to Mayfield estimates. Traylor et al. (2004) found simple Mayfield estimates of white-winged scoter (*Melanitta fusca deglandi*) nest survival were positively biased by as much as 10%, relative to a model-based, constant-survival option within program MARK (Dinsmore et al. 2002). Similarity among my estimates may relate to: how I sampled nests, and the way in which I defined a nest. Burrowing owls are semi-colonial (Desmond and Savidge 1996), and colony-nesting birds tend to initiate synchronously and are more easily detected than solitary nests (Johnson and Shaffer 1990). When searches are conducted repeatedly in areas of easily detected nests, the apparent estimator can be an accurate measure of nest survival (Johnson and Shaffer 1990). Burrowing owl nests in TBNG were clustered, and repeated nest visits resulted in frequent, incidental detections of additional nesting pairs within the cluster. Incidental nests were typically detected in early stages. While apparent estimates usually miss nests that failed early (Mayfield 1961), they may be accurate and acceptable when coloniality promotes detection of most nests early in the nesting cycle.

It is important to consider how researchers vary in their definition of a nest when comparing methods or comparing estimates across studies. The way in which nests are defined may influence bias in nest survival estimates just as much as the method of estimation. For example, I defined a burrowing owl nest as any burrow in which eggs or juveniles were confirmed in the nest chamber, and I excluded all nesting attempts discovered after the last known hatch date for the population within that season. Annual nest survival estimates may have been higher had I included nesting attempts discovered after juveniles were independent of the nest chamber, or those nesting attempts discovered after the last known hatch date. According to the MSYT model, DSR was highest for nests active later in the breeding season. By restricting my nest definition to include only those burrows at which eggs or juveniles were confirmed, I might have excluded nests that failed early in the season, prior to confirmation. Excluding these early nests may have produced a positive bias in apparent nest success similar to that of previous studies in which nests may not have been discovered until late in the breeding season. Or, such exclusion may have produced higher estimates than those of other studies that defined burrows as nests without visual confirmation of eggs or juveniles.

The clear advantage of the logistic-exposure approach was that I could model changes in survival probability over time within season (Figure 2.4). Both Mayfield and apparent estimates assumed constant daily survival. When I varied daily survival in the logistic-exposure model, there was a clear upward trend in the probability of nesting attempt success as the breeding season progressed. Moreover, the logistic-exposure model illustrated the decreasing risk in daily nest mortality within breeding seasons (Figure 2.2). The model-based approach was more biologically informative because I was able to conclude that burrowing owl nest survival was not constant throughout the breeding season.

MANAGEMENT IMPLICATIONS

This study illustrates an important distinction between annual fecundity and annual nest survival. Birds can have high daily nest survival but low fecundity within the same year. Clutch-, brood-, and fledge counts can be useful when monitoring annual demographic trend in burrowing owl populations (Thompson et al. 2001). Indeed, nest survival probabilities do not measure annual contribution to the juvenile stage class. In contrast, annual fecundity may not be as informative as a model-based approach to estimating nest survival in detecting the effects of site, time, and climate on the probability of nest success.

Apparent success, brood size, clutch size, and fledge success was comparable to other populations. This may be a reassuring indication of stable habitat quality in Wyoming. However, future changes in land use may begin to differentially affect habitat quality among populations. Thus, I recommend continued measurement of reproductive parameters for multiple Burrowing Owl populations to monitor annual trends.

DSR of burrowing owl nests in TBNG varied annually and seasonally. I was not able to determine the reasons for this variation within the scope of my study. I recommend future research examine why nest survival varies among years and within seasons. There may be a functional response in burrowing owl reproductive success and survival to fluctuating predator and prey densities. Future studies should estimate predator and prey densities and evaluate their association with burrowing owl reproductive trend. In addition, I recommend future research examine nest initiation dates for migratory females and their timing of migration, and how these two behaviors are affected by overwinter habitat quality.

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Table 2.1. Twenty-eight daily nest survival models for burrowing owls breeding in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004. Models were grouped by the potential effect of time, weather, habitat. Abbreviations for explanatory variables were: M = Midpoint of observation interval (day), MM = M, quadratic term, S = Nesting stage (egg-laying, incubation, nestling), Y = Year (2003, 2004), T = Average, weekly maximum temperature (°C) , TT = T, quadratic term, L = Nest tunnel length (m), B = Available burrows in 30m, H = Shrub cover in 30m (%), D = Prairie dog activity 100m (%).

Model Notation
Global
1) M MM S Y T TT L B H D
Temporal Effects
2) M MM S Y
3) M S Y
4) M S
5) M Y
6) S Y
7) M
9) S
10) Y
Weather Effects
11) T TT
12) T
Habitat Effects
13) L B H D
14) B D
15) B
16) H
17) D
Temporal and Weather Effects
18) M MM S Y T TT
19) M S Y T TT
20) M S Y T
21) M T
22) S T
Temporal and Habitat Effects
23) M S Y L B H D
24) M B D
Weather and Habitat Effects
25) L B H D T
Temporal, Weather, and Habitat Effects
26) Y B H D T
27) M B H D T
Null
28.

Table 2.2. Means, 95% Confidence Intervals (CI), and sample sizes of reproductive parameters measured at burrowing owl nests in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004.

Parameter	2003	2004
Number of nests[a]	65 (32)	71 (45)
Number of successful nests	52	54
Nest initiation date	12 May	17 May
95% CI	9 – 14 May	16 – 18 May
n	63	67
Clutch size	6.9	7.4
95% CI	6.1 – 7.7	6.9 – 7.9
n[b]	21	38
Hatch initiation date	5 June	10 June
95% CI	3 – 8 June	7 – 12 June
n	24	39
Brood size	4.4	4.5
Range	1 – 8	1 – 11
95% CI	4.0 – 4.9	4.2 – 4.9
n	59	71
Egg success[c]	0.55	0.57
95% CI	0.38 – 0.72	0.48 – 0.66
n	21	38
Young fledged per successful nest (44d)	3.9	2.7
95% CI	3.4 – 4.4	2.3 – 3.1
n	52	54

[a] Nest defined as ≥ 1 egg laid. Number in parentheses is sample size of nests used in logistic-exposure and Mayfield estimators.

[b] Sample size reduced to number of nests with reliable underground information.

[c] Proportion of eggs hatched, based on maximum number of young observed.

Table 2.3. Means and 95% Confidence Intervals (CI) for seasonal midpoint and habitat covariates included in models of burrowing owl nest survival in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003-2004.

Variable	Failed		Successful	
	$\bar{x}$	95% CI	$\bar{x}$	95% CI
Observation midpoint (day)	31 May	25 May – 5 Jun	15 Jun	13-18 Jun
Nest tunnel length (m)	3.3	2.7 – 3.8	3.9	3.1 – 4.8
Available burrows	29	24 – 34	30	27 – 33
Shrub cover (%)	4	2.1 – 5.9	7	4.3 – 9.6
Prairie dog activity (%)	45	34.0 – 55.2	45	39.0 – 50.9

Table 2.4. Model ranking results for burrowing owl nest survival in the Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004. Models were ranked by ascending ΔAIC_c, w_i is the model weight, and K is the number of parameters. Deviance is $-2[\log_e(L(\theta))-2\log_e(L_s(\theta))]$, where θ is a maximum likelihood estimate evaluated for the model in question $L(\theta)$ and for the saturated model $L_s(\theta)$.

Model	Deviance	K	AIC_c	ΔAIC_c	*w*i
M S Y T	173.08	6	185.10	0.00	0.184
M Y	180.01	3	186.02	0.92	0.116
M S Y B L H D	168.02	9	186.06	0.96	0.114
M T	180.11	3	186.11	1.02	0.111
M S Y	176.12	5	186.13	1.04	0.110
M1 S Y	174.24	6	186.26	1.16	0.103
M S Y T1	172.87	7	186.89	1.80	0.075
M1 S Y T1	171.36	8	187.39	2.29	0.059
GLOBAL	164.08	12	188.15	3.06	0.040
M	184.31	2	188.32	3.22	0.037
M S	180.91	4	188.92	3.83	0.027
M B H D T	178.04	6	190.06	4.96	0.015
M B D	183.31	4	191.31	6.22	0.008

Table 2.5. Estimated odds ratios and 95% Confidence Intervals (CI) for parameters within the MSYT model of burrowing owl nest survival in Thunder Basin National Grassland, northeastern Wyoming, USA.

Variable	Odds Ratio	95% CI
Observation Midpoint	1.12	1.08, 1.17
Egg-laying vs. Nestling Stage	3.33	0.32, 34.96
Incubation vs. Nestling Stage	1.03	0.33, 3.18
2003 vs. 2004	0.36	0.15, 0.89
Temperature	0.96	0.91, 1.01

Table 2.6. Model-averaged odds ratios and 95% Confidence Intervals (CI) for all variables included in the candidate set of 27 models (excluding the null) of burrowing owl nest survival in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004. Models averages were calculated as the sum of model coefficients multiplied by their Akaike weights (w_i). Explanatory variables not contained within a model were given $\beta = 0$.

Variable	No. Models	Odds Ratio	CI
Observation Midpoint	27	1.082	0.963, 1.215
Midpoint**2	27	1.000	0.999, 1.001
Egg-laying versus nestling	27	2.727	0.256, 29.041
Incubation versus nestling	27	1.135	0.479, 2.686
2003 vs. 2004	27	0.972	0.841, 1.124
Nest tunnel length	27	1.011	0.962, 1.064
Available burrows	27	0.999	0.995, 1.006
Shrub cover	27	1.008	0.978, 1.039
Prairie dog activity	27	1.000	0.998, 1.002
Temperature	27	0.972	0.841, 1.124
Temperature**2	27	1.000	0.999, 1.000

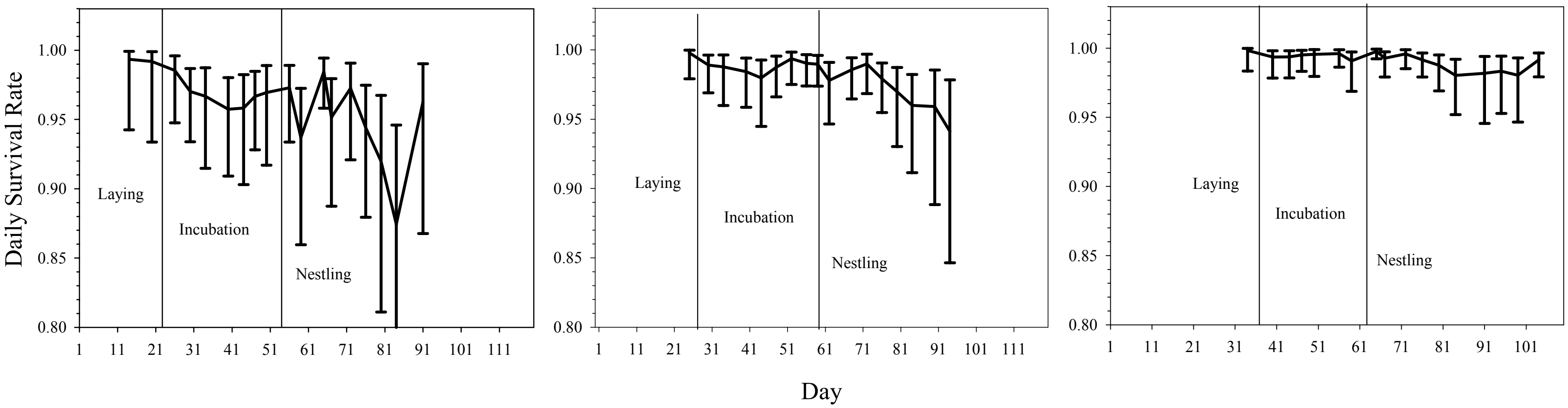

Figure 2.1. Daily survival rates (DSR) for three burrowing owl nests in Thunder Basin National Grasslands, northeastern Wyoming, USA, 2003 breeding season. Graphs depict daily nest survival for nests with early-, moderate- and late observation midpoints within the breeding season. From left to right, the early observation midpoint was day 14, the moderate observation midpoint was day 24, and the late observation midpoint was day 34. Observation midpoints were used as a proxy for nest initiation.

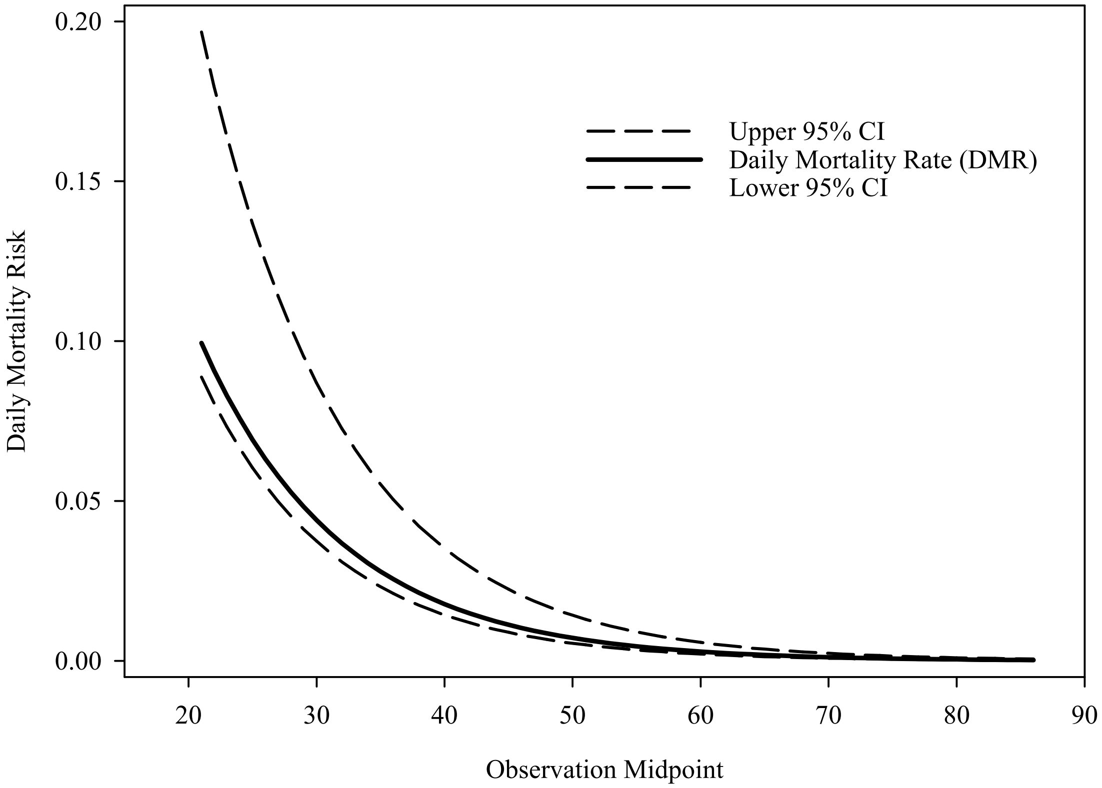

Figure 2.2. Daily mortality risk within the breeding season for burrowing owl nests in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004. Observation midpoint was used as a proxy for nest initiation date. Nests with later observation midpoints, therefore later nest initiation dates, had a lower daily risk of mortality.

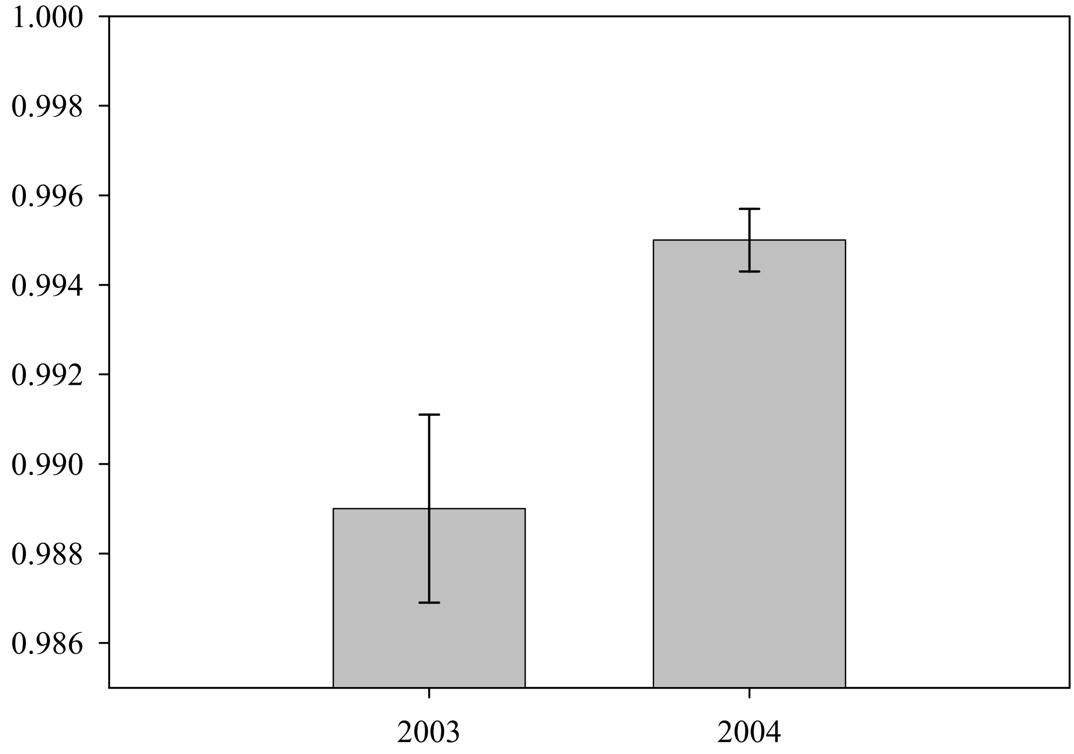

Figure 2.3. Annual difference in daily nest survival (DSR), estimated from constant-survival model (null model) for burrowing owls breeding in the Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004.

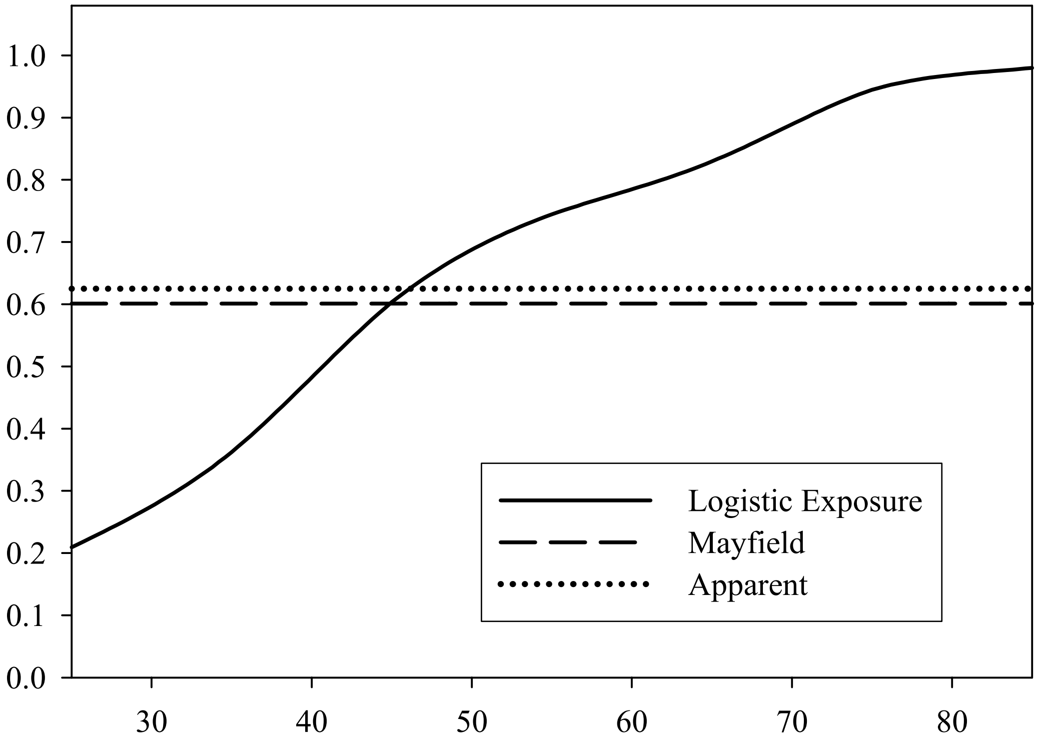

Figure 2.4. Overall probability of burrowing owl nest survival, estimated with the logistic-exposure model (curve) and compared to empirical estimates of apparent nest success and Mayfield nest success (horizontal lines). The logistic-exposure model allowed the probability of nest success to vary daily within the breeding season, whereas apparent success and the Mayfield estimator assumed constant survival over the breeding season. The probability of burrowing owl nest survival was higher for nests that were active later in the breeding season. Data were from burrowing owl nests in the Thunder Basin National Grassland, northeastern Wyoming, USA, 2003 – 2004.