

Factors Affecting Daily Nest Survival of Burrowing Owls Within Black-Tailed Prairie Dog Colonies

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ABSTRACT Identifying environmental parameters that influence probability of nest predation is important for developing and implementing effective management strategies for species of conservation concern. We estimated daily nest survival for a migratory population of burrowing owls (*Athene cunicularia*) breeding in black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Wyoming, USA. We compared estimates based on 3 common approaches: apparent nesting success, Mayfield estimates, and a model-based logistic-exposure approach. We also examined whether 8 intrinsic and extrinsic factors affected daily nest survival in burrowing owls. Positive biases in apparent nest survival were low (3–6%), probably because prior knowledge of nest locations and colonial behavior among nesting pairs facilitated discovery of most nests early in the nesting cycle. Daily nest survival increased as the breeding season progressed, was negatively correlated with ambient temperature, was positively correlated with nest-burrow tunnel length, and decreased as the nesting cycle progressed. Environmental features were similar between failed and successful nests based on 95% confidence intervals, but the seasonal midpoint was earlier for failed nests (31 May) compared to successful nests (15 Jun). The large annual variation in nest survival (a 15.3% increase between 2003 and 2004) accentuates the importance of multiyear studies when estimating reproductive parameters and when examining the factors that affect those parameters. Failure to locate and monitor nests throughout the breeding season may yield biased estimates of nesting success in burrowing owls (and possibly other species), and some of the variation in nesting success among years and across study sites may be explained by annual and spatial variation in ambient temperature. Any management actions that result in fewer prairie dogs, shorter burrow lengths, or earlier nesting may adversely affect reproductive success of burrowing owls. (JOURNAL OF WILDLIFE MANAGEMENT 73(2):232–241; 2009)

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Predation is one of the most important ecological processes because predation influences the evolution of behavior, morphology, and life-history traits (Kerfoot and Sih 1987). In birds, nest predation is a particularly important process because nest predation accounts for approximately 80% of mortality during the first few weeks of development (Ricklefs 1969, Martin 1993). Hence, identifying environmental parameters that influence probability of nest predation is important for advancing our understanding of both applied and basic science. For basic science, environmental factors that influence nest predation are often correlated with life-history traits in birds (Martin 1995). For applied science, identifying habitat features that influence probability of successful reproduction is critical for developing effective conservation plans (Martin 1992).

Most studies of avian-habitat relationships have examined correlations between habitat features and either occupancy or breeding density (Donovan et al. 2002). However, correlations between habitat features and either occupancy or density are often confounded by source and sink population dynamics, where species presence does not guarantee species persistence (Pulliam 1988) and site tenacity can reflect past rather than current habitat quality (Van Horne 1983). Instead, identifying habitat features that are correlated with reproductive parameters is considered

more important information when developing management strategies for species of conservation concern (Martin 1992, Christoferson and Morrison 2001, Donovan et al. 2002). Moreover, reproductive parameters are not static, but rather can be influenced by fluctuations in annual, seasonal, and diurnal factors. Failure to account for these temporal effects can produce biased estimates or invalid comparisons. For example, daily nest survival can either decrease or increase as the breeding season progresses (Dinsmore et al. 2002, Hazler 2004, Jehle et al. 2004, Peak et al. 2004). Such patterns in daily nest survival have important management implications if anthropogenic changes (e.g., climate change) alter breeding phenology of migratory birds (Brown et al. 1999, Price and Root 2000, Root and Schneider 2006). Hence, we need to identify both the environmental stressors on and the temporal patterns in reproductive parameters such as daily nest survival. This information is particularly important for species exhibiting population declines.

The western burrowing owl (*Athene cunicularia hypugaea*) is a migratory raptor that breeds in grassland, shrub-steppe, desert, and agricultural landscapes throughout western North America. Western burrowing owls (hereafter, burrowing owls) prefer flat, sparsely vegetated areas where digging activity by fossorial mammals provides many potential nest burrows. In the Great Plains of North America, burrowing owls are strongly associated with colonial, burrowing mammals, particularly the black-tailed prairie dog. Density of nesting burrowing owls was higher within black-tailed prairie dog colonies relative to the

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surrounding landscape in Oklahoma (Butts and Lewis 1982), Nebraska (Desmond and Savidge 1996), Colorado (VerCauteren et al. 2001), and eastern Wyoming (Conway and Simon 2003), USA. Burrowing owls likely select black-tailed prairie dog colonies in response to proximate cues created by prairie dog activity: increased burrow availability and short vegetation (Lantz et al. 2007).

Many populations of burrowing owls have declined along the periphery of their breeding range since the 1970s (James and Espie 1997, Wellicome and Holroyd 2001, Klute et al. 2003, Conway and Pardieck 2006). In recent decades, many of the western landscapes preferred by burrowing owls have been altered or fragmented by urbanization, prairie dog (*Cynomys* spp.) eradication efforts, agricultural conversion, and mineral extraction (Knopf 1994, Vickery et al. 1999, Klute et al. 2003). Indeed, many authors have suggested that habitat alteration has caused burrowing owl population declines (Haug et al. 1993, Sheffield 1997, Dechant et al. 1999, Klute et al. 2003). However, few studies have sought to quantify how changes to specific habitat features affect burrowing owl demographic traits, such as nest survival (but see Plumpton 1992, Ronan 2002). Moreover, all 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, Conway et al. 2006). Apparent nest survival usually overestimates true nest survival to some extent because unsuccessful nesting attempts survive only briefly and are less likely to be detected compared to successful nesting attempts (Mayfield 1961). Thus, failures that occurred early in the nesting cycle were likely underrepresented in previous burrowing owl studies that reported estimates of nest survival.

An alternative to apparent nest survival involves estimating a daily survival rate (DSR) based on exposure days (Mayfield 1961, Hensler and Nichols 1981). Overall nest survival (e.g., from the first egg laid to fledging) is then DSR^d , where d is the average number of days between nest initiation and fledging. This approach assumes DSR is constant over the course of the nesting cycle, and optimal use of the Mayfield estimator assumes that critical dates within the nesting cycle (e.g., date first egg laid, hatch date, fledge date, and date of nest failure) are known exactly. However, most researchers visit nests at irregular intervals, either for logistical reasons or to minimize disturbance to nesting birds (Bart and Robson 1982, Dinsmore et al. 2002, Shaffer 2004).

Because burrowing owls nest underground, identifying and monitoring the fate of nesting attempts presents some challenges relative to open-cup-nesting birds (Garcia and Conway 2009b). For example, observers tend to spend more time observing burrowing owl nests to obtain reliable estimates of fecundity than would be necessary for open-cup-nesting birds (Gorman et al. 2003). Extended observations at each nest then preclude daily nest visits when investigators are monitoring a large number of nests. Also, underground refugia may preclude accurate ageing of eggs

and juveniles. Although rigorous methods should be used to determine nesting stage and fate, exact dates are rarely known. Given these challenges, the optimal method for estimating nest survival in burrowing owls would be one that accounts for the potential bias in undetected early nest failures, accounts for irregular nest visits, and is more tolerant of imprecise estimates of nest initiation, hatch date, and fledge date. The logistic-exposure method (Shaffer 2004) is such a method.

We measured daily and overall nest survival for a migratory population of burrowing owls breeding in black-tailed prairie dog (*C. ludovicianus*) colonies in northeastern Wyoming. Our first objective was to compare apparent and Mayfield nest survival estimates with a model-based logistic-exposure approach that addressed the challenges of estimating nest survival in burrowing owls. Our second objective was to identify intrinsic and extrinsic factors that influence daily nest survival in burrowing owls.

STUDY AREA

We conducted our study in the Thunder Basin National Grassland (TBNG) in northeastern Wyoming, near the towns of Wright (43°44'N, 105°28'W), Newcastle (43°51'N, 104°12'W), and Douglas (42°45'N, 105°22'W; Lantz 2005, Lantz et al. 2007). The TBNG encompassed 2,300 km² of the southern Powder River Basin and contained more land occupied by black-tailed prairie dogs (7,381 ha) than any of the other United States Forest Service Great Plains National Grasslands (Luce 2003). Elevation ranged from 1,090 m to 1,580 m, ambient temperature varied between -10° C and 41° C throughout the year, and annual precipitation varied from 15 cm to 40 cm (Western Regional Climate Center 2008). Vegetation was dominated by grasses (western wheatgrass [*Pascopyrum smithii*], buffalo grass [*Buchloe dactyloides*], blue grama [*Bouteloua gracilis*]), sedges (*Carex* spp.), and shrubs (big sagebrush [*Artemisia tridentata*], silver sagebrush [*Artemisia cana*], and greasewood [*Sarcobatus vermiculatus*]). Much of TBNG was used for cattle and sheep grazing and mineral extraction.

METHODS

Given the association between burrowing owls and black-tailed prairie dog colonies in the Great Plains, we restricted our nest searches to black-tailed prairie dog colonies within the study area. In 2003 and 2004, we used 3 methods to locate burrowing owl nests: standardized surveys, visits to historical nest burrows, and repeated visits to owl-occupied black-tailed prairie dog colonies. First, we used standardized, call-broadcast surveys (Conway and Simon 2003, Conway et al. 2008) along dirt roads within 73 black-tailed prairie dog colonies in TBNG. Upon completion of a survey, we revisited areas where we detected burrowing owls and conducted thorough ground searches to look for nest burrows. We used the following signs to indicate a potential nest burrow: shredded cow or horse manure, prey remains, owl feces, and regurgitated castings at burrow entrances

(Haug et al. 1993, Smith and Conway 2007, Garcia and Conway 2009b). We used an underground, infrared video-scope (Sandpiper Technologies, Manteca, CA) to examine the contents of all potential nest burrows within 1–4 days after discovery (and periodically thereafter). Repeated use of the infrared videoscope does not affect reproductive parameters in western burrowing owls (Garcia and Conway 2009a). We included a burrow as a nest in our analyses only if we eventually confirmed that ≥ 1 egg was laid.

Second, we visited burrowing owl nest burrows located during previous years of an ongoing demographic study (Conway and Hughes 2002, Lantz 2005, Conway et al. 2008). Burrowing owls exhibit nest-site fidelity and will often return to former nest burrows or territories (Millsap and Bear 1997, Lutz and Plumpton 1999, Conway et al. 2006). We monitored nest sites that were occupied in past years every 3–7 days at the beginning of each breeding season. If nest sites became active, we continued to monitor those nests every 3–7 days. If nest sites remained unoccupied, we attenuated the frequency of nest visits as the season progressed. Confirmation of nesting activity at these historical burrows followed the protocol described above.

Lastly, burrowing owls are semicolonial, and nests are particularly clustered within black-tailed prairie dog colonies (Haug et al. 1993, Desmond and Savidge 1996). Because we visited active nest burrows every 3–7 days throughout the breeding season, we were able to conduct repeated visual scan surveys for additional nesting pairs within each prairie dog colony. Clusters of burrowing owl nests were common in the prairie dog colonies in TBNG, and nests we detected during these visual scan surveys contributed substantially to our final sample of nest burrows. Frequent visits to prairie dog colonies also facilitated detection of nests early in the nesting cycle (often prior to egg-laying). However, we did not include nest burrows detected after the last known hatch date (19 Jul in 2003 [$n = 0$], and 26 Jun in 2004 [$n = 4$] in TBNG).

During each nest visit, we first scanned the nest area from 125 m to 300 m away with binoculars and a spotting scope. We approached the nest burrows on foot every other visit (approx. once per week) to help determine the stage of the nesting cycle. We recorded the distance from the nest to the observer when adults flushed or retreated into burrows and used these as clues to help determine whether eggs or juveniles were present in the nest burrow. Signs of depredation at the nest included burrow excavation or presence of dirty eggs or owl carcasses outside the nest entrance. On visits when we approached the nest burrow, we used a videoscope to examine contents of the nest chamber. We recorded presence and sex of adult owls (based on size and plumage), clutch size, and number of juvenile owlets observed. We estimated the age of each owlet based on morphological development, percent of down feathers, percent of flight feather emergence, and behavior (hopping, wing flapping, and flight behaviors) after emergence from the burrow based on an aging guide adapted from Priest (1997).

We used a combination of these above- and below-ground observations to estimate the stage of the nesting cycle (laying, incubation, or nestling) during each nest visit. We were unable to view contents of the nest chamber at some nests ($n = 5$ in 2003, $n = 11$ in 2004) due to sharp bends in the nest tunnel or sandy soil. At these nests, we had to estimate stage of the nesting cycle on each visit based on adult behavior and estimates of nestling age based on future nest visits. Exact dates of nest initiation and transitions to subsequent nesting stages were not absolutely necessary, but approximate dates were essential to assign each nest visit to an appropriate stage of the nesting cycle. To maintain objectivity, we used a standardized protocol to estimate stage of the nesting cycle on each nest visit (Garcia et al. 2007). If accurate brood counts could not be obtained because burrow tunnels were too long or bent at angles too sharp for the videoscope to navigate, we assumed 8 eggs were laid at that nest (mean for our population) when determining critical dates (first egg laid, initiation of incubation, hatching, first juv fledged).

Female burrowing owls typically lay 6–12 eggs over a period of 8–17 days, and incubation typically begins at the midpoint of clutch completion (Wellicome 2005). Therefore, we defined the egg-laying stage as the interval between the first egg laid to the midpoint of laying (i.e., day 5 for a clutch of 8 eggs) and the incubation stage (median = 26 days) as the interval from the midpoint of laying until the first egg hatched. The nestling stage began when the first egg hatched and ended when the first juvenile reached 44 days (Landry 1979). We included nests we discovered during the nestling stage only if we discovered them prior to the last known hatch date for the season (see above) and only if we could accurately age juveniles in the nest chamber.

We recorded nesting stage and fate for each observation interval (the interval between 2 successive nest visits). A nest survived an observation interval if it had ≥ 1 surviving egg or juvenile. For successful nests, the end of the last observation interval was the estimated date that ≥ 1 juvenile had reached 44 days of age. For failed nests, the end of the last observation interval was the first nest visit in which we confirmed failure. We estimated fledge date of successful nests based on estimates of juvenile age from previous nest visits. Estimating a failure date at failed nests required making a decision about when a nesting attempt actually terminated. Many researchers assign failure to the midpoint of the last observation interval (Manolis et al. 2000), and such decisions may be appropriate when all observation intervals are of equal length (Shaffer 2004). But when nest survival is only assumed to be constant within a given observation interval, and observation intervals vary across nests, our assumption that failure did not occur until the last day of the last observation interval is just as appropriate as assuming failure at the midpoint.

Based on our previous research at this study site (Lantz et al. 2007), we included 4 important habitat features in our nest-survival analysis: tunnel length of the nest burrow (m), number of usable satellite burrows (burrows near the nest

Table 1. The top 13 (out of 27 examined) most plausible logistic-exposure models of daily nest survival for burrowing owls ($n = 77$) in the Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004. The other 14 models had $\Delta\text{AIC}_c > 30.5$ and $w_i < 0.001$.

Model ^a	Deviance ^b	K^c	AIC_c^d	ΔAIC_c	w_i^e
M S Y T	173.1	6	185.1	0.00	0.184
M Y	180.0	3	186.0	0.92	0.116
M S Y B L H D	168.0	9	186.1	0.96	0.114
M T	180.1	3	186.1	1.02	0.111
M S Y	176.1	5	186.1	1.04	0.110
M ² S Y	174.2	6	186.3	1.16	0.103
M S Y T ²	172.9	7	186.9	1.80	0.075
M ² S Y T ²	171.4	8	187.4	2.29	0.059
M M ² S Y T T ² B L H D (full model)	164.1	12	188.2	3.06	0.040
M	184.3	2	188.3	3.22	0.037
M S	180.9	4	188.9	3.83	0.027
M B H D T	178.0	6	190.1	4.96	0.015
M B D	183.3	4	191.3	6.22	0.008

^a M = midpoint of observation interval (day); M² = quadratic of the midpoint of observation interval; S = stage of nesting cycle (egg-laying, incubation, nestling); Y = yr (2003, 2004); T = average ambient temp of observation interval (°C); T² = quadratic of T; L = nest tunnel length (m); B = no. of available burrows within 30 m; H = shrub cover within 30 m (%); D = prairie dog activity within 100 m (%).

^b Deviance is $-2\{\log_e[L(\theta)] - 2\log_e[L_c(\theta)]\}$, where θ is a max. likelihood estimate evaluated for the model in question $[L(\theta)]$ and for the full model $[L_c(\theta)]$.

^c No. of parameter estimates in the model.

^d Akaike's Information Criterion.

^e Model wt.

burrow that are used regularly by nesting owls) within 30 m of the nest, shrub cover (%) within 30 m, and prairie dog activity (%) within 100 m. We also examined the effect of 3 temporal parameters on burrowing owl nest survival: year, stage of the nesting cycle, and season. Year (2003, 2004) and stage of the nesting cycle (egg laying, incubation, nestling) were categorical variables. To measure seasonal effects, we used the midpoint between the first and last observation day at each nest as a proxy for early, mid-, and late-season nesting attempts (Hazler 2004). To examine the possible effects of ambient temperature on burrowing owl daily nest survival, we used the average daily maximum temperature (°C) for each observation interval at each nest. We used temperature data collected at the Dull Center weather station, centrally located within our study area (Western Regional Climate Center 2008).

One of our objectives was to compare methods for estimating burrowing owl nest survival and to assess the extent of potential biases associated with the different methods. Because historical information may not always be available in burrowing owl studies, we restricted our method comparisons to a subset of nests; we included only newly discovered nests from each year and excluded known nest burrows from previous years. Excluding nesting attempts within burrows located in past years was important because biases associated with apparent nest survival are caused by previously unknown nest sites being located late in the nesting cycle. We compared the overall probability of nest survival from the null logistic-exposure model to estimates

derived from apparent nest survival and the Mayfield estimator. For the estimate based on logistic-exposure, we held survival constant over the 75-day nesting period.

We used the logistic-exposure approach (Shaffer 2004, 2006; SAS version 8, SAS Institute, Cary, NC) to model the effects of our 7 explanatory variables on daily survival of burrowing owl nests. 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 to account for variation in length of observation intervals. This modification converts survival probabilities for observation intervals into daily probabilities. Underlying assumptions are that fates are independent among nests, daily survival probabilities are constant within each observation interval, and survival probabilities are homogeneous among nest-days with the same values of the explanatory variables (Rotella et al. 2004, Shaffer 2004).

We compared 27 alternative logistic-exposure models (Table 1). We included quadratic terms for observation midpoint and ambient temperature to examine the possibility of important but nonlinear effects (i.e., whether daily nest survival peaked mid-season or if some intermediate range of temperatures were optimal for daily nest survival). We tested for multicollinearity among the 4 habitat variables by examining their variance inflation factors (VIF) and tolerance values. A VIF that strongly deviated from 1.0 (i.e., a VIF closer to 0.1 or 10) and a tolerance value that approached zero indicated a lack of independence (Chatterjee and Price 1991). We ranked candidate models by ascending Akaike's Information Criterion (AIC_c) values, adjusting for the small-sample bias (Burnham and Anderson 2002). We examined ΔAIC_c , Akaike weights (w_i), and deviance to evaluate how well each model fit our data. To further elucidate differences between failed and successful nests, we also compared the means of influential variables between failed and successful nests. We used a t -test to examine whether nest initiation dates differed between years. We used the null logistic-exposure model to estimate the overall probability of burrowing owl nest survival.

RESULTS

We found 77 burrowing owl nests in black-tailed prairie dog colonies of TBNG during the 2003 ($n = 32$) and 2004 ($n = 45$) breeding seasons. Nest initiation dates were earlier in 2003 (14 Apr–30 May) compared to 2004 (26 Apr–2 Jun; $t = 2.1$, $df = 74$, $P = 0.040$). Hatch dates occurred between 18 May and 28 June in 2003 and between 29 May and 29 June in 2004. Habitat features were similar between failed and successful burrowing owl nests in TBNG (Table 2), but the seasonal midpoint was earlier for failed nests (31 May) compared to successful nests (15 Jun), with nonoverlapping 95% confidence intervals. We did not detect multicollinearity among any of the continuous or categorical variables (tolerance > 0.65 ; $1.1 < \text{VIF} < 1.5$).

The logistic-exposure estimate of nest survival was 17% higher in 2004 compared to 2003 (Fig. 1), and estimates

Table 2. Breeding phenology and habitat parameters at failed and successful burrowing owl nests in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Habitat parameters	Failed ($n = 22$)		Successful ($n = 55$)	
	\bar{x}	95% CI	\bar{x}	95% CI
Midpoint of observation interval (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 (%)	4.0	2.1–5.9	6.9	4.3–9.6
Prairie dog activity (%)	44.6	34.0–55.2	44.9	39.0–50.9

based on apparent survival were 3–6% higher than those based on logistic-exposure (Table 3). To estimate nest survival for the study population in TBNG, we returned to the full data set and used all 77 nests. Fewer nests fledged ≥ 1 juvenile in 2003 (20 of 32) compared to 2004 (35 of 45).

The Hosmer and Lemeshow (2000) goodness-of-fit test suggested adequate fit of the full model ($\chi^2 = 9.2$, $df = 8$, $P = 0.326$). We found a large natural break in the weight of evidence (w_i) between models that included the observation midpoint variable and those that did not (Table 1). Among the top 13 models, weight of evidence and ΔAIC_c did not differ markedly (w_i ranged 0.184–0.008).

Based on the prevalence of variables in top-ranking models, daily nest survival of burrowing owl nests differed between years, increased as the season progressed, was influenced by ambient temperature, was positively correlated with nest-burrow tunnel length, and decreased with each successive change in the nesting cycle (Tables 1, 4). Odds of daily nest survival increased 12%/day as the breeding season progressed (Table 4; Fig. 2). For every 1° C increase in ambient temperature, odds of daily nest survival decreased by 4%. Odds of daily nest survival were 2 times higher during the egg-laying stage relative to the nestling stage. However, the odds ratio estimate for the egg-laying stage was not very accurate (95% CI = 0.32–34.96). The large variability is not surprising given the minor contribution of egg-laying observations to the overall sample (9% as

opposed to 36% from incubation and 55% from nestling). Odds of daily nest survival were also higher during the incubation stage relative to the nestling stage, but the associated 95% confidence interval included 1.0.

DISCUSSION

Daily nest survival was higher for burrowing owl nesting attempts that initiated later in the breeding season, and daily nest survival was slightly higher during the laying and incubation stages relative to the nestling stage. Mountain plover (*Charadrius montanus*) nests in Montana, USA, also had higher daily nest survival for late-season nests, but daily nest survival was higher during the nestling stage (Dinsmore et al. 2002). In contrast, lark bunting (*Calamospiza melanocorys*) nests in Colorado had lower daily nest survival for late-season nests, and daily nest survival was lower during later stages of the nesting cycle (Jehle et al. 2004). Although we did not measure prey densities in TBNG, invertebrates and small mammals (common prey items for burrowing owls; Marti 1974, Gleason and Craig 1979, Green et al. 1993) may have been more abundant later in the breeding season.

Our results differ from most multivariate modeling studies where daily nest survival increases with successive stages of the nesting cycle (Martin 1992, Dinsmore et al. 2002, Stephens 2003, Peak et al. 2004, Traylor et al. 2004). Studies for which daily nest survival decreased with successive stages of the nesting cycle typically cite increased predation risk for nests with juveniles compared to nests with eggs (Burhans et al. 2002, Jehle et al. 2004). Burrowing owl nests may be more susceptible to predation during the nestling stage because nestlings begin to spend considerable time loafing in and around the entrance of the burrow (whereas eggs are likely less vulnerable to many predators because they remain ≥ 3 m below ground). Moreover, nesting activity at the burrow entrance likely increases visibility of the nest to potential predators. We did document some predation on nestlings, but the causes of nest failure for burrowing owls in TBNG were largely unknown.

Paradoxically, burrowing owl daily nest survival was higher for late-season nests even though increased temperatures that occurred later in the breeding season had a slightly negative effect on nest survival. Paradoxes are not uncommon in a multivariate framework and are best explained by looking at the parameter weight of each variable to assess

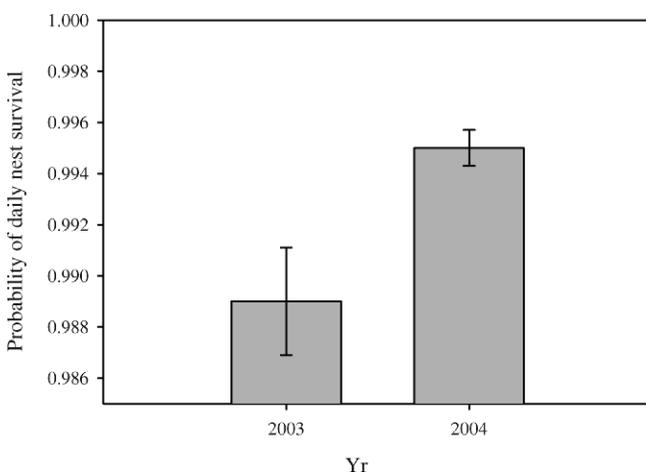


Figure 1. Annual difference in daily nest survival, estimated from constant-survival model (null model) for burrowing owls breeding in the Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Table 3. Apparent, Mayfield, and logistic-exposure estimates of nesting success in burrowing owls in Thunder Basin National Grassland, northeastern Wyoming, USA. Estimates for a restricted sample ($n = 32$) that excluded nesting attempts within burrows located in previous years differed more than estimates for the full sample of nests located in 2003 and 2004 ($n = 77$).

Nest and yr	Date of nest discovery		% nesting success		
	\bar{x}	Range	Apparent	Mayfield	Logistic-exposure
New nests only					
2003 ($n = 13$)	9 May	7 Apr–28 May	46.2	42.6	43.3
2004 ($n = 19$)	30 Apr	4 Apr–5 Jun	73.6	72.2	67.1
All nests					
2003 ($n = 32$)	20 Apr	6 Apr–28 May	62.5	60.4	60.5
2004 ($n = 45$)	16 Apr	3 Apr–5 Jun	77.8	77.4	77.5

relative influence on daily nest survival. Time within breeding season influenced daily odds of burrowing owl nest survival by 12%, whereas temperature influenced daily odds by -4% . This suggests that the benefits of initiating nests later in the breeding season outweigh the negative influence of increasing temperature. However, we did not directly measure the benefits (e.g., increased prey availability or decreased predation risk) of nesting later in the breeding season. Daily nest survival might decrease with increasing temperature due to temperature-related changes in prey activity or mobility. For example, many invertebrates are less mobile when ambient temperatures are low (possibly making them easier to catch) and many small mammals remain underground (and hence are not accessible) when ambient temperatures are low. Our results highlight the value of including nesting stage, time within breeding season, and ambient temperature all in the same model; we were able to examine the effect of each variable after controlling for the other 2 variables. Future studies should examine the ubiquity and cause of the relationship between daily nest survival and ambient temperature and should also examine effects of rainfall and other weather variables (especially those that may affect foraging time or prey activity) on daily nest survival.

Although only present in a few of the top-ranking models, we found some indication that burrow tunnel length, satellite-burrow availability, shrub cover, and prairie dog activity influenced burrowing owl daily nest survival. These same factors influenced nest-site selection on our study site (Lantz et al. 2007). However, whereas temporal factors were present in all of the top 13 models, habitat effects were present in only 4 of the top 13 models. The weak influence

of habitat effects is consistent with other burrowing owl studies, where site characteristics had little (or no) effect on reproductive parameters (Plumpton 1992, Ronan 2002). Based on 95% confidence intervals, the 4 habitat features did not differ between successful and failed nests. These habitat features may influence daily nest survival of burrowing owls at larger spatial scales than what we measured. For example, effects of habitat features on daily nest survival may have been more evident if we had included burrowing owl nests both on and off prairie dog colonies.

Our estimates of apparent nest survival in TBNG (62.5% in 2003, 77.8% in 2004) were within the range of estimates reported in previous studies. Apparent burrowing owl nest survival within black-tailed prairie dog colonies was 85% in Colorado (Plumpton 1992) and 92% in Montana (Restani et al. 2001). Apparent nest survival in eastern Washington, USA, was 41% in urban areas and 51% in agricultural areas (Conway et al. 2006). Apparent nest survival was 53–57%

Table 4. Estimated odds ratios and 95% confidence intervals for parameters within the top-ranking model of burrowing owl nest survival in Thunder Basin National Grassland, northeastern Wyoming, USA, 2003–2004.

Variable	Odds ratio	95% CI
Midpoint of observation interval	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
Yr (2003 vs. 2004)	0.36	0.15, 0.89
Ambient temp	0.96	0.91, 1.01

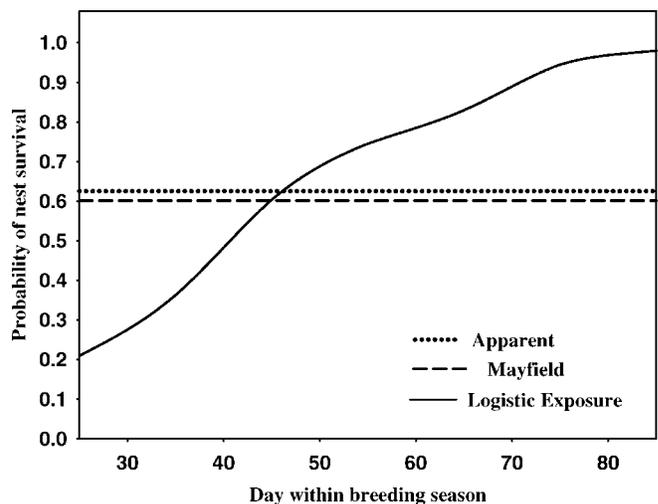


Figure 2. Overall probability of burrowing owl nest survival estimated with the logistic-exposure model (solid line) and compared to empirical estimates of apparent nest survival (dotted line) and Mayfield nest survival (dashed line). The logistic-exposure model allowed the probability of nest survival to vary daily within the breeding season, whereas apparent nest survival and Mayfield nest survival 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.

in the shrub-steppe of north-central Oregon, USA (Green and Anthony 1989, Holmes et al. 2003). Apparent nest survival estimates were 59–69% in Saskatchewan, Canada (Haug 1985, James and Espie 1997, Wellicome et al. 1997), 67–68% in Idaho, USA (Olenick 1990, Lehman et al. 1998), 76% in South Dakota, USA (Griebel and Savidge 2007), and 69% in urban Florida, USA (Millsap and Bear 2000). The large annual variation in apparent nest survival estimates (a 15.3% increase between 2003 and 2004) accentuates the importance of multiyear studies when estimating reproductive parameters and when examining factors that affect those parameters.

Constant-survival models from the logistic-exposure approach have typically produced estimates similar to, if not slightly less than, Mayfield estimates for other species (Peak et al. 2004, Shaffer 2004). Of the 3 methods we compared, the logistic-exposure method frequently yielded the lowest estimate of burrowing owl nest survival. The logistic-exposure estimator may be more appropriate than apparent and Mayfield methods, particularly when 1) observations are limited by inaccessibility of nest contents (as they frequently are with cavity and burrow-nesting birds), 2) nests are found during all stages of the nesting cycle, and 3) observation intervals vary in length.

However, the positive bias we identified in our apparent nest survival estimates is still less than the biases identified by other studies that compared these methods. Hensler and Nichols (1981) used Monte Carlo simulations to illustrate a 9–27% positive bias in apparent estimates compared to Mayfield estimates. Simple Mayfield estimates of white-winged scoter (*Melanitta fusca*) nest survival were positively biased by as much as 10% (Traylor et al. 2004) relative to a model-based, constant-survival option within Program MARK (Dinsmore et al. 2002). Extent of bias undoubtedly depends on the proportion of nests that were found late in the nesting cycle, length of the nesting cycle, extent to which daily nest survival differs among nesting stages, and probability of nest failure (bias will increase as the probability of nest failure increases). Because bias is positively correlated with the proportion of nests found late in the nesting cycle, bias will be higher when field work begins after some birds have already laid, and in studies where prior knowledge of nest locations is not available. Moreover, the extent of bias in our estimates was likely affected by the criteria we used to determine whether a nesting attempt had been initiated at an occupied burrow, by the frequency with which we searched for nests, and by the frequency of our nest visits. Indeed, the criteria used to identify nesting attempts introduce more bias into estimates of burrowing owl nest survival than the analytical methods used to estimate nest survival. For example, estimates of nesting success varied from 49% to 84% depending on the criteria used to identify an active nest in one study (Garcia and Conway 2009b). When searches are conducted repeatedly in areas of easily detected nests, apparent nest survival will be an accurate estimate 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. Apparent nest survival is less biased when coloniality promotes detection of most nests early in the nesting cycle.

Interestingly, our subsample of new nests had much lower nest survival compared to our full sample of all nests. All things being equal, we would have expected nest survival estimates to be higher among new nests because we discovered those nests later in the nesting cycle when they would be more likely to succeed. This opposite pattern suggests that nests that were occupied in a previous year were much more likely to succeed (i.e., nest-burrow fidelity among burrowing owls may be positively correlated with high nest-survival rates). Though we were unable to document the identity of both adults at all of our nest burrows, we were able to positively identify some adults marked in previous years nesting in burrows that were occupied in a previous year (Conway and Hughes 2002, Lantz et al. 2004, Conway et al. 2005). The lower nest survival that we observed at new nest sites may reflect differences in nesting success between first-year breeders at a site and returning (and hence experienced) breeders that often re-nest at the same site in subsequent years (Millsap and Bear 1997).

The positive bias in our nest survival estimates may also have been reduced because we discovered several of our new nests prior to egg-laying during visual scan surveys near known burrowing owl nests from previous years. Without that prior knowledge of nearby burrowing owl occupancy, we may not have discovered those new nests until later in the nesting cycle. Thus, during the first year of a study, apparent nest survival may be more positively biased because all nests cannot be found during early stages, and some early failures will go undetected. In subsequent years of a study, researchers typically search areas previously occupied and the positive bias will be reduced because most nests are detected earlier in the breeding season. Hence, apparent nest survival may be biased high during the first year of a study. To address this issue, we recommend researchers report the average (and range) date of nest discovery for each year of study.

The extent to which researchers vary in the criteria they use to determine whether an occupied burrow is included as a nesting attempt affects comparisons of nest survival among estimators or across studies (Garcia and Conway 2009b). For example, we included all burrows in which we confirmed eggs or juveniles in the nest chamber, and we excluded all nesting attempts discovered after the last known hatch date for the population within that season. Our nest-survival estimates would have been higher had we included nesting attempts discovered after the last known hatch date, regardless of the estimator used. And our estimates would have been lower had we included all burrows that were lined with manure (a common cue used to identify burrowing owl nests; Haug et al. 1993, Garcia and Conway 2009b). Our analysis suggested that daily nest survival was highest for nests active later in the

breeding season, but nestling stage had the lowest daily nest survival. If we had restricted our analysis to include only those burrows at which we confirmed eggs or juveniles, we might have excluded nests that failed early in the season before we were able to confirm eggs or juveniles. Excluding these early failures may have caused us to underestimate the difference among the 3 estimators of nest survival. Exclusion of these early failures may also have produced estimates of nesting success that were higher than those from studies that defined burrows as nests without visual confirmation of eggs or juveniles (Green and Anthony 1989, Holmes et al. 2003, Conway et al. 2006).

One advantage of the logistic-exposure modeling approach is that the probability of daily nest survival can be evaluated over a continuous range of values for influential explanatory variables. Apparent and Mayfield estimators assume constant daily nest survival probabilities, whereas our analysis suggested that the daily probability of nest survival increased as the season progressed (Fig. 2). Hence, the model-based approach was more biologically informative because we were able to conclude that daily nest survival of burrowing owls was not constant throughout the breeding season.

MANAGEMENT IMPLICATIONS

Management actions that result in shorter burrow lengths may adversely affect reproductive success of burrowing owls. Managing for healthy populations of prairie dogs is one way to ensure deep tunnels are available for nesting burrowing owls. Any anthropogenic changes that cause burrowing owls to breed earlier may result in lower nesting success. Future surveys for burrowing owls in northeastern Wyoming (and similar regions) should start in mid-April and continue until mid-July to overlap the prelaying through pre fledging stages of the nesting cycle. Frequent nest visits will increase accuracy in determining critical dates in the nesting cycle (e.g., date the first egg is laid, date the first nestling fledges, date the nest failed); the more frequent the better, but we recommend visiting each nest at least every 7 days. The analytical method used to estimate nesting success in burrowing owls appears to introduce less bias than the criteria used to determine whether an occupied site is included as a nesting attempt in that analysis.

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