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RESEARCH ARTICLE

Northern bobwhite breeding season and nest survival are greater on native grasslands

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Abstract

Northern bobwhites (*Colinus virginianus*) are declining across their range. Population recovery requires a better understanding of the influence of management strategies and land cover on specific demographic components of full annual cycle population dynamics. We used known-fate daily survival models to relate adult breeding season survival and nest survival to land cover composition, woody cover, and management actions on 5 study sites in southwest Missouri, USA. We collected 3,516 observations of daily nest survival from 364 bobwhite nests for 7,509 exposure days and 34,386 observations of adult survival from 955 bobwhites for 85,225 exposure days during breeding seasons in 2014–2018. The most supported model for nest and adult breeding season survival included environmental covariates for percent native grass and agricultural cover, distance to shrub, and distance to tree. Both nest and adult breeding season survival were positively related to distance to trees. Nest survival was negatively related to percent agricultural crop cover. Areal nest and adult breeding season survival were greater on native grassland sites compared to conservation areas that maintained small units of strip crop and wooded cover. Management to sustain or expand native grass cover and reduce tree cover should benefit bobwhite nest survival and adult breeding season survival in the landscapes we studied.

KEYWORDS

breeding season, *Colinus virginianus*, habitat management, native grasslands, nest survival, Northern bobwhite

The northern bobwhite (*Colinus virginianus*; bobwhite) is an economically important upland gamebird of the eastern United States. While bobwhite occupy a variety of early successional landscapes, habitat loss, fragmentation, and degradation have resulted in long-term, range-wide population declines (Leopold 1931, Brennan 1991, Hernández et al. 2013). Bobwhite population decline has accelerated over the past 15 years in Missouri, USA (Sauer et al. 2017). Purposeful management for bobwhites can support local population stability despite range-wide declines (McConnell et al. 2018). For some bobwhite populations, growth is sensitive to breeding season adult survival and number of young hatched (Folk et al. 2007, Sandercock et al. 2008, Williams et al. 2012). These vital rates are sensitive to vegetation type, habitat management, and land cover composition (Roseberry and Sudkamp 1998, Janke et al. 2015, Malone et al. 2022, Sinnott et al. 2022, Thompson et al. 2022). Population recovery on altered landscapes requires a better understanding of the influence of land cover composition and management strategies on these components of full annual cycle population dynamics. Many studies report seasonal survival and nesting success; however, few studies have used statistical models to directly relate multiple vegetation features and management practices directly to breeding season adult survival or nesting success.

Bobwhite breeding habitat typically consists of open, herbaceous cover and a lesser component of short woody cover. Grassland cover and grasslands that provide taller canopies, more forb and shrub cover, and less bare ground can increase nesting success and breeding season survival (Lusk et al. 2006, Lohr et al. 2011, Potter et al. 2011). Additionally, disturbances such as fire, grazing, disking, and herbicide applications may increase brood and adult summer survival (Peters et al. 2015, Sinnott et al. 2022). But relationships between breeding season vital rates and vegetation structure, composition, and management may vary based on region and scale of evaluation (Taylor et al. 1999*b*, Townsend et al. 2001, Brooke et al. 2017).

Predation is a substantial source of mortality for bobwhite chicks in summer and juveniles and adults in fall and winter in Missouri (Mosloff 2020, Sinnott et al. 2022). Land cover composition and land management practices influence the suitability of landscapes for predators, and consequently predation risk and demographic rates of bobwhite occupying those landscapes (Rectenwald et al. 2021, Peterson et al. 2022). Trees can harbor predators such as Virginia opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), and raptors (Dijak and Thompson 2000, Byrne and Chamberlain 2011). Racoons are more abundant in agricultural landscapes, especially along forest edges adjacent to agricultural fields (Pedlar et al. 1997, Dijak and Thompson 2000). Nest proximity to features such as trees, roads, or human structures can increase the likelihood of encounters with raccoons or striped skunks (*Mephitis mephitis*; Peterson et al. 2022). Shrubs can provide escape cover for bobwhites from predators (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). Successful bobwhite broods in Missouri showed stronger selection for areas with greater shrub cover and distance to trees than broods that failed (Sinnott et al. 2021). Additionally, bobwhites in Missouri selected sites closer to tree cover in fall and winter; however, survival was lower closer to tree cover, creating a potential ecological trap (Mosloff 2020).

We investigated bobwhite demography across 5 sites that ranged from predominately large patches of native grassland managed with prescribed fire and grazing to sites consisting of a mix of smaller patches of grassland, cropland, and woody cover. A site-level, full annual cycle bobwhite demographic analysis revealed sites with larger continuous tracts of native grassland cover had greater adult breeding season and nest survival compared to sites with mixed cover types (Sinnott et al. 2023*b*). Our objectives here were to further evaluate variation in breeding season demography among sites by determining relationships between management actions and vegetation composition on bobwhite nest and adult breeding season survival. We used known-fate daily survival models to relate adult breeding season survival and nest survival to vegetation composition, woody cover, and management actions. We predicted that adult breeding-season survival and nest survival would be positively related to the amount of grassland managed by grazing and burning, shrub cover, and distance to mature trees. We also predicted that survival would be negatively related to distance to shrub cover and the amount of agricultural crop and mature tree cover. We reasoned that the disturbed grassland and shrub provided suitable cover and protection from predators, whereas mature tree cover provided refuge or perch sites for predators.

STUDY AREA

We studied bobwhite adult and nest survival in the eastern tallgrass prairie region of southwest Missouri from 1 May through 30 September 2014–2018 (Figure 1). This region's rolling plains were once tallgrass prairie, dominated by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*) and Indian grass (*Sorghastrum nutans*) interspersed with oak (*Quercus* spp.) woodlands and savannas. Dominant avifauna on study sites include mourning dove (*Zenaida macroura*), American goldfinch (*Spinus tristis*), field sparrow (*Spizella pusilla*), and eastern meadowlark (*Sturnella magna*). Common nest predators of bobwhites include, raccoons, skunks, opossums, and snakes (Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005, Harris and O'Connell 2023). Elevation ranged from approximately 249 m to 385 m. While historical prairies in the region have been largely converted to cool-season pastures and row crop fields, areas of southwest Missouri were identified by the National Bobwhite Conservation Initiative as having high potential for bobwhite recovery (Palmer et al. 2011).

Regional climate was characterized by hot, humid summers and cool, relatively dry winters. Thirty-year average annual precipitation was 116.0 cm and most rainfall occurred between April and June (77.7 cm; PRISM Climate Group 2021). Thirty-year average monthly temperatures ranged from 0.36°C (−5.25°C average minimum, 5.96°C average maximum) in January to 25.43°C (19.04°C average minimum, 31.89°C average maximum) in August (PRISM Climate Group 2021).

We studied breeding season demography on 5 sites: Shawnee Trail Conservation Area (1,471 ha; Shawnee Trail), Robert E. Talbot Conservation Area (1,764 ha; Talbot), Wade and June Shelton Memorial Conservation Area (130 ha; Shelton), Stony Point Prairie Conservation Area (516 ha including 169 ha of adjacent private land;

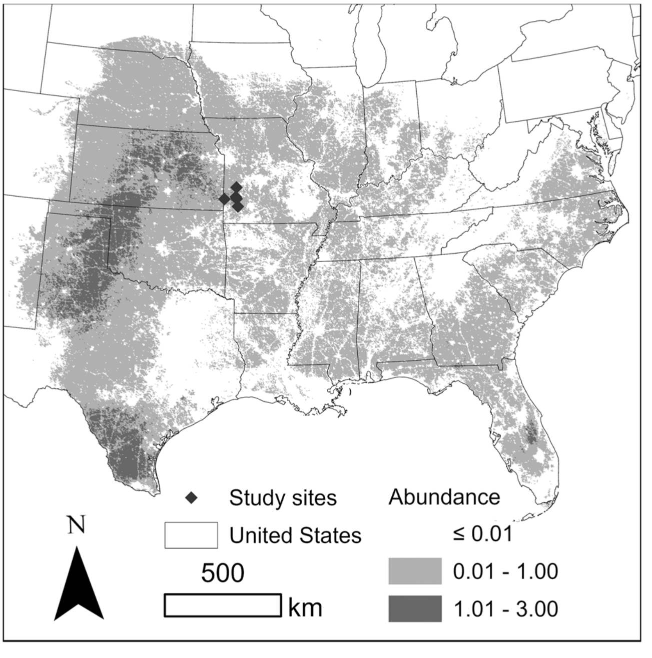

FIGURE 1 Northern bobwhite's distribution (grey) and the 5 study sites (♦) in which we estimated bobwhite breeding season survival and nest survival in southwest Missouri, USA, 2014–2018. Mean relative abundance is estimated as the number of bobwhites detected by an average eBirder during 1 hour, traveling 1 km at the optimal time for bobwhite detection (Fink et al. 2022). Study sites managed by Missouri Department of Conservation included Shawnee Trail and Robert E. Talbot conservation areas, Shelton Memorial Prairie, Stony Point Prairie, and Wah'Kon-Tah Prairie.

Stony Point), and Wah'Kon-Tah Prairie (1,226 ha). Shawnee Trail and Talbot were intensively managed sites composed of small units (<1–24 ha) of food plots, woody vegetation, grassland, and some larger cropland and grassland units (Figure 2). Management practices consisted of prescribed grazing, mowing, and burning of grassland units and habitat improvement practices such as planting food plots or crop fields and maintaining woody strip cover (Figure 2). Shelton, Stony Point, and Wah'Kon-Tah Prairie were >80% native grassland; they had no food plots or cropland and were managed by fire, grazing, and brush hogging, which created heterogeneity in grassland composition and structure and varying amounts of scattered shrub cover (Figure 2). Prescribed burning and conservation grazing used low-intensity grazing of 1 animal unit (454 kg of cattle) per 1.6–2 ha for 90 to 120 days from April to August and grazing units were rested every 1–4 years depending on grazing management. One-third of a unit was burned annually or biannually with rest periods at the end of a burn cycle or after each burn in a burning cycle. Prescribed burns occurred September–April.

METHODS

We captured bobwhite using funnel traps baited with cracked corn and milo in February and March of each year (Stoddard 1931). We pre-baited capture sites for 4–10 days and placed traps at a site when there was evidence bobwhite were using a site. We attached a uniquely numbered leg band and necklace style radio-transmitter with mortality signal that weighed 5–6 g (model AWE-QII, American Wildlife Enterprises, Monticello, FL, USA) to captured birds (Brogan et al. 2022). Radio-transmitters had an expected battery life of 9 months. We located birds approximately 3 times/week by homing in on birds and recorded locations on a hand-held global positioning system unit along with the bird's status as alive or dead while attempting to avoid flushing the bird. We located the transmitter within 1 day when we detected a mortality signal and determined the proximate cause of mortality based on evidence at the recovery site and transmitter condition.

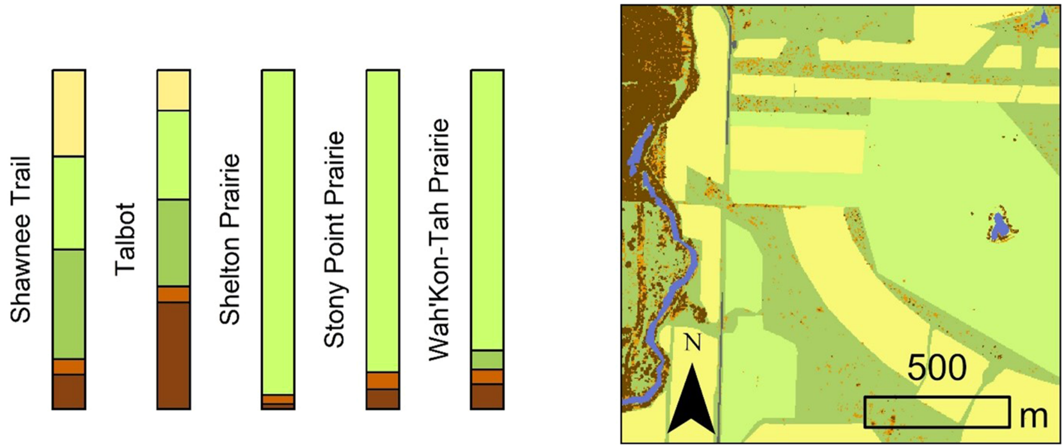

FIGURE 2 Composition of herbaceous and woody vegetation among the 5 study sites in which we estimated nest survival and adult breeding season survival of northern bobwhites in southwest Missouri, USA, 2014–2018. All sites included native grassland cover (light green) and shrub cover (orange). Two intensively managed sites incorporated agricultural cover (yellow) as strip crops and food plots. Most sites had a smaller component of non-native grassland cover (dark green), and tree cover (brown). Shawnee Trail and Robert E. Talbot conservation areas employed fine-scale management practices that included strip crops, food plots, and linear wooded edges among grassland units. Shelton Memorial, Stony Point, and Wah'Kon-Tah Prairie were continuous tracts of remnant or reconstructed prairies managed with fire, grazing, and mowing to maintain native grassland habitat.

We located nests during the breeding season from 1 May–30 September when we tracked adults to the same location on consecutive visits. We tracked incubating birds 3–5 times per week. If an adult was at a nest, we assumed it was active and incubating. If an adult was not at a nest, we inspected the nest and verified the status (e.g., active, hatched, or failed) and the number of eggs. We monitored most nests daily within a couple days of the estimated hatch date. We classified a nest as successful during the interval from the previous visit to the current visit if it was active (incubated) or if it hatched during the interval as evident by ≥1 eggshell with evidence of pipping or chicks located with the adult. We considered nests depredated if there were strewn and crushed eggshell fragments and obvious disturbance of the nest bowl. We classified nests as abandoned if the incubating individual did not return to the nest after 5 consecutive days. We summarized nest interval data for each nest into 2 intervals that represented the period from the first location determined to be incubating to the last location when known active and the interval from the last location known active to the final fate (e.g., hatched, depredated, abandoned).

Environmental covariates

We quantified local cover type composition as percent cover within a 100-m radius of each bird and nest location. While bobwhites likely respond to vegetation composition and structure at micro and macro scales (Taylor et al. 1999*a*, Yeiser et al. 2021, Sinnott et al. 2023*b*), we restricted our scale of interest to a radius in which vegetation composition and structure could vary daily with movements of individual bobwhites and that captured proximity of vegetation features associated with predator risk (Peterson et al. 2022, Sinnott et al. 2022). We selected a scale of interest based on prior knowledge of bobwhite and predator movements and vegetation associations, but we did not identify the optimal scale to evaluate demographic–environmental relationships (Monroe et al. 2022).

We delineated polygons that classified annual management activities and herbaceous cover types across the study extent using field observations and National Agriculture Imagery Program data in ArcMap10.4.1 (U.S. Army Corps of Engineers 2015, 2016; Esri, Redlands, CA, USA). We then overlayed the management and herbaceous cover type maps with shrub and tree cover classified using light detection and ranging data (LiDAR). We used cropland data layers (U.S. Department of Agriculture 2018) to classify a limited area of remote private lands surrounding public conservation areas where property access was limited. The final maps of annual management activities, herbaceous, and woody cover had a 3.6-m resolution, which matched the grain at which LiDAR data best classified shrub and tree cover.

We classified herbaceous cover types as native grasslands, non-native grasslands, or agricultural crop cover. Native grasslands included remnant and reconstructed prairies and native warm-season grass plantings that included grasses such as big bluestem and little bluestem, and forbs such as prairie blazing star (*Liatris pycnostachya*) and pale purple coneflower (*Echinacea pallida*). Native grassland management units were 10–55 ha. Non-native grasslands included cool-season pastures on surrounding private lands (primarily tall fescue [*Festuca arundinacea*]), and mixed grasslands that included old fields, native and non-native grasses, and sericea lespedeza (*Lespedeza cuneata*) or ragweed (*Ambrosia* spp.). We characterized grassland management practices for each field or management unit as burned, grazed, or burned and grazed if these practices occurred within the previous 2 years. We characterized grasslands as idle if not grazed or burned in the previous 2 years. Agricultural crops included soybean, corn, sunflower, and winter wheat. Agricultural units ranged in size from <1 ha to 25 ha on public lands and could exceed 120 ha on surrounding private lands.

We used LiDAR data to classify vegetation 0.7–3.5 m tall as shrubs and vegetation 3.5–40 m tall as trees (Sinnott et al. 2022). We quantified the percent composition of herbaceous cover types, shrubs, and trees within 100 m of nest and adult locations and measured Euclidean distance (m) from nest or bird to the nearest woody vegetation in ArcMap10.4.1 using the near proximity analysis tool (Esri). Common shrub species included plum (*Prunus* spp.) and sumac (*Rhus* spp.), and dominant trees included oaks.

Survival analysis

The development of a flexible generalized linear mixed model to estimate survival from nest monitoring and radio-tracking data have provided a rigorous framework for relating survival to intrinsic (sex, age), temporal (day of year, nest attempt, season, year), and environmental covariates (nest site, patch, and landscape characteristics; Dinsmore et al. 2002, Rotella et al. 2004). Logistic-exposure models are tailored to the interval nature of nest monitoring and radio-tracking observations, which are typically collected at daily or irregular multiday intervals (Shaffer 2004). The recent extension of these models to a Bayesian framework allows development of more complex models with fixed and random effects that provide reasonable estimates of model fit and uncertainty (Schmidt et al. 2010).

We used observations of birds fitted with radio transmitters from 1 May–30 September to estimate adult breeding season survival. We right-censored observations for individuals that experienced transmitter signal loss or dropped collars but included observations up to the last observation of known fate (Tanner et al. 2019). We used observations of nests attended by radio-marked adults to estimate nest survival. Nest monitoring began with the first observation of an incubating adult and continued to the final fate of the nest. We estimated daily adult and nest survival probability (P_i) based on observations of individual bird's or nest's status (alive or dead, successful or failed, respectively; y_i), the days elapsed since the previous observation (t), and the relationship between the probability of survival across an interval (s) and associated effects (β) of intrinsic, temporal, and environmental covariates (X; Shaffer 2004, Sinnott et al. 2022).

$$y_i \sim \text{Bernoulli}(P_i) \tag{1}$$

$$P_i = s_i^{t_i} \tag{2}$$

$$logit(s_i) = \beta X_i \tag{3}$$

We standardized values of continuous environmental variables to mean 0 and 1 unit of standard deviation. We ensured predictor variables in a model had a variance inflation factor <2.5 to avoid multicollinearity. We fit survival models in a Bayesian framework in Program R version 3.6.1 (R Core Team 2023) using JAGS (Plummer 2003) via the JagsUI package (Kellner 2021). We specified vague priors for normally distributed parameters with mean 0 and precision 0.001. We ran models using 3 chains, each contained 10,000 iterations including a burn-in of 4,000, and a thin rate of 3, yielding 6,000 posterior samples for each parameter. We evaluated model convergence by checking for $\hat{R} < 1.1$ for all model parameters (Gelman and Hill 2007) and inspected trace plots to check that chains were well mixed (Link and Barker 2010). We also assessed goodness of fit for each model by calculating posterior predictive P-values. We interpreted adequate model fit to our data if the proportion of posterior simulations that equaled or exceeded the realized value was >0.10 and <0.90.

We evaluated support for our competing hypotheses by ranking models based on leave-one-out cross-validation information criteria (LOOIC), which we calculated in R using the package loo (Vehtari et al. 2017, 2023). We evaluated support for parameter effects based on f values, which are the proportion of posterior samples with the same sign as the mean and can be interpreted as the probability an effect was negative or positive. We derived estimates of 154-day adult breeding season period survival and 23-day nest period survival across gradients of grassland and agricultural cover and shrub and tree proximity by varying each environmental covariate of interest while holding all others at their mean then exponentiating daily estimates of survival across the breeding season or peak nesting period. We produced spatial predictions of period survival at Talbot, an intensively managed site, and Wah'Kon-Tah, a managed native grassland site, using the raster calculator tool in ArcGIS using mean estimates of environmental effects from the linear predictor of the top model and spatial covariate values from environmental rasters.

RESULTS

We collected 3,516 observations of daily nest survival from 459 nests incubated by 364 bobwhites for 7,509 exposure days across 5 study sites in southwest Missouri from 2014 to 2018 (Sinnott et al. 2023*a*). Interval lengths for nest survival observations averaged 2.1 days and ranged from 1–13 days. Two hundred eighty-six nests failed, and 173 nests successfully hatched young. The primary cause for failure was predation, but abandonment and

TABLE 1 Candidate models relating nest survival of northern bobwhites to land cover composition, sex of incubating adults, site, time of year, and annual variation in southwest Missouri, USA, 2014–2018. Models are ranked by leave-one-out cross-validation information criteria (LOOIC). We also report differences (Δ) between candidate models and the top model in LOOIC and expected log pointwise predictive density (ELPD) and standard errors (SE) around LOOIC and ELPD calculations. All models included fixed effects for sex and quadratic day of year and random effects for site and year.

Rank	Model	LOOIC (SE)	ΔLOOIC	ΔELPD (SE)
1	Native grass + agriculture + log distance to shrub + log distance to tree + sex + day + day^2 + conservation area + year	1,966.6 (80.9)	0.0	0.0 (0.0)
2	Idle native grass + grazed native grass + burned native grass + burned and grazed native grass + agriculture + log distance to shrub + log distance to tree + sex + day + day^2 + conservation area + year	1,969.2 (81.1)	2.6	1.3 (2.0)
3	Native grass + agriculture + log % shrub + log % tree + sex + day + day^2 + conservation area + year	1,974.1 (80.8)	7.5	3.8 (4.5)
4	Native grass + agriculture + distance to shrub + distance to shrub^2 + distance to tree + distance to tree^2 + sex + day + day^2 + conservation area + year	1,980.5 (81.1)	13.9	7.0 (3.2)
5	Sex + day + day^2 + conservation area + year	1,986.2 (80.7)	19.6	9.8 (5.8)

TABLE 2 Candidate models relating adult breeding-season survival of northern bobwhites to land cover composition, sex of incubating adults, site, time of year, and annual variation in southwest Missouri, USA, 2014–2018. Models are ranked by leave-one-out cross-validation information criteria (LOOIC). We also report differences (Δ) between candidate models and the top model in LOOIC and expected log pointwise predictive density (ELPD) as well as standard errors (SE) around LOOIC and ELPD calculations. All models included fixed effects for sex and quadratic day of year and random effects for site and year.

Rank	Model	LOOIC (SE)	ΔLOOIC	ΔELPD (SE)
1	Native grass + agriculture + log distance to shrub + log distance to tree + sex + day + day^2 + conservation area + year	4,741.8 (179.0)	0.0	0.0
2	Idle native grass + grazed native grass + burned native grass + burned and grazed native grass + agriculture + log distance to shrub + log distance to tree + sex + day + day^2 + conservation area + year	4,746.2 (179.2)	4.4	2.2 (1.5)
3	Native grass + agriculture + distance to shrub + distance to shrub^2 + distance to tree + distance to tree^2 + sex + day + day^2 + conservation area + year	4,761.2 (179.7)	19.4	9.7 (4.7)
4	Native grass + agriculture + log % shrub + log % tree + sex + day + day^2 + conservation area + year	4,768.9 (179.9)	27.1	13.6 (5.3)
5	Sex + day + day^2 + conservation area + year	4,774.5 (180.0)	32.7	16.4 (7.0)

vehicles or farming equipment also led to nest failure. Bobwhite nest predators included the western ratsnake (*Pantherophis obsoletus*), Great Plains ratsnake (*P. emoryi*), raccoon, opossum, striped skunk, and coyote (*Canis latrans*). Predators of adults included coyote, bobcat (*Lynx rufus*), Cooper's hawk (*Accipiter cooperii*), and great horned owl (*Bubo virginianus*). We concurrently collected 34,386 observations of adult survival from 955 bobwhites, including 455 females and 500 males, for 85,225 exposure days during the breeding season. Interval lengths for survival observations of radio-tagged adults averaged 2.5 days and ranged from 1–14 days. There were 443 mortalities during the breeding season and the primary cause was predation. Occasionally equipment led to nesting or brooding adult mortality.

We fit 5 candidate models for nest survival and adult breeding season survival; all models included fixed effects for sex and day of year and random effects for site and year. The most supported models for nest and adult survival

TABLE 3 Parameter estimates from the top-ranked model evaluating relationships between northern bobwhite nest survival, land cover composition, sex of incubating adults, site, time of year, and annual variation in southwest Missouri, USA, 2014–2018. Parameter summaries include mean coefficient estimate, 95% credible interval (2.5%, 97.5%), and proportion of posteriors with the same sign as the mean (*f*). Agricultural cover within 100 m of a nest was negatively related to survival, while distance to tree was positively related to survival. Survival of male-incubated nests were greater than female-incubated nests and nests incubated earlier in the breeding season had greater survival. We also report the grand mean (μ) and standard deviation (σ) of conservation area (CA) and year random effects.

	Mean	2.5%	97.5%	*f*
Native grass	0.05	−0.09	0.19	0.75
Agriculture	−0.14	−0.24	−0.03	0.99
Distance to shrub	−0.04	−0.19	0.10	0.73
Distance to tree	0.26	0.12	0.41	1.00
Female	0.00	0.00	0.00	1.00
Male	0.27	−0.03	0.59	0.96
μ.CA	3.11	2.79	3.39	1.00
σ.CA	0.14	0.00	0.55	1.00
Shawnee Trail	3.09	2.75	3.38	1.00
Shelton	3.06	2.74	3.34	1.00
Stony Point	3.16	2.89	3.43	1.00
Talbot	3.15	2.85	3.44	1.00
Wah'Kon-Tah	3.09	2.79	3.36	1.00
Day	−0.16	−0.29	−0.04	0.99
Day^2	0.06	−0.06	0.18	0.83
2014	0.06	−0.12	0.35	0.69
2015	−0.01	−0.23	0.21	0.54
2016	0.02	−0.20	0.26	0.57
2017	−0.05	−0.31	0.13	0.69
2018	0.00	−0.24	0.24	0.51
σ.year	0.13	0.01	0.47	1.00

included environmental covariates for percent native grass and agriculture, distance to shrub, and distance to tree (Tables 1 and 2). Models that included log-transformed distance to woody vegetation were more supported than those that included a quadratic relationship between survival and distance to woody cover and those that included percent cover of woody vegetation (Tables 1 and 2). Models with percent grassland cover were more supported than those that incorporated grassland management practices. Null models with no environmental covariates had the least support for both nest survival and adult survival (Tables 1 and 2).

Daily nest survival and adult survival declined through the breeding season from 0.977 (95% credible interval [CRI] = 0.957, 0.989) to 0.953 (95% CRI = 0.921, 0.976) and 0.996 (95% CRI = 0.994, 0.998) to 0.995 (95% CRI = 0.991, 0.997), respectively (Tables 3 and 4). Survival of nests incubated by females (0.557, 95% CRI = 0.453, 0.643) was less than survival of nests incubated by males (0.637, 95% CRI = 0.523, 0.730; Table 3). Female adult breeding season survival (0.483, 95% CRI = 0.316, 0.635) was lower than male adult breeding season survival (0.556, 95% CRI = 0.400, 0.695; Table 4).

TABLE 4 Parameter estimates from the top-ranked model evaluating relationships between northern bobwhite adult breeding season survival, land cover composition, sex of incubating adults, site, time of year, and annual variation in southwest Missouri, USA, 1 May–30 September 2014–2018. Parameter summaries include mean coefficient estimate, 95% credible interval (2.5%, 97.5%), and proportion of posteriors with the same sign as the mean (*f*). Distance to tree was positively related to survival. Male survival was greater than female survival and survival declined later in the breeding season. We also report the grand mean (μ) and standard deviation (σ) of conservation area (CA) and year random effects.

	mean	2.5%	97.5%	*f*
Native grass	0.05	−0.07	0.18	0.81
Agriculture	0.02	−0.10	0.13	0.60
Distance to shrub	−0.04	−0.15	0.07	0.74
Distance to tree	0.29	0.18	0.40	1.00
Female	0.00	0.00	0.00	1.00
Male	0.22	0.03	0.41	0.99
μ.CA	5.33	4.86	5.81	1.00
σ.CA	0.38	0.12	1.03	1.00
Shawnee Trail	4.97	4.65	5.31	1.00
Shelton	5.36	5.03	5.70	1.00
Stony Point	5.52	5.21	5.85	1.00
Talbot	5.29	4.98	5.62	1.00
Wah'Kon-Tah	5.52	5.17	5.90	1.00
Day	−0.12	−0.22	−0.03	0.99
Day^2	0.06	−0.04	0.16	0.87
2014	0.00	0.00	0.00	1.00
2015	−0.17	−0.48	0.11	0.87
2016	−0.26	−0.59	0.03	0.96
2017	−0.53	−0.85	−0.18	1.00
2018	−0.22	−0.54	0.07	0.92
σ.year	0.54	0.13	1.55	1.00

Nest survival probability was negatively related to percent agricultural crop cover; survival decreased from 0.573 (95% CRI = 0.469, 0.659) to 0.268 (95% CRI = 0.073, 0.521) as crop cover increased from 0% to 100% within 100 m of a nest (Figure 3B). Nest survival was positively related to distance to tree; survival increased from 0.279 (95% CRI = 0.113, 0.466) to 0.691 (95% CRI = 0.581, 0.782) as distance increased from 0 to 292 m (Figure 3D). Adult survival was lower closer to trees; female seasonal survival probability increased from 0.260 (95% CRI = 0.109, 0.443) to 0.660 (95% CRI = 0.503, 0.784) as distance to tree increased from 0 to 556 m (Figure 4D). There was a weak positive relationship between nest and adult survival and native grassland cover (Tables 3 and 4). Nest survival increased from 0.534 (95% CRI = 0.413, 0.641) to 0.574 (95% CRI = 0.460, 0.668) from 0% to 100% cover within 100 m of a nest (Figure 3A), and adult survival increased from 0.460 (95% CRI = 0.289, 0.623) to 0.506 (95% CRI = 0.328, 0.661) across the same range (Figure 4A).

We estimated areal survival of bobwhite nests and adults across the study extent by predicting survival at a 3.6-m resolution based on surrounding cover and mean effect sizes from the most supported models. Areal survival, or predicted survival across the entire area of each site, was greatest on managed native grassland sites compared to intensively managed conservation areas (Figure 5). Interspersion of agricultural cover and woodland units among grasslands reduced areal survival on Shawnee Trail and Talbot, and continuous native grasslands had higher mean areal survival (Figure 6).

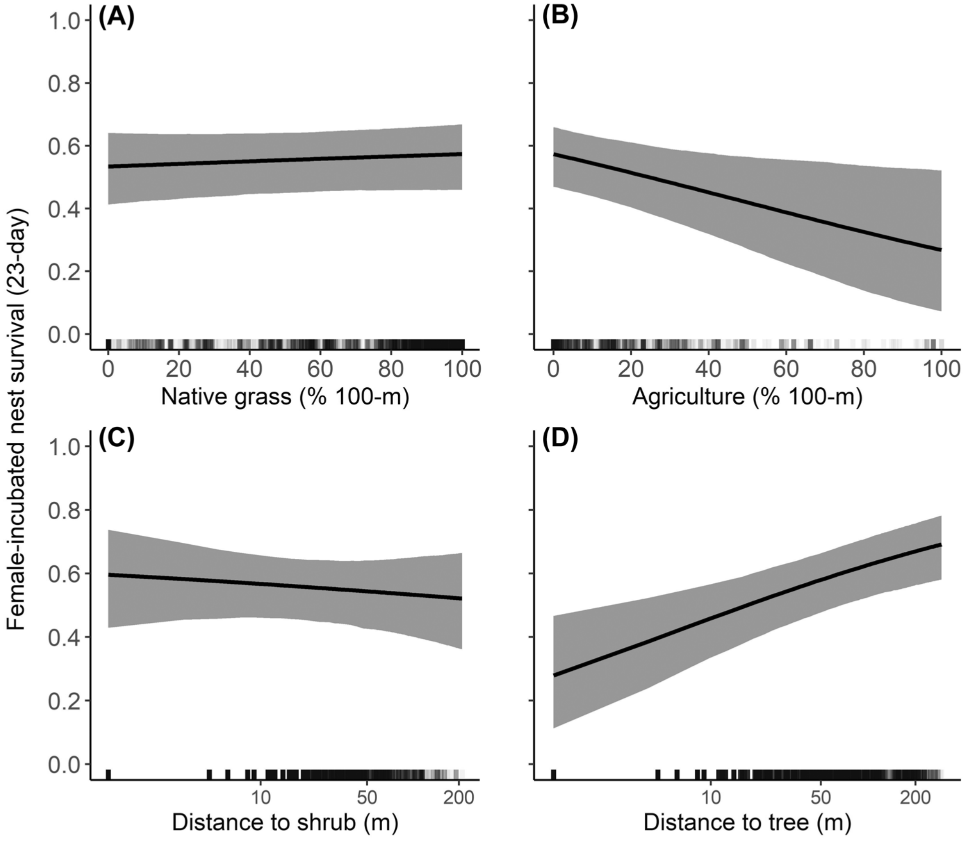

FIGURE 3 Relationships between predicted female-incubated nest survival probability of northern bobwhites and vegetation composition from 1 May to 30 September in southwest Missouri, USA, 2014–2018. Nest survival probability increased with decreasing agricultural crop cover within 100 m of nests and with distance to nearest tree. Native grassland cover had a weak, positive relationship with nest survival. The rug along the *x*-axis reflects the density of observations across each environmental gradient.

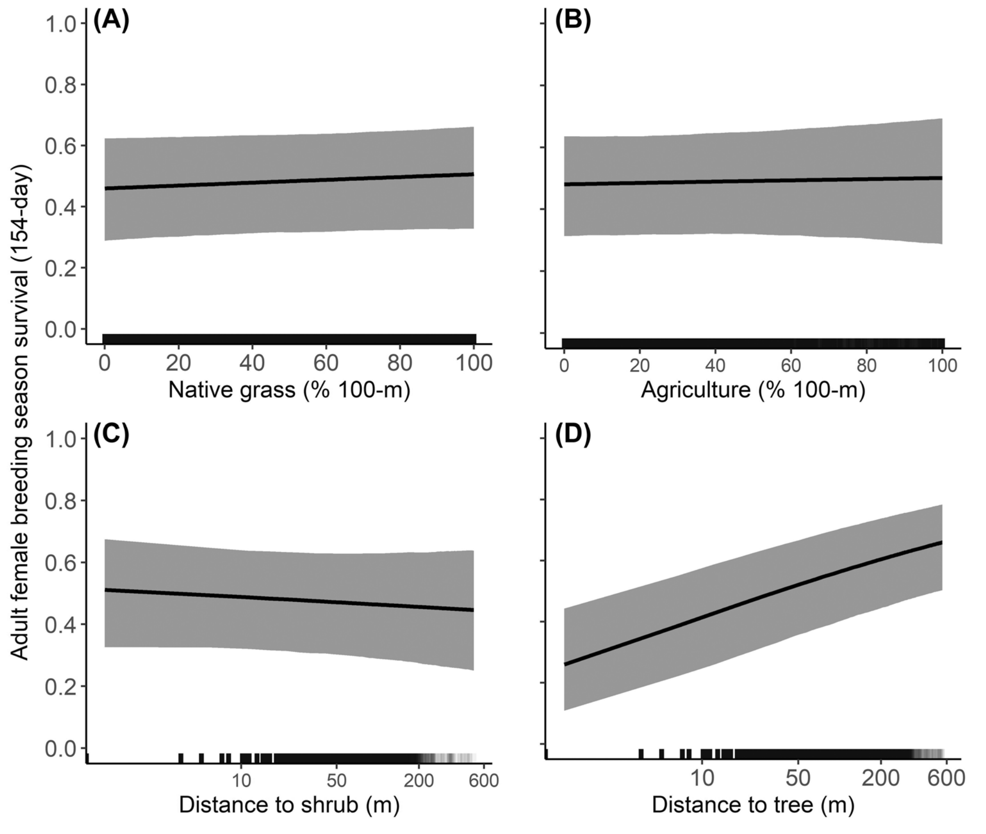

FIGURE 4 Relationships between predicted adult female northern bobwhite seasonal survival probability and vegetation composition from 1 May to 30 September in southwest Missouri, USA, 2014–2018. Survival probability increased with greater distances to trees and native grassland cover had a weak, positive relationship with nest survival. The rug along the *x*-axis reflects the density of observations across each environmental gradient.

DISCUSSION

Nest survival was negatively related to agricultural cover and nest and adult survival declined with proximity to trees. Areal nest and adult survival estimates also supported our prediction that nest survival and breeding season adult survival were greater on managed native grassland sites compared to intensively managed sites interspersed with agricultural plots and small or linear units of mature woody cover. It is not surprising that we found similar patterns in nest and adult survival given that individuals are tied to nests for much of the breeding season. Survival estimates were within the range of those observed throughout the species' distribution (Burger et al. 1995, Lohr et al. 2011, Potter et al. 2011, Brooke et al. 2017, Doggett and Locher 2018).

Both bobwhite nest survival and adult breeding season survival probability were lower closer to trees. We hypothesized tree cover was negatively related to survival because many of the frequent predators of bobwhite nests and adults use trees or forest edge as perch sites or refuge from predators. Predation contributes substantially to bobwhite adult mortality and nest failure (Rollins and Carroll 2001). Mammals and snakes are responsible for 40.2%, and 31.7% of nests depredated, respectively, and raccoons are the most common mammalian predator of bobwhites in Georgia, USA (Terhune et al. 2008). Raccoons select trees and agriculture while avoiding open grasslands (McClain 2017, Peterson et al 2022). They also use tree lines, fencerows, timber-grassland edges, and woody draws as movement corridors (Pedlar et al. 1997, Barding and Nelson 2008, McClain 2017, Peterson et al. 2022).

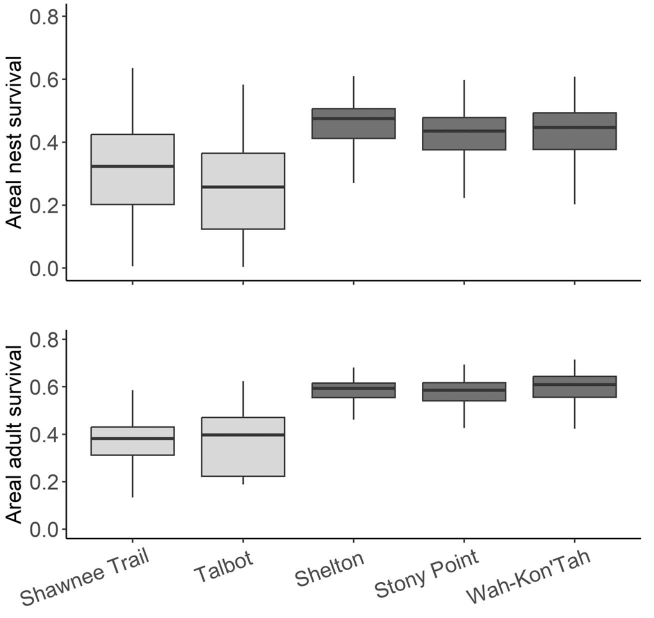

FIGURE 5 Distributions of areal nest and adult breeding season survival predictions of northern bobwhite across 2 intensively managed conservation areas (light grey; Shawnee Trail and Robert E. Talbot Memorial conservation areas) and 3 managed native grasslands (dark grey; Shelton Memorial Conservation Area, Stony Point Prairie Conservation Area, and Wah-kon'tah Prairie) in southwest Missouri, USA, 2014–2018. Intensively managed conservation areas incorporated small or linear woodland units and agricultural fields among grasslands, while managed native grasslands were continuous tracts of original and reconstructed prairie.

Mesocarnivores likely remain near woody cover and avoid open grassland to avoid predation by coyotes or bobcats (*Lynx rufus*; Tewes et al. 2002, Kamler and Gipson 2003). Snakes and avian predators also use forest edges. Western ratsnakes (*Pantherophis obsoletus*) preferentially select habitat characteristics and thermal conditions associated with forest edges (George et al. 2017). Raptors are infrequent predators of bobwhite nests (Terhune et al. 2008) but contributed to adult mortalities we observed. These results are consistent with Lohr et al. (2011), who reported bobwhite breeding season survival in New Jersey, USA, was positively related to use of grassland cover and negatively related to use of forest.

Areal survival on managed native grassland sites was greater than that on intensively managed sites. Bobwhites generally prefer nest sites with greater grass and forb cover, greater vegetation height, less bare ground, and greater visual obstruction or vegetation complexity created by grasses, forbs, and shrubs (Taylor et al. 1999*a*, Townsend et al. 2001, Lusk et al. 2006, Rader et al. 2007, Brooke et al. 2017). Successful nests are also associated with more grass, forb cover, and shrub cover, taller canopies, and less bare ground compared to failed nests (Lusk et al. 2006, Potter et al. 2011). These reported nest-site preferences are generally consistent with our conclusion that more grassland was better for nest survival. The same has been true for adult breeding season survival (Taylor et al. 1999*b*, Lohr et al. 2011).

Few studies directly relate adult summer survival to management practices. We found no difference in survival among burned, grazed, or idle grasslands. Disturbance may not be important for nesting cover because the ultimate benefit of grassland for nesting is concealment, whereas burned and grazed grasslands benefit chick survival presumably because they facilitate greater chick mobility and insect prey abundance (Engle et al. 2008, Doxon and Carroll 2010, Sinnott et al. 2022). Disking, burning, and herbicide application to reduce dominance of non-native vegetation and cover of densely planted native grasses on strip-mined sites in Kentucky, USA, resulted in greater adult summer survival, while litter depth and canopy cover were negatively related to survival (Peters et al. 2015).

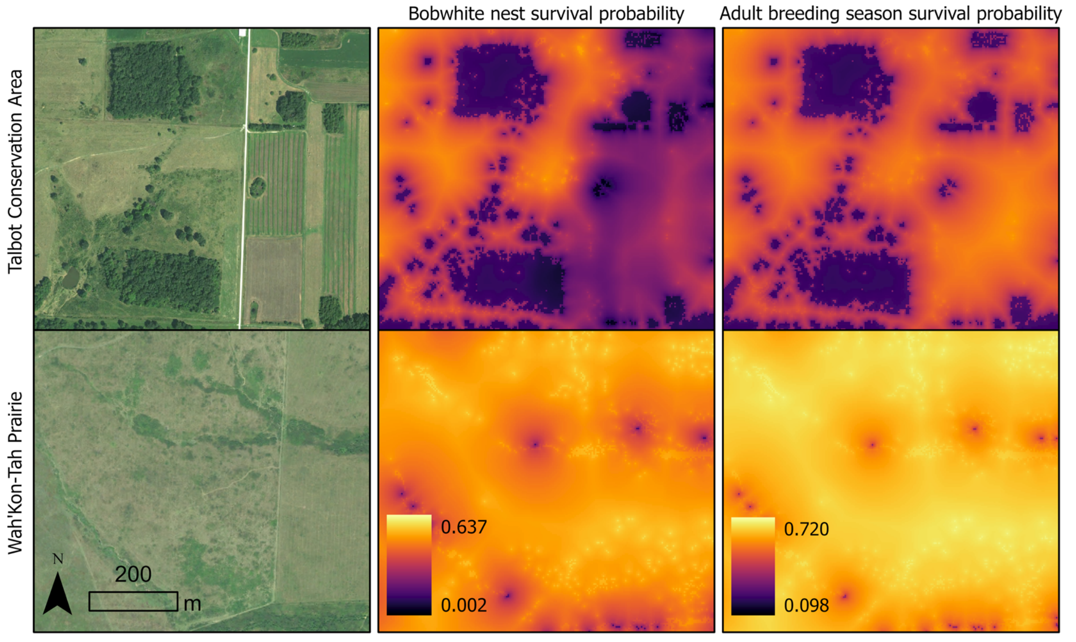

FIGURE 6 Comparison of cover type and associated areal predictions of northern bobwhite nest and adult breeding season survival in southwest Missouri, USA, 2014–2018. Intensively managed conservation areas such as Talbot (top) incorporate agricultural and woodland units among grasslands, resulting in lower areal nest and adult breeding season survival rates compared to continuous managed native grasslands such as Wah'Kon-Tah (bottom).

These results might seem inconsistent with the lack of support for burning and grazing effects in our study; however, their study was on revegetated strip mines with dense planted native grass and sericea lespedeza and ours was in grassland landscapes with native or restored prairie.

Bobwhites occupy mixed agricultural landscapes in the central United States along the forest-prairie ecotone (Roseberry and Sudkamp 1998). We detected relationships between breeding season demography and land cover composition that may be contributing to population declines regionally. On conservation areas purposefully managed for wildlife, nest survival and adult breeding season survival declined with increasing agricultural cover and proximity to trees. If we scale that relationship up to the forest-prairie ecotones of the central United States, woody encroachment and agricultural intensification may be contributing to depressed breeding season survival and productivity rates of declining bobwhite populations (MacDonald et al. 2013, Stanton et al. 2018). Bobwhite populations are responsive to broad land cover features and these relationships may be correlated or interact with local vegetation structure and composition (Yeiser et al. 2021, Sinnott et al. 2022). Additional understanding of relationships between demography and broader land cover structure and composition would support regional conservation planning.

Our results add to a body of evidence that traditional, fine-scale practices promoting woody field edges and food plots implemented on public areas managed for bobwhite do not optimize breeding season productivity or adult survival (Williams et al. 2004, Thompson et al. 2022, Sinnott et al. 2023*b*). We did not find support for a difference in nest survival or adult survival during the breeding season among native grass that was burned, grazed, or not disturbed, though there are benefits during the brood period (Sinnott et al. 2021, 2022). Rotational fire and grazing can prevent succession and sustain native grasslands that benefit nest and adult breeding season survival while providing recently disturbed patches preferred by broods. Burning on a 3-year cycle also provides for dispersed low shrub cover that adults prefer in winter (Mosloff 2020, Mosloff et al. 2021).

MANAGEMENT IMPLICATIONS

Management to sustain or expand native grass cover should benefit bobwhite nest survival and adult breeding season survival in the Midwest. Replacing agricultural strips with reconstructed prairie plantings should improve nest survival on areas managed for wildlife, while removal of tree cover and fire-return intervals that permit some shrub cover should result in greater survival of bobwhite in all life stages.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Capture and handling protocols were approved by the University of Missouri Animal Care and Use Committee (protocol 8766). These methods were part of the study plan approved by the Missouri Department of Conservation.

DATA AVAILABILITY STATEMENT

Data and code used in this analysis are archived publicly at https://doi.org/10.5061/dryad.kkwh70s9f.

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