Factors associated with nest survival of Black-throated Sparrows, desert-breeding nest-site generalists

Jeffrey M. Kozma,[1,3,4] Laura M. Burkett,[1,5] Andrew J. Kroll,[2] Jamie Thornton,[2] and Nancy E. Mathews[1,6]

[1] *United States Geological Survey-Biological Resources Discipline, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, Texas 79409, USA*
[2] *Strategy & Technology, Weyerhaeuser, P.O. Box 9777, Federal Way, Washington 98063, USA*

ABSTRACT. Black-throated Sparrows (*Amphispiza bilineata*) are common breeding birds throughout the desert regions of North America and can be considered nest-site generalists. Information about how spatial (e.g., vegetation) and temporal factors influence nest survival of these sparrows is lacking throughout their range. Our objective was to examine the spatial and temporal factors associated with nest survival of Black-throated Sparrows at the nest and nest-patch scales in the predator-rich environment of the northern Chihuahuan Desert of New Mexico. We used a logistic-exposure model fit within a Bayesian framework to model the daily survival probability of Black-throated Sparrow nests. Predation was the leading cause of nest failure, accounting for 86% of failed nests. We found evidence of negative associations between nest survival and both vegetative cover above nests and shrub density within 5 m of nests. We found no support for other habitat covariates, but did find strong evidence that daily survival rate was higher earlier in the breeding season and during the egg-laying stage. A decline in nest survival later in the breeding period may be due to increased predator activity due to warmer ambient temperatures, whereas lower survival during the incubation and nestling stages could be a result of increased activity at nests. A generalist approach to nest-site selection may be an adaptive response to the presence of a diverse assemblage of nest predators that results in the reduced influence of spatial factors on nest survival for Black-throated Sparrows.

RESUMEN. **Factores asociados a la supervivencia de nido del Zacatonero Garganta Negra, un generalista de sitio de nidada que cría en el desierto.**
Los Zacatoneros Garganta Negra (*Amphispiza bilineata*) son aves que crían comúnmente a lo largo de regiones desérticas de Norte América y que pueden ser considerados generalistas de sitio de nidada. Se carece de información de cómo factores espaciales (e. g. vegetación) y temporales influencian la supervivencia de nido en estos gorriones a lo largo de su rango de distribución. Nuestro objetivo fue examinar los factores espaciales y temporales asociados a la supervivencia de nido de los Zacatoneros Garganta Negra a escala del nido y del parche de nidada en un ambiente rico en depredadores del norte del desierto de Chihuahua en Nuevo México. Usamos un modelo de exposición logística en un contexto Bayesiano a fin de modelar la probabilidad de supervivencia diaria de los nidos del Zacatonero Garganta Negra. La depredación fue la principal causa de fracaso en nidos, explicando el 86% de los nidos que fracasaron. Encontramos evidencia de una asociación negativa entre la supervivencia de nido y tanto la cobertura vegetal como la densidad de arbustos dentro de 5 metros de distancia de los nidos. No encontramos respaldo para asociaciones con otras covariables de hábitat, pero si encontramos fuerte evidencia de que la tasa de supervivencia diaria es más alta al principio de la temporada reproductiva y durante la etapa de puesta de huevos. Una disminución en la supervivencia de nido más tarde en el período reproductivo puede deberse al aumento de actividad de los depredadores debido a temperaturas ambientales más cálidas, mientras que la baja supervivencia durante la etapa de incubación y de volantones puede ser el resultado del aumento de actividad en el nido. Una estrategia generalista en cuanto a la selección de sitio de nidada puede ser una respuesta adaptativa al diverso ensamble de depredadores de nido, que resulta en una influencia reducida de los factores espaciales en la supervivencia de nido de los Zacatoneros Garganta Negra.

Key words: *Amphispiza bilineata*, Bayesian framework, Chihuahuan Desert, logistic-exposure model, New Mexico, temporal factors

---

[3] Corresponding author. Email: kozj@yakamafish-nsn.gov
[4] Current address: Yakama Nation, Timber, Fish and Wildlife/Fisheries Resource Management, P.O. Box 151, Toppenish, Washington, USA.
[5] Current address: U.S. Department of Agriculture-Agricultural Research Service Jornada Experimental Range, New Mexico State University, MSC 3JER, P.O. Box 30003, Las Cruces, New Mexico, USA.
[6] Current address: Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Dr. Aiken Center 220D, Burlington, Vermont, USA.

Black-throated Sparrows (*Amphispiza bilineata*) may be the most abundant birds in the hot deserts (Sonoran, Chihuahuan, and Mojave) of southwestern North America (Coe and Rotenberry 2003). These sparrows occupy numerous desert vegetation types dominated by creosote bush (*Larrea tridentata*), white-thorn acacia (*Vachellia constricta*), black grama (*Bouteloua gracilis*), yucca (*Yucca* spp.), and crucifixion thorn (*Canotia holacantha*) depending on location (Coe and Rotenberry 2003, Pidgeon et al. 2003, Johnson and van Riper 2004). Kozma and Mathews (1997) classified Black-throated Sparrows as nest-site generalists because they used a greater variety of plant species ($N = 25$) for nesting than 26 other species of birds breeding in desert shrublands in the northern Chihuahuan Desert. Early studies focused on their physiological adaptations (Smyth and Bartholomew 1966), distribution (Raitt and Maze 1968, Tomoff 1974, Naranjo and Raitt 1993), and foraging ecology (Zimmer 1983, Parker 1986). In more recent studies, investigators evaluated nest-site use (Kozma and Mathews 1997) and nesting success (Coe and Rotenberry 2003, Pidgeon et al. 2003, Hargrove and Rotenberry 2011) of Black-throated Sparrows, as well as the effects of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*; Johnson and van Riper 2004). Quantifying spatial variation (vegetation characteristics at different scales) in nest survival is critical to inform management decisions for Black-throated Sparrows and their habitat (Dearborn and Sanchez 2001, Bulluck and Buehler 2008). Also, even though these sparrows are common throughout their range, climate change is expected to exert negative effects on desert-breeding birds through delays in nest initiation due to drought, which can lower nest success and productivity (McCreedy and van Riper 2014). Thus, nest-survival estimates can be used in population viability analyses for evaluating common and stable species such as Black-throated Sparrows (Morrison et al. 2006).

Understanding adaptive pressures that influence habitat selection and productivity of birds is essential for their conservation (Grant et al. 2005). Predation is the primary cause of reproductive failure for most species of birds (Ricklefs 1969, Martin 1992) and, therefore, should influence the choices birds make when they select habitat features associated with nest sites (Martin and Roper 1988, Davis 2005). New modeling techniques allow researchers to quantify spatial and temporal variation in nest survival while accounting for the hierarchical design of nest survival sampling (visits to individual nests and numerous nests in a study site). In arid environments, temporal factors such as a lack of precipitation can influence nestling growth rates and clutch size (Tieleman et al. 2004), as well as the ability to re-nest (Keynan and Yosef 2010). Likewise, high temperatures can delay nestling growth and increase the risk of nest failure (Cunningham et al. 2013), and can influence nest-site selection and predation risk (Yanes et al. 1996, Tieleman et al. 2008). However, the influence of spatial factors on nest survival in desert environments remains largely unexplored (Pidgeon et al. 2003).

We quantified spatial and temporal variation in nest survival of Black-throated Sparrows in the Chihuahuan Desert of south-central New Mexico, U.S.A. (Kozma 1995, Myers 1998). Our objectives were to describe population demographic variables of Black-throated Sparrows (e.g., clutch size and mean number of young produced per nest) and examine the spatial and temporal factors associated with nest survival at the nest and nest-patch scales. Because Black-throated Sparrows are nest-site generalists, we predicted that spatial factors (e.g., nest height, shrub density, and spinescent foliage) would have little influence on daily nest survival, a pattern observed with other bird species that can be considered nest-site generalists (Filliater et al. 1994, Ricketts and Ritchison 2000, Siepielski et al. 2001, Kus et al. 2008). We also predicted a decline in nest survival during the nesting season, a common pattern for many bird species (Verhulst et al. 1995, Grant et al. 2005, Fields et al. 2006).

METHODS

Study area. We conducted our study ~47.5 km southwest of Alamogordo in Otero County, New Mexico (32.54°N, −105.88°W), in the foothills of the Sacramento Mountains on the northern portion of the McGregor Range in the Fort Bliss Military Reservation from 1993 to 1997.

Elevation ranged from 1276 to 1512 m, with an average annual rainfall of 20.3–25.4 cm (Budd et al. 1979). Approximately 65–80% of the annual precipitation occurs as rain from June through September (Shreve 1942). Dominant upland shrubs, by decreasing density, were mariola (*Parthenium incanum*), creosote bush, tarbush (*Flourensia cernua*), white-thorn acacia, banana yucca (*Yucca baccata*), honey mesquite (*Prosopis glandulosa*), and rough jointfir (*Ephedra aspera*) (Kozma and Mathews 1997). Dominant shrubs in arroyos, by decreasing density, were mariola, creosote bush, tarbush, white-thorn acacia, little-leaf sumac (*Rhus microphylla*), and honey mesquite (Kozma and Mathews 1997).

We chose eight arroyos and their adjacent uplands for our study plots. Each arroyo was 1400 m long and upland plots extended 400 m to one side of the arroyos. Upland plots did not intersect other major arroyos and retained continuity of cover. Arroyo vegetation comprised ~20% (~11.2 ha) of each plot with the remainder in upland vegetation (~44.8 ha per plot).

Nest searching. We began nest searching during the first week of May in each year. We found nests by following adults carrying nesting material or food, flushing adults from nests by accident, and searching for nests in potential sites. We searched for and monitored nests on each plot every other day when possible, and rotated observers among plots. We recorded whether adults were present, nest contents (e.g., clutch size, number of cowbird eggs, and number of nestlings), and nest fate. We classified a nest as deserted if no adults were observed for five or more consecutive checks and if the contents of the nest remained unchanged. We assigned a fate of predated if all eggs or young were gone before the anticipated time of incubation or nestling stage was complete. We considered nests with one or more cowbird nestlings as having failed at the point where nestling sparrows were found dead in nests or were missing, but the cowbird nestling remained. To confirm suspected fledging, we checked nests for the presence of fecal material in nest cups or on nest rims, and searched the areas around nests for parents carrying food or giving scolding calls (Manolis et al. 2000, McCreedy and van Riper 2014). We calculated nest-initiation date by backdating from the day of hatching or fledging, or from the age of young estimated from feather development (Keyser et al. 2004) using a period length of 3 d for laying, 12 for incubation, and 10 for the nestling stage (Johnson et al. 2002). We calculated egg success by dividing the number of young fledged by the number of eggs laid (Murray 2000).

Vegetation sampling. We modified guidelines proposed by James and Shugart (1970) and Martin et al. (1997) to sample vegetation characteristics associated with each nest after the nesting season was complete. At each nest, we recorded variables associated with the nest and nest substrate, which included species and height of nest shrubs, height of nests above ground, and nest concealment 0.5 m above the nest. We counted the total number of shrubs within a 5-m radius centered on a single point directly under the nest to determine shrub density.

Statistical analyses. We used a logistic-exposure model fit within a Bayesian framework to model the daily survival probability of Black-throated Sparrow nests (Shaffer 2004, Schmidt et al. 2010). We specified a multilevel structure that allowed us to incorporate the inherent nested design of nest-survival studies. The Bayesian framework supports inclusion of spatial and temporal covariates as fixed or random effects at different levels of nesting as appropriate and allows for easy calculation of derived quantities, such as period survival.

We denoted the interval survival of the observed nests as $y_{i,j}$ where $y_{i,j} = 1$ if nest i survives interval j, and $y_{i,j} = 0$ if nest i fails during interval j. Observed nest survival was assumed to follow a Bernoulli distribution, $y_{i,j} = \text{Bern}(\theta_{i,j})$ where $\theta_{i,j}$ is the probability that nest i survives interval j. The daily nest survival probability for nest i during interval j is $s_{i,j}$ so $\theta_{i,j} = s^{t_{i,j}}$, where $t_{i,j}$ is the length of interval j for nest i. The daily nest survival probability is modeled as a function of covariates using a logit link function, $\text{logit}(s_{i,j}) = X\beta$ where X is the design matrix of the covariates of interest and β is the parameter vector.

We modeled daily survival as a function of seven covariates. To account for temporal variation, we included two interval-specific covariates as fixed effects: nest stage (laying, incubation, and nestling; Kroll and Haufler 2009) and ordinal date (Grant et al. 2005,

Kozma and Kroll 2010, 2012). Year, represented as a categorical variable, was included as a random effect, allowing the model intercept to vary by year. To account for spatial variation, we included the total number of shrubs in each plot, vegetation coverage above each nest, nest height, and an indicator variable of whether nests were in either spiny or non-spiny plants as fixed effects. We included study plot as a random effect to account for spatial variation not modeled with covariates (Hane et al. 2012). We also included a nest random effect, allowing the model intercept to vary by nest. We chose specific covariates because each has been associated with nest survival in previous studies of songbirds (Martin and Roper 1988, Götmark et al. 1995, Kozma and Mathews 1997, Noa et al. 2007, Aldinger et al. 2015). We centered and scaled all continuous covariates to have a mean of zero and a standard deviation of one: coverage, total shrubs, and nest height for the nest level and ordinal date for the visit level. The daily nest survival probability model was:

$$\text{logit}(s_{i,j}) = \alpha_0 + \gamma_{Plot_i} + \tau_{Year_i} + \varpi_{Nest_i} + \alpha_1 \cdot \text{Spine}_i + \alpha_2 \cdot \text{Total Shrubs}_i + \alpha_3 \cdot \text{Height}_i + \alpha_4 \cdot \text{Coverage}_i + \alpha_5 \cdot \text{Incubation}_{i,j} + \alpha_6 \cdot \text{Nestling}_{i,j} + \alpha_7 \cdot \text{Ordinal Date}_{i,j}$$

where Spine, Incubation, and Nestling are all indicator variables, taking the value of 1 if the argument is true and 0 otherwise, γ_{Plot_i} is a random intercept adjustment for each of the eight plots in our study, $\gamma_{Plot_i} \sim N(0, \sigma^2_{Plot})$; τ_{Year_i} is a random intercept adjustment for each of the 5 y of the study, $\tau_{Year_i} \sim N(0, \sigma^2_{Year})$; and ϖ_{Nest_i} is a random intercept adjustment for

each of the 265 nests, $\varpi_{Nest_i} \sim N(0, \sigma^2_{Nest})$. When summarizing the model, we calculated 90% credible intervals for coefficients and derived quantities because a 90% credible interval provides sufficient confidence around the estimates.

We used coefficient estimates to calculate daily and period survival probabilities (the probabilities that a nest survives a single day in a given stage and the entire nesting period, respectively). Given our assumption of a typical nesting period with 3 d for laying, 12 for incubation, and 10 for the nestling stage, for a total of 25 d, we approximated an ordinal date for each nesting stage by centering the full nesting period at the mean ordinal date for all nests and then calculating the median ordinal date for each individual stage. We used day 2 as the median for the nesting stage (median of day 1–3), day 9.5 as the median for the incubation stage (median of days 4–15), and day 20.5 as the median for the nestling stage (median of days 16–25). Centering the full nestling period (median of full period is day 13) on the mean ordinal date for all nests, which is ~154, we estimated the following ordinal dates for the medians of each stage: laying = 143, incubation = 150.5, and nestling = 161.5. Placing these ordinal dates on the same scale as the centered and scaled values used in the model by subtracting the mean (153.9) and dividing by the standard deviation (15.4), we use these ordinal date covariate values to calculate survival probabilities: laying = −0.703, incubation = −0.217, and nestling = 0.496. Using the coefficient estimates and the other nest specific covariates, we estimated the daily survival rate for nest i during each of the three stages, laying, incubation, and nestling, as:

$$s_{i,Laying} = \text{logit}^{-1}\left(\begin{array}{l} \alpha_0 + \gamma_{Plot_i} + \tau_{Year_i} + \varpi_{Nest_i} + \alpha_1 \cdot \text{Spine}_i + \alpha_2 \cdot \text{Total Shrubs}_i + \alpha_3 \cdot \text{Height}_i + \\ \alpha_4 \cdot \text{Coverage}_i + \alpha_7 \cdot -0.703 \end{array} \right)$$

$$s_{i,Incubation} = \text{logit}^{-1}\left(\begin{array}{l} \alpha_0 + \gamma_{Plot_i} + \tau_{Year_i} + \varpi_{Nest_i} + \alpha_1 \cdot \text{Spine}_i + \alpha_2 \cdot \text{Total Shrubs}_i + \alpha_3 \cdot \text{Height}_i + \\ \alpha_4 \cdot \text{Coverage}_i + \alpha_5 \cdot \text{Incubation}_i + \alpha_7 \cdot -0.217 \end{array} \right)$$

$$s_{i,Nestling} = \text{logit}^{-1}\left(\begin{array}{l} \alpha_0 + \gamma_{Plot_i} + \tau_{Year_i} + \varpi_{Nest_i} + \alpha_1 \cdot \text{Spine}_i + \alpha_2 \cdot \text{Total Shrubs}_i + \alpha_3 \cdot \text{Height}_i + \\ \alpha_4 \cdot \text{Coverage}_i + \alpha_6 \cdot \text{Nestling}_i + \alpha_7 \cdot 0.496 \end{array} \right)$$

where

$$\text{logit}^{-1}(x) = {e^x}/{(1 + e^x)}$$

Using the nest specific daily survival rates, we calculated the period survival probability, P, using the assumed stage lengths:

$$P_i = \left(s_{i,Laying}{}^3\right) \cdot \left(s_{i,Incubation}{}^{12}\right) \cdot \left(s_{i,Nestling}{}^{10}\right)$$

In addition to nest-specific daily survival rates and period survival probabilities, we compared survival rates of nests under different assumed conditions, e.g., in spiny plants versus plants with no spines, by calculating daily nest survival rates and period survival probabilities using the average value for the continuous variables. As with the continuous covariates, the random plot, year, and nest effects were taken as zero for γ_{Plot}, τ_{Year}, and ϖ_{Nest_i}. As with the nest specific survival probabilities, we used the median stage specific ordinal dates as a covariate:

$$s_{Laying,Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_1 \cdot \text{Spine} + \alpha_7 \\ \cdot - 0.703\right);$$

$$s_{Incubation,Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_1 \cdot \text{Spine} + \alpha_5 \\ \cdot \text{Incubation} + \alpha_7 \cdot -0.217\right);$$

$$s_{Nestling,Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_1 \cdot \text{Spine} + \alpha_6 \\ \cdot \text{Nestling} + \alpha_7 \cdot 0.496\right)$$

$$s_{Laying,Non-Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_7 \cdot -0.703\right)$$

$$s_{Incubation,Non-Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_5 \\ \cdot \text{Incubation} + \alpha_7 \cdot -0.217\right)$$

$$s_{Nestling,Non-Spine} = \text{logit}^{-1}\left(\alpha_0 + \alpha_6 \\ \cdot \text{Nestling} + \alpha_7 \cdot 0.496\right)$$

$$P_{Spine} = \left(s_{Laying,Spine}{}^3\right) \cdot \left(s_{Incubation,Spine}{}^{12}\right) \\ \cdot \left(s_{Nestling,Spine}{}^{10}\right)$$

$$P_{Non-spine} = \left(s_{Laying,Non-Spine}{}^3\right) \cdot \\ \left(s_{Incubation,Non-Spine}{}^{12}\right) \cdot \\ \left(s_{Nestling,NonSpine}{}^{10}\right)$$

We fit our model using JAGS (Plummer 2003) called from R (R Development Core Team, 2010) using the "jags" function from package R2jags (Su and Yajima 2012). We used an $N(4, 4)$ (mean, variance) prior distribution for the overall intercept coefficient, a *Uniform* (0.1, 2) prior distribution for the random effect standard deviations, and an $N(0, 3)$ prior distribution for all other coefficients. We used a prior distribution centered at 4 for the overall intercept because daily nest survival probabilities need to be sufficiently high for some nests to survive the full nesting period. Centering the prior distribution for the overall intercept at zero would mean that the daily survival probabilities were near 0.5 ($\text{logit}^{-1}(0) = 0.5$), but using a daily survival probability of 0.5 over the course of a 25-d nesting period gives a period survival probability of nearly zero. Using a prior distribution centered at 4 and a relatively large standard deviation allows the model to identify reasonable overall intercept values. We ran three Markov chains of length 200,000 with a burn-in period of 100,000 and 1/50 thinning. We assessed convergence using the Gelman-Rubin statistic (Gelman et al. 2004) and visual inspection of chains. All of our coefficient estimates showed Gelman-Rubin statistics between 1.001 and 1.02, which support our assumption of convergence. We provide code for the nest survival model (Appendix S1). A posterior predictive check (Appendix S2) to assess the model fit yielded no evidence for a lack of fit. We provide R code for the posterior predictive checks in Appendix S3 and nest survival data to run the nest survival model in Appendix S4. Values are provided as means ± 1 SD.

RESULTS

We found 297 Black-throated Sparrow nests and were able to use 265 to model nest survival. We were not able to use all nests because of unknown nest fates, data-collection errors, and missing vegetation measurements. Of the nests used, 48 (18%), 170 (64%), and 47 (18%) were found during the laying, incubation, and nestling stages, respectively. We located 29 nests in arroyos and 268 nests in uplands. The average number of visits to nests was 4.4 ± 2.3 (range = 1−10) and the average interval between nest visits was 3 ± 1.5 d (range = 1−13 d; N = 1160 intervals). Average clutch

size was 2.7 ± 0.6 eggs (range = 2–4 eggs; N = 278 nests), the average number of young fledged per successful nest was 2.2 ± 0.7 (range = 1–4 young; N = 107), and the average number of young fledged across all nests was 0.8 ± 1.2 (range = 0–4; N = 290). We found that 32% of eggs resulted in fledged young and an apparent nest success rate of 36%. Predation was the leading cause of nest failure, accounting for 86% of failed nests. Other causes of nest failure included 6% from unknown causes, 4% abandoned, 2% from weather (e.g., nestlings died in the nest from exposure), and 2% due to cowbirds. Brown-headed Cowbirds parasitized 19 nests for a parasitism rate of 7%. Only two parasitized nests resulted in a fledged cowbird.

Sparrows nested in 32 species of plants and 45% of nests were in plants with spinescent foliage. Average height of all nests was 27.9 ± 22.7 cm (range = 0–75 cm; N = 292) and average coverage of vegetation above the nest was 55 ± 30% (range = 2.5–87.5%; N = 290). The average number of shrubs within 5 m of nests was 92.4 ± 48.3 (range = 16–357; N = 292).

At the nest level, we found no evidence of a difference in period survival rate between nests in plants with and without spiny foliage (average difference = 0.040; 90% CRI: −0.069, 0.150). We did find that daily survival was associated negatively with vegetative cover over nests (Table 1, Fig. 1), but found no evidence for an association with nest height (Table 1, Fig. 2). At the nest-patch

Table 1. Parameter estimates from a multilevel nest survival model for Black-throated Sparrows in southern New Mexico, USA, 1993–1997.

Parameter	Level	Mean	90% credibility interval
Intercept (fixed effect)	Nest	4.230	3.215, 5.330
Vegetation coverage (fixed effect)	Nest	−0.217	−0.386, −0.053
Nest height (fixed effect)	Nest	−0.121	−0.290, 0.055
Spine (fixed effect)	Nest	0.120	−0.214, 0.447
Total shrub count (fixed effect)	Nest patch	−0.177	−0.335, −0.023
Ordinal date (fixed effect)	Visit	−0.389	−0.578, −0.217
Incubation (fixed effect)	Visit	−1.018	−2.001, −0.159
Nestlings (fixed effect)	Visit	−1.564	−2.550, −0.678
Plot 1 (random effect)	Study plot	−0.030	−0.585, 0.533
Plot 2 (random effect)	Study plot	−0.245	−1.010, 0.497
Plot 3 (random effect)	Study plot	0.683	0.104, 1.324
Plot 4 (random effect)	Study plot	0.234	−0.307, 0.814
Plot 5 (random effect)	Study plot	−0.386	−0.986, 0.176
Plot 6 (random effect)	Study plot	0.834	0.239, 1.504
Plot 7 (random effect)	Study plot	−0.639	−1.240, −0.084
Plot 8 (random effect)	Study plot	−0.375	−0.942, 0.183
Plot.sigma	Study plot	0.716	0.373, 1.258
Year 1 (random effect)	Study plot	−0.041	−0.422, 0.291
Year 2 (random effect)	Study plot	0.003	−0.352, 0.346
Year 3 (random effect)	Study plot	0.053	−0.303, 0.455
Year 4 (random effect)	Study plot	0.027	−0.376, 0.469
Year 5 (random effect)	Study plot	−0.021	−0.340, 0.285
Year.sigma	Study plot	0.286	0.108, 0.711
Nest.sigma[a]	Nest	0.504	0.149, 0.940

[a]We present nest.sigma as a summary of nest-specific random effects due to the space requirements for means for each of 265 nests. These estimates are available from the corresponding author upon request. Estimates for fixed effects are constant for all nests in the study; random effects are specific to the plot and year in which nests were observed. Fixed effects are interpreted as the additive effect, on the logit scale, for the given parameter for the average nest. Random effects are interpreted as random intercept adjustments to allow for correlation between nests observed within the same plot or year, and account for any unmeasured variation
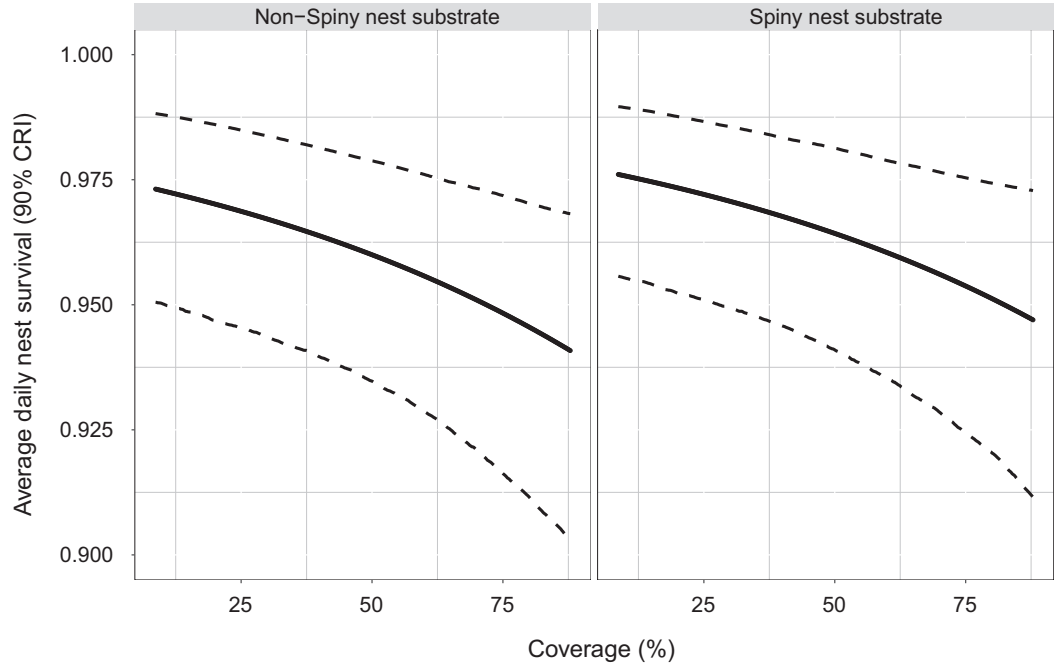
Fig. 1. Association between plant coverage of nests and daily survival rate for Black-throated Sparrows in southern New Mexico, USA, 1993–1997. Estimates are shown for nests in both non-spiny and spiny substrates. Plant coverage values were back transformed to the original scale using a standard deviation of 20 and a mean of 61.15.

level, we found a negative association between daily survival and total number of shrubs (Table 1, Fig. 3) and, at the visit level, a negative association between daily survival and date (Table 1, Fig. 4). We also found that daily survival rate was lower for the incubation and nestling stages than the laying stage (Table 1, Fig. 4). As a result, and due to differences in stage length, estimated period survival rate was substantially lower during both the incubation and nestling stages than the laying stage (Fig. 5). Estimated standard deviations for plot (0.716; 90% CRI: 0.373, 1.258), year (0.286; 90% CRI: 0.108, 0.711) and nest (0.504, 90% CRI: 0.149, 0.940) indicated variation at the study plot and nest level not accounted for by fixed effects (Table 1). We retained random effects in the model even though credible intervals contained zero for many plot, year, and nest-specific random effects (Table 1). If we had not included these random effects, we would be making inference under the unreasonable assumption that all nests (with identical covariate information) from all plots or all years behaved identically.

DISCUSSION

The nest-concealment hypothesis states that birds should locate their nests in areas with dense foliage and the probability of nest predation should decline as foliage density increases (Martin and Roper 1988, Borgmann and Conway 2015). However, the results of studies investigating this relationship have been equivocal (Borgmann and Conway 2015). Our results suggest that greater shrub density within 5 m of the nest was negatively associated with daily nest survival. In contrast, other investigators have reported that successful nests were located in areas of greater plant density (Kelly 1993, Liebezeit and George 2002, Smith et al. 2007, Schill and Yahner 2009). We offer three hypotheses that may explain our results. First, as shrub density increases, the ability of incubating/brooding females to detect approaching predators may
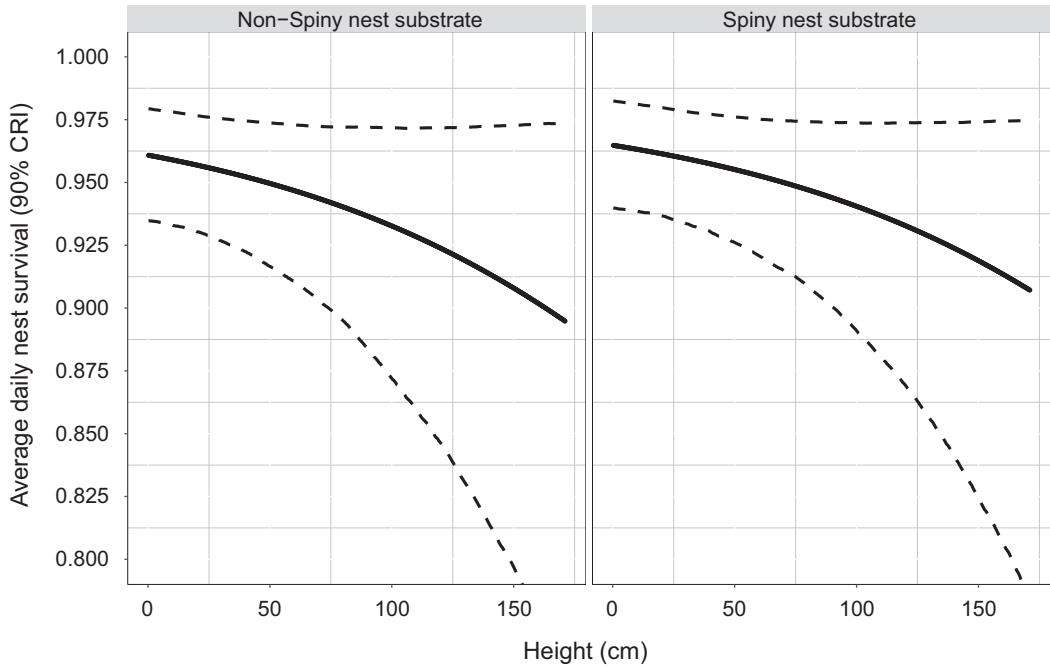
Fig. 2. Association between nest height and daily survival rate for Black-throated Sparrows in southern New Mexico, USA, 1993–1997. Estimates are shown for nests in both non-spiny and spiny substrates. Nest height values were back transformed to the original scale using a standard deviation of 22.81 and a mean of 27.76.

be reduced, thereby causing them to flush late and reveal a nest's location (Burhans and Thompson 2001). Next, if snakes and terrestrial mammals are important predators, nest concealment may have less influence on risk of predation because these predators find nests primarily through olfaction and parental activity (Eichholz and Koenig 1992, Burhans and Thompson 1998, Schmidt 1999). Finally, dense patches of shrubs may be searched more frequently by predators because such patches contain more potential sites where prey may reside (Martin and Roper 1988). Predators of songbird nests are typically generalists (Davis 2005, Weidinger 2008) and find food by searching in habitats with specific features rather than attempting to visually locate nests (Howlett and Stutchbury 1996, Schmidt et al. 2001, Cox et al. 2013). For example, snakes may search for nests in dense shrub patches more frequently because they can move easily among the branches of interconnecting shrubs. Furthermore, other prey such as rodents that also are potential nest predators may be more

abundant in dense shrub patches because they offer more abundant food and are safer from predators (Brown et al. 1988). Indeed, in our study area, Jorgensen et al. (1995) found that rodents in arroyos, where vegetation is patchily distributed, avoided open/exposed patches. Therefore, Black-throated Sparrows may experience lower daily nest survival because of incidental nest predation in dense shrub patches if snakes and other nest predators occur there more frequently (Schmidt et al. 2001, Borgmann et al. 2013).

We found no support for a difference in the survival rates of nests of Black-throated Sparrows in plants with spiny foliage versus those located in spineless plants. In our study area, we identified a diverse suite of potential nest predators including Swainson's Hawks (*Buteo swainsoni*), Barn Owls (*Tyto alba*), Greater Roadrunners (*Geococcyx californianus*), American Kestrels (*Falco sparverius*), Chihuahuan Ravens (*Corvus cryptoleucus*), Loggerhead Shrikes (*Lanius ludovicianus*), snakes (*Masticophis* spp., *Crotalus* spp., *Lampropeltis getula*, and *Pituophis catenifer*),
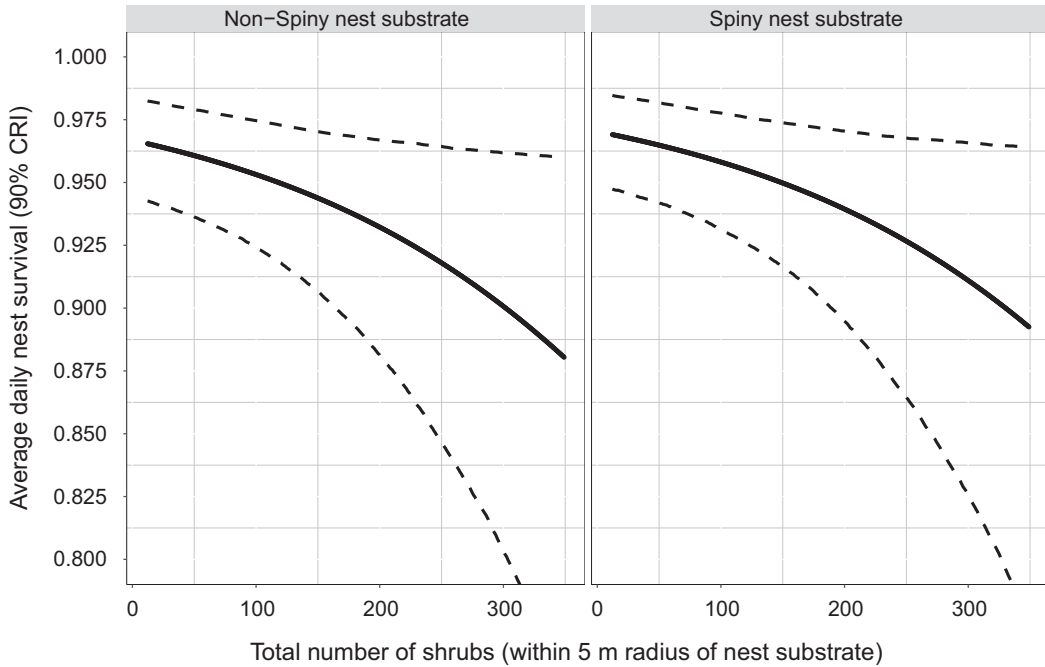
Fig. 3. Association between total number of shrubs in nest patches (within a 5-m radius centered on each nest) and daily survival rate for Black-throated Sparrows in southern New Mexico, USA, 1993–1997. Estimates are shown for nests in both non-spiny and spiny substrates. Total number of shrub values were back transformed to the original scale using a standard deviation of 47.7 and a mean of 87.45.

rodents (*Peromyscus* spp. and *Spermophilus* spp.), kit foxes (*Vulpes macrotis*), long-tailed weasels (*Mustela frenata*), American badgers (*Taxidea taxus*), and coyotes (*Canis latrans*). Spinescent plants may offer protection against large predators such as raptors, ravens, and canids, but offer less protection from small mammals and snakes because they can navigate the spines to reach nest contents (Austin et al. 1972, Ricketts and Ritchison 2000). Indeed, Mezquida and Marone (2002) found that nests in shrubs with thorns had higher rates of nest failure because the predators that accounted for most nest failures were birds that were able to move among thorns because they nest in thorny shrubs. In our study, most nest failures resulted from the disappearance of nest contents with no nest disturbance, suggesting that small mammals, snakes, and birds were likely responsible (Filliater et al. 1994, Howlett and Stutchbury 1996). However, avian predators are uncommon in our study area so we suspect that small mammals and snakes accounted for most nest predation. We acknowledge the

potential inaccuracy of inferring predators from nest remains (Larivière 1999, Pietz and Granfors 2000) and suggest further investigation to determine the important nest predators in desert shrublands.

We found no evidence for an association between nest height and daily nest survival. Black-throated Sparrows nest close to the ground (81% of nests ≤ 40 cm high) because most upland shrubs are short. This lack of variability in nest height may have prevented us from detecting a relationship between nest height and daily nest survival. In addition, plants such as bush muhly (*Muhlenbergia porteri*) and broom snakeweed (*Gutierrezia sarothrae*) are frequently present at the base of shrubs where Black-throated Sparrows nest. Locating their nests lower in shrubs where other plants are present may provide greater nest support and thermal protection. Although some studies have revealed that passerine nest survival increases with nest height (Burhans et al. 2002, Noa et al. 2007, Smith et al. 2007), our results support the findings of others that nest height does not
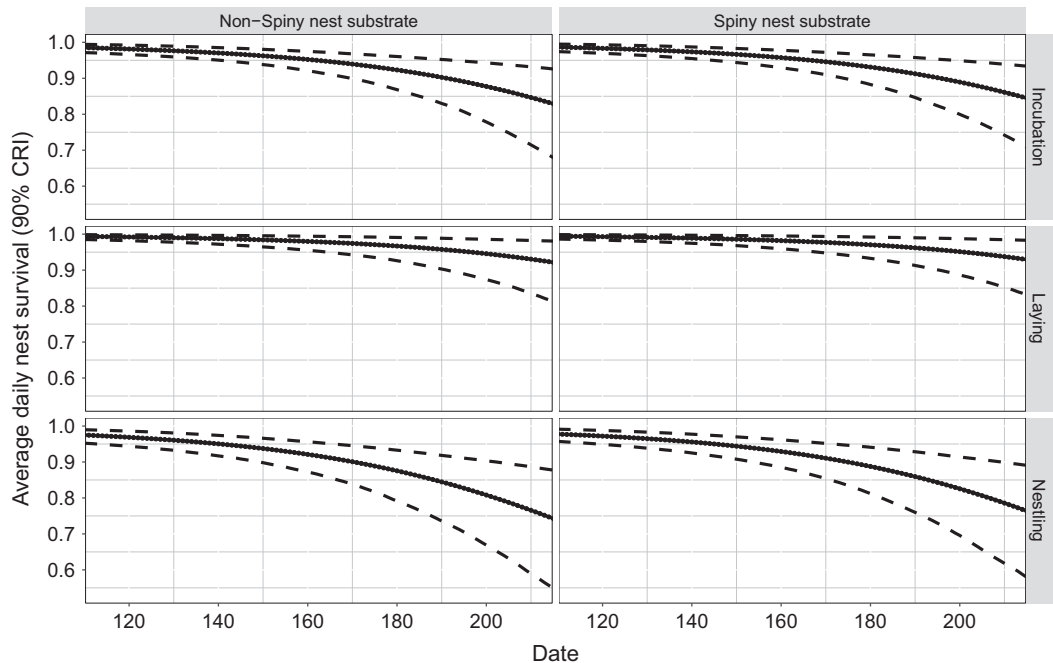
Nest Survival of Black-throated Sparrows

Fig. 4. Association between ordinal date, lay stage, and daily survival rate for Black-throated Sparrows in southern New Mexico, USA, 1993–1997. Estimates are shown for nests in both non-spiny and spiny substrates. Ordinal date values used for estimating survival rates were standardized using a mean of 153.85 and a standard deviation of 15.43.
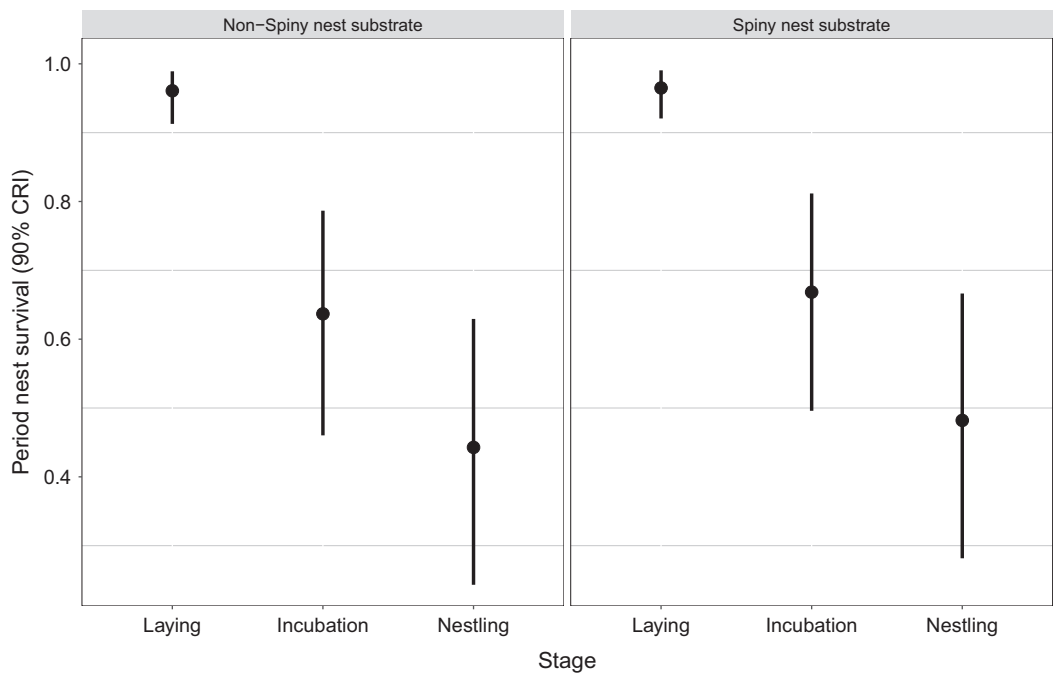

Fig. 5. Period survival rates by nesting stage for Black-throated Sparrows in southern New Mexico, USA, 1993–1997. Estimates are shown for nests in both non-spiny and spiny substrates.

influence nest survival (Howlett and Stutchbury 1996, Farnsworth and Simons 1999, Ricketts and Ritchison 2000, Bulluck and Buehler 2008).

We found that daily survival rates decreased as vegetative cover over nests increased. In contrast, other investigators have found that more concealed nests experience lower rates of predation (Martin and Roper 1988, Grant et al. 2006, Segura et al. 2012, Aldinger et al. 2015, although Smith et al. 2007, also found higher nest survival for less-concealed nests). Nesting close to the ground forces females to weigh the advantages of sitting tight and relying on camouflage to avoid revealing a nest's location or flushing, which might reveal a nest's location (Burhans and Thompson 2001). Overhead concealment of nests may be more important for reducing nest predation by avian predators (Segura et al. 2012). However, because avian predators are uncommon in our study area, sparrows may choose nest sites with less overhead cover, which would provide an escape route from terrestrial predators. This could allow incubating/brooding females to leave nests without revealing their location and reduce the risk of predation to themselves. In arid environments where rates of nest predation are high, species of birds that nest on or close to the ground have been found to place their nests in more exposed locations to reduce predation risk for incubating parents (Yanes et al. 1996, Tieleman et al. 2008).

At the visit level, we found evidence of a negative association between daily survival and date, supporting our prediction that daily survival probability would be higher earlier in the season. The results of recent studies have revealed that, as temperatures increase during the breeding season, rates of nest predation by some predators also increase (Sperry et al. 2008, Cox et al. 2013). For example, Cox et al. (2013) found that rates of nest predation by snakes increased with increasing temperatures, whereas rates of predation by mammals were virtually unchanged by an increase in temperature. Snakes become more active and exhibit improved locomotor performance in arboreal environments as temperatures increase (Gerald et al. 2008). In our study area, maximum daily temperatures increase throughout the nesting period and range from an average of 25.1°C in April to

34.9°C in June (Western Regional Climate Center at http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nmalam). Therefore, daily nest survival may decline throughout the breeding period as snakes and other predators become more active due to warmer temperatures. If so, higher temperatures resulting from climate change could contribute to more extended droughts that may cause Black-throated Sparrows to delay nest initiation (McCreedy and van Riper 2014). Delayed nest initiation would force sparrows to nest later when temperatures are higher and predators are more active, resulting in lower nest survival rates.

Daily survival rates in our study were lower during the incubation and nestling stages than during the egg-laying stage. The increased activity and greater olfactory cues from the presence of adults during the incubation stage, enhanced by the presence of young during the nestling period, could make it easier for predators such as snakes and mammals that rely on these cues to find nests. During egg-laying, nests are usually left unattended until the last egg is laid (Johnson et al. 2002), so there is little activity at nests. In addition, the egg-laying period is brief so there is less time for predators to find nests. The number of nest visits increases during incubation as females go to and from nests during foraging bouts, likely explaining the lower daily survival rates during this period. Previous studies of songbirds have also revealed that daily nest survival is high during egg laying and declines with the onset of incubation (Filliater et al. 1994, Grant et al. 2005, Kroll and Haufler 2009, Kozma and Kroll 2010). Similarly, nestling begging after hatching and an increase in parental activity during feeding by both adults may account for the lower daily survival we observed during the nestling stage (Haskell 1994, Martin et al. 2000, Muchai and du Plessis 2005, Heltzel and Earnst 2006).

The nests of Black-throated Sparrows are potentially exposed to a diverse predator community. When predator communities are diverse and have varied search strategies, the possibility of finding a safe nest site is reduced because all nest locations may be subject to similar predation risk (Filliater et al. 1994, Braden 1999, Mezquida 2004). Thus, females may employ a diversified bet-hedging strategy to spread risk when they locate their nests (Chalfoun and Schmidt 2012), and the

limited effect of spatial factors on daily nest survival in our study may be a result of this generalized nest location approach. A generalized nest location strategy may prevent predators from developing specific search images for sparrow nests because nests are not located in similar microhabitats (Martin and Roper 1988, Borgmann et al. 2013). Use of a variety of plant species as nest substrates may explain why Black-throated Sparrows are so abundant across diverse arid vegetation types throughout the desert southwest.

ACKNOWLEDGMENTS

LITERATURE CITED

ALDINGER, K. R., T. M. TERHUNE II, P. B. WOOD, D. A. BUEHLER, M. H. BAKERMANS, J. L. CONFER, D. J. FLASPOHLER, J. L. LARKIN, J. P. LOEGERING, K. L. PERCY, A. M. ROTH, AND C. G. SMALLING. 2015. Variables associated with nest survival of Golden-winged Warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. Avian Conservation and Ecology 10: 6.

AUSTIN, G. T., E. YENSEN, AND C. S. TOMOFF. 1972. Snake predation on Cactus Wren nestlings. Condor 74: 492.

BORGMANN, K. L., AND C. J. CONWAY. 2015. The nest-concealment hypothesis: new insights from a comparative analysis. Wilson Journal of Ornithology 127: 646–660.

———, ———, AND M. L. MORRISON. 2013. Breeding phenology of birds: mechanisms underlying seasonal declines in the risk of nest predation. PLoS ONE 8: e65909.

BRADEN, G. T. 1999. Does nest placement affect the fate or productivity of California Gnatcatcher nests? Auk 116: 984–993.

BROWN, J. S., B. P. KOTLER, R. J. SMITH, AND W. O. WIRTZ. 1988. The effects of owl predation on the foraging behavior of desert rodents. Oecologia 76: 408–415.

BUDD, L. F., R. B. AREND, J. W. HURST, AND V. H. ANDERSON. 1979. Fort Bliss environmental analysis and impact assessment. Photographic Interpretation Corporation, Hanover, NH.

BULLUCK, L. P., AND D. A. BUEHLER. 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. Auk 125: 551–559.

BURHANS, D. E., D. DEARBORN, F. R. THOMPSON III, AND J. FAABORG. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66: 240–249.

———, AND F. R. THOMPSON III. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. Condor 100: 663–672.

———, AND ———. 2001. Relationship of songbird nest concealment to nest fate and flushing behavior of adults. Auk 188: 237–242.

CHALFOUN, A. D., AND K. A. SCHMIDT. 2012. Adaptive breeding-habitat selection: is it for the birds?. Auk 129: 589–599.

COE, S. J., AND J. T. ROTENBERRY. 2003. Water availability affects clutch size in a desert sparrow. Ecology 84: 3240–3249.

COX, A., F. R. THOMPSON III, AND J. REIDY. 2013. The effects of temperature on nest predation by mammals, birds, and snakes. Auk 130: 784–790.

CUNNINGHAM, S. J., R. O. MARTIN, C. L. HOJEM, AND P. A. R. HOCKEY. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savannah: a study of Common Fiscals. PLoS ONE 8: e74613.

DAVIS, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107: 605–616.

DEARBORN, D. C., AND L. L. SANCHEZ. 2001. Do Golden-cheeked Warblers select nest locations on the basis of patch vegetation? Auk 118: 1052–1057.

EICHHOLZ, M. W., AND W. D. KOENIG. 1992. Gopher snake attraction to bird's nests. Southwestern Naturalist 37: 293–298.

FARNSWORTH, G. L., AND T. R. SIMONS. 1999. Factors affecting nesting success of Wood Thrushes in Great Smoky Mountain National Park. Auk 116: 1075–1082.

FIELDS, T. L., G. C. WHITE, W. C. GILGERT, AND R. D. RODGERS. 2006. Nest and brood survival of Lesser Prairie-Chickens in west central Kansas. Journal of Wildlife Management 70: 931–938.

FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96: 761–768.

GELMAN, A., J. B. CARLIN, H. S. STERN, AND D. B. RUBIN. 2004. Bayesian data analysis, 2nd ed. Chapman & Hall/CRC, Boca Raton, FL.

GERALD, G. W., M. J. MACKEY, AND D. L. CLAUSSEN. 2008. Effects of temperature and perch diameter on arboreal locomotion in the snake *Elaphe guttata*. Journal of Experimental Zoology 309A: 147–156.

GÖTMARK, R. T., D. BLOMQVIST, O. C. JOHANSSON, AND J. BERGKVIST. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? Journal of Avian Biology 26: 305–312.

GRANT, T. A., E. M. MADDEN, T. L. SHAFFER, P. J. PIETZ, G. B. BERKEY, AND N. J. KADRMAS. 2006. Nest survival of Clay-colored and Vesper sparrows

in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70: 691–701.

———, T. L. SHAFFER, E. M. MADDEN, AND P. J. PIETZ. 2006. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122: 661–672.

HANE, M. E., A. J. KROLL, J. R. JOHNSON, M. ROCHELLE, AND E. B. ARNETT. 2012. Experimental effects of structural enrichment on avian nest survival. Forest Ecology and Management 282: 167–174.

HARGROVE, L., AND J. T. ROTENBERRY. 2011. Breeding success at the range margin of a desert species: implications for a climate-induced elevational shift. Oikos 120: 1568–1576.

HASKELL, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proceedings of the Royal Society B 257: 161–164.

HELTZEL, J. M., AND S. L. EARNST. 2006. Factors influencing nest success of songbirds in aspen and willow riparian areas in the Great Basin. Condor 108: 842–855.

HOWLETT, J. S., AND B. J. STUTCHBURY. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. Auk 113: 1–9.

JAMES, F. C., AND H. H. SHUGART, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727–736.

JOHNSON, M. J., AND C. VAN RIPER III. 2004. Brown-headed Cowbird parasitism of the Black-throated Sparrow in central Arizona. Journal of Field Ornithology 75: 303–311.

———, ———, AND K. M. PEARSON. 2002. Black-throated Sparrow (*Amphispiza bilineata*). In: The Birds of North America (P. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

JORGENSEN, E. E., S. DEMARAIS, AND S. NEFF. 1995. Rodent use of microhabitat patches in desert arroyos. American Midland Naturalist 134: 193–199.

KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. Condor 95: 83–93.

KEYNAN, O., AND R. YOSEF. 2010. Annual precipitation affects reproduction of the Southern Grey Shrike (*Lanius meridionalis*). Wilson Journal of Ornithology 122: 334–339.

KEYSER, A. J., M. T. KEYSER, AND D. E. L. PROMISLOW. 2004. Life-history variation and demography in Western Bluebirds (*Sialia mexicana*). Auk 121: 118–133.

KOZMA, J. M. 1995. Neotropical migrant and Chihuahuan Desert bird community use of arroyo-riparian habitat and adjacent upland. M.S. thesis, Texas Tech University, Lubbock, TX.

———, AND A. J. KROLL. 2010. Nest survival of Western Bluebirds using tree cavities in managed ponderosa pine forests of central Washington. Condor 112: 87–95.

———, AND ———. 2012. Woodpecker nest survival in burned and unburned managed ponderosa pine forests of the northwestern United States. Condor 114: 173–184.

———, AND N. E. MATHEWS. 1997. Breeding bird communities and nest plant selection in Chihuahuan Desert habitats in south-central New Mexico. Wilson Bulletin 109: 424–436.

KROLL, A. J., AND J. B. HAUFLER. 2009. Age and clutch size variation in Dusky Flycatcher nest survival. Journal of Ornithology 150: 409–417.

KUS, B. E., B. L. PETERSON, AND D. H. DEUTSCHMAN. 2008. A multiscale analysis of nest predation on Least Bell's Vireos (*Vireo bellii pusillus*). Auk 125: 277–284.

LARIVIÈRE, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101: 718–721.

LIEBEZEIT, J. R., AND T. L. GEORGE. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. Condor 104: 507–517.

MANOLIS, J. C., D. E. ANDERSON, AND F. J. CUTHBERT. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117: 615–626.

MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? In: Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III AND D. W. Johnston, eds.), pp. 455–473. Smithsonian Institution Press, Washington, D.C.

———, C. PAINE, C. J. CONWAY, W. M. HOCHACHKA, P. ALLEN, AND W. JENKINS. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.

———, AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

———, J. S. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society B 267: 2287–2293.

MCCREEDY, C., AND C. VAN RIPER III. 2014. Drought-caused delay in nesting of Sonoran Desert birds and its facilitation of parasite- and predator-mediated variation in reproductive success. Auk 132: 235–247.

MEZQUIDA, E. T. 2004. Nest site selection and nesting success of five species of passerines in a South American open *Prosopis* woodland. Journal of Ornithology 145: 16–22.

———, AND L. MARONE. 2002. Microhabitat structure and avian nest predation risk in an open Argentinean woodland: an experimental study. Acta Oecologica 23: 313–320.

MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN. 2006. Wildlife-habitat relationships, 3rd ed. Island Press, Washington, D.C.

MUCHAI, M., AND M. A. DU PLESSIS. 2005. Nest predation of grassland bird species increases with parental activity at the nest. Journal of Avian Biology 36: 110–116.

MURRAY, B. G., Jr. 2000. Measuring annual reproductive success in birds. Condor 102: 470–473.

MYERS, L. M. 1998. The influence of habitat and predation on nesting assemblages of breeding birds in the northern Chihuahuan Desert. M.S. thesis, Texas Tech University, Lubbock, TX.

NARANJO, L. G., AND R. J. RAITT. 1993. Breeding bird distribution in Chihuahuan Desert habitats. Southwestern Naturalist 38: 43–51.

NOA, L. A., D. H. HIRTH, T. M. DONOVAN, AND D. CIMPRICH. 2007. Demographic differences of Black-capped Vireos in 2 habitat types in central Texas. Journal of Wildlife Management 71: 1042–1049.

PARKER, K. C. 1986. Partitioning of foraging space and nest sites in a desert shrubland bird community. American Midland Naturalist 115: 255–267.

PIDGEON, A. M., V. C. RADELOFF, AND N. E. MATHEWS. 2003. Landscape-scale patterns of Black-throated Sparrow (*Amphispiza bilineata*) abundance and nest success. Ecological Applications 13: 530–542.

PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and nest fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64: 71–87.

PLUMMER, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: 3rd International Workshop on Distributed Statistical Computing (DSC 2003) (K. Hornik, F. Leisch, and A. Zeileis, eds.), pp. 20–22. Austrian Association for Statistical Computing, Vienna, Austria.

RAITT, R. J., AND R. L. MAZE. 1968. Densities and species composition of breeding birds of a creosote bush community in southern New Mexico. Condor 70: 193–205.

R DEVELOPMENT CORE TEAM. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RICKETTS, M. S., AND G. RITCHISON. 2000. Nesting success of Yellow-breasted Chats: effects of nest site and territory vegetation structure. Wilson Bulletin 112: 510–516.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9: 1–48.

SCHILL, K. L., AND R. H. YAHNER. 2009. Nest-site selection and nest survival of early successional birds in central Pennsylvania. Wilson Journal of Ornithology 121: 476–484.

SCHMIDT, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. Oikos 85: 151–160.

———, J. R. GOHEEN, AND R. NAUMANN. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. Ecology 82: 2937–2947.

SCHMIDT, J. H., J. A. WALKER, M. S. LINDBERG, D. S. JOHNSON, AND S. E. STEPHENS. 2010. A general Bayesian hierarchical model for estimating survival of nests and young. Auk 127: 379–386.

SEGURA, L. N., D. A. MASSON, AND M. G. GANTCHOFF. 2012. Microhabitat nest cover effect on nest survival of the Red-crested Cardinal. Wilson Journal of Ornithology 124: 506–512.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121: 526–540.

SHREVE, F. 1942. The desert vegetation of North America. Botanical Review 8: 195–246.

SIEPIELSKI, A. M., A. D. RODEWALD, AND R. H. YAHNER. 2001. Nest site selection and nesting success of the Red-eyed Vireo in central Pennsylvania. Wilson Bulletin 113: 302–307.

SMITH, L. A., E. NOL, D. M. BURKE, AND K. A. ELLIOTT. 2007. Nest-site selection of Rose-breasted Grosbeaks in southern Ontario. Wilson Journal of Ornithology 119: 151–161.

SMYTH, M., AND G. A. BARTHOLOMEW. 1966. The water economy of the Black-throated Sparrow and the Rock Wren. Condor 68: 447–458.

SPERRY, J. H., R. G. PEAK, D. A. CIMPRICH, AND P. J. WEATHERHEAD. 2008. Snake activity affects seasonal variation in nest predation risk. Journal of Avian Biology 39: 379–383.

SU, Y.-S., AND M. YAJIMA [online]. 2012. R2jags: a package for running Jags from R. <http://CRAN. R-project.org/package=R2jags> (Accessed 14 April 2017).

TIELEMAN, B. I., H. J. VAN NOORDWUK, AND J. B. WILLIAMS. 2008. Nest site selection in a hot desert: trade-off between microclimate and predation risk. Condor 110: 116–124.

———, J. B. WILLIAMS, AND G. H. VISSER. 2004. Energy and water budgets of larks in a life history perspective: parental effort varies with aridity. Ecology 85: 1399–1410.

TOMOFF, C. S. 1974. Avian species diversity in desert scrub. Ecology 55: 396–403.

VERHULST, S., J. H. VAN BALEN, AND J. M. TINBERGEN. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? Ecology 76: 2392–2403.

WEIDINGER, K. 2008. Identification of nest predators: a sampling perspective. Journal of Avian Biology 39: 640–646.

YANES, M., J. HERRANZ, AND F. SUÁREZ. 1996. Nest microhabitat selection in larks from a European semi-arid shrub-steppe: the role of sunlight and predation. Journal of Arid Environments 32: 469–478.

ZIMMER, K. J. 1983. The Foraging Ecology of Nesting Black-throated Sparrows. M. S. thesis, New Mexico State University, Las Cruces, NM.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. R code for Bayesian nest survival model.

Appendix S2. Details of posterior predictive checks for Bayesian nest survival model for Black-throated Sparrow nest survival data, New Mexico, USA, 1993 - 1997.

Appendix S3. R code for posterior predictive checks for Bayesian nest survival model.

Appendix S4. Black-throated Sparrow nest survival data, New Mexico, USA, 1993 - 1997.