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RESEARCH ARTICLE

Northern Bobwhite juvenile survival is greater in native grasslands managed with fire and grazing and lower in non-native field borders and strip crop fields

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ABSTRACT

Effective species conservation requires understanding environmental effects on stage-specific demographics driving population change. Northern Bobwhite (*Colinus virginianus*) is an early-successional shrub-obligate species that has experienced long-term, range-wide declines due to fire suppression, agricultural intensification, and sprawling development. Local habitat features and landscape context may interactively influence vital rates. Management affects food, cover, and other resources available locally, while surrounding landscapes often determine degree of isolation and predator communities. We evaluated relationships between juvenile bobwhite survival and local (50 m) and landscape (1 km) scale cover type composition and grassland management (i.e. conservation grazing, prescribed burns, mowing/haying) on 3 native grasslands and 2 traditionally managed conservation areas in southwest Missouri, USA, 2016–2018. We radio-tracked brood-attending adults and young from hatch to a maximum of 114 days and estimated juvenile survival with a Bayesian known-fate logistic exposure model. Juvenile survival was greatest on native grasslands that were burned and grazed at least once in the previous 2 years. Percent shrub cover was positively related to survival. Survival was relatively high in local agriculture, but these relationships were sensitive to surrounding landscape composition. For example, small patches of cropland surrounded by nonagriculture such as strip crops surrounded by grassland units on traditionally managed sites had low survival. Relationships between survival and agricultural landscape cover were dependent on local cover types; survival was high within crop fields but low in non-native grasslands surrounded by crop fields such as agricultural field borders. Patch-burn grazing practices on native grasslands provided the best habitat for bobwhite juvenile survival. Agricultural landscapes can support the recruitment of bobwhite if appropriately managed native grasslands are also available.

Keywords: agricultural landscape, eastern tallgrass prairie, juvenile survival, logistic exposure, Northern Bobwhite, patch-burn grazing management

LAY SUMMARY

- Local vegetation structure and composition shaped by habitat management practices can drive bird population dynamics, and the magnitude and direction of relationships may vary depending on composition of the surrounding landscape. Thus, effective conservation planning requires understanding the effects of both local management and landscape context on survival and recruitment of sensitive species such as Northern Bobwhite (*Colinus virginianus*).
- While Northern Bobwhites occupy many early successional and agricultural landscapes, habitat-specific survival probabilities during this vulnerable life stage are unknown.
- We estimated juvenile survival from hatch to 90 days using nest monitoring, brood capture, and radio-telemetry data within a logistic exposure model.
- Across our 5 study sites in southwest Missouri, juvenile survival was greatest on local native grasslands managed with fire and grazing. Juvenile survival was relatively high in agricultural crop fields but low in non-native field borders and in strip crop fields. Relationships between survival and local cover type varied depending on proportion of agricultural land cover in the surrounding landscape.
- Native grassland management using fire and grazing may better support Northern Bobwhite juvenile survival and recruitment compared with management that includes food plots and planted strips of woody vegetation.

La supervivencia de los juveniles de *Colinus virginianus* es mayor en los pastizales nativos manejados con fuego y pastoreo, y menor en los bordes de campos no nativos y campos de cultivos en franja

RESUMEN

La conservación efectiva de especies requiere comprender los efectos ambientales sobre la demografía específica de las etapas que impulsan los cambios poblacionales. *Colinus virginianus* es una especie obligada de la sucesión temprana arbustiva, que ha experimentado disminuciones a largo plazo en todo su rango debido a la supresión de incendios, la intensificación agrícola y la expansión urbana. Las características del hábitat local y el contexto del paisaje pueden influir de forma interactiva en las tasas vitales. El manejo afecta los alimentos, la cobertura y otros recursos disponibles localmente, mientras que los paisajes circundantes a menudo determinan el grado de aislamiento y las comunidades de depredadores. Evaluamos las relaciones entre la supervivencia de los juveniles de *C. virginianus* y la composición del tipo de cobertura y el manejo de los pastizales (i.e. pastoreo de conservación, quemas prescritas, siega/heno) a escala local (50 m) y de paisaje (1 km) en tres pastizales nativos y dos áreas de conservación manejadas de modo tradicional en el suroeste de Misuri, EEUU, entre 2016 y 2018. Seguimos con telemetría por radio a adultos que asistían a las crías y a juveniles desde la eclosión hasta los 114 días y estimamos la supervivencia de los juveniles con un modelo bayesiano de exposición logística de destino conocido. La supervivencia de los juveniles fue mayor en los pastizales nativos que se quemaron y que fueron pastoreados al menos una vez en los dos años anteriores. El porcentaje de cobertura de arbustos se relacionó positivamente con la supervivencia. La supervivencia fue relativamente alta en la agricultura local, pero estas relaciones fueron sensibles a la composición del paisaje circundante. Por ejemplo, pequeños parches de tierras de cultivo rodeados de áreas no agrícolas, como cultivos en franja rodeados por pastizal en sitios manejados de modo tradicional, tuvieron una baja supervivencia. Las relaciones entre la supervivencia y la cobertura del paisaje agrícola dependieron de los tipos de cobertura local; la supervivencia fue alta dentro de los campos de cultivo, pero baja en los pastizales no nativos rodeados de campos de cultivo, como los bordes de los campos agrícolas. Las prácticas de pastoreo con quema de parches en los pastizales nativos proporcionaron el mejor hábitat para la supervivencia de los juveniles de *C. virginianus*. Los paisajes agrícolas pueden sustentar el reclutamiento de *C. virginianus* si también se dispone de pastizales nativos adecuadamente gestionados.

Palabras clave: Colinus virginianus, exposición logística, paisaje agrícola, pradera oriental de pastos altos, supervivencia de juveniles, manejo de pastoreo con quema de parches

INTRODUCTION

Wildlife population dynamics are driven by quality and quantity of available resources, and associations of neighboring land cover (Kane et al. 2017). Understanding the magnitude and direction of relationships of local habitat and landscape composition on demography can substantially improve conservation and management actions (Wisdom et al. 2000). Modern grassland management activities such as haying, grazing, and prescribed burning drive local food availability, protective cover, and predator foraging behavior and success (Perlut et al. 2006, Engle et al. 2008). For example, Upland Sandpiper (*Bartramia longicauda*) nest survival is greater in non-burned and non-grazed grasslands that provide better concealment from nest predators (Sandercock et al. 2015). Yet, landscape composition and broad-scale land use change associated with conversion of eastern tallgrass prairie to cool-season pastures and crop fields can also affect demographic rates. For example, Dickcissel (*Spiza americana*) nest survival is reduced on landscapes with greater corn and soybean cover (1-km radius), possibly due to greater abundance of nest predators along agricultural edges (Pedlar et al. 1997, Nelson et al. 2018).

Despite substantial evidence that landscape context modifies wildlife responses to local vegetation composition and structure, few studies estimate habitat-specific vital rates at both local and landscape scales (Prevedello and Vieira 2010, Tscharntke et al. 2012). Landscape composition can modify physiological stress responses of birds to local land management practices within agricultural landscapes, and these stress responses are linked to survival (Latimer et al. 2020). Additionally, landscape composition can modify relationships between local habitat and survival by influencing predator community composition. Spillover of organisms from adjacent landscapes may alter local trophic structures and predator–prey dynamics (Tscharntke et al. 2012). For example, local edge effects resulted in higher nest depredation rates of ground-nesting songbirds in highly and moderately fragmented forested landscapes but not in unfragmented forested landscapes (Donovan et al. 1997). In shrub-obligate birds such as Northern Bobwhite (*Colinus virginianus*), abundance can increase in agricultural-dominated landscapes with the establishment of local field borders, yet populations may not respond to the same management practice in the same way within forested landscapes (Riddle et al. 2008).

Northern Bobwhites (hereafter "bobwhite") have experienced long-term, range-wide declines due to fire suppression, agricultural intensification, and sprawling low-density housing development (Hernández et al. 2013). Annual survival of adult bobwhite can average 13% in

stable populations, and thus recruitment is an important contributor to population growth (McConnell et al. 2018). Survival of young is low but improves with rapid growth in body size and mobility (Lusk et al. 2005, Tanner et al. 2019). While survival and habitat utility may change with age and growth, current estimates of juvenile survival do not represent the full developmental period from hatch during this vulnerable life stage (Lusk et al. 2005, Kamps et al. 2017, Tanner et al. 2019). Survival estimates based on nest monitoring and brood count data at roost locations only evaluate the first 2 to 3 weeks of life (DeVos and Mueller 1993, Kamps et al. 2017). Telemetry-based estimates of survival start between 8- and 21-days old and end between 34- and 56-days old (Suchy and Munkel 2000, Tanner et al. 2019). Juveniles grow rapidly in the first 74 days of life, from less than 10 to 149 g, and then steadily up to 180 g at ~145 days (Roseberry and Klimstra 1971). Longer period estimates are important for understanding patterns of juvenile survival. Additionally, habitat-specific demographic responses to daily use of different vegetation types and management practices on altered landscapes have not yet been estimated (Kamps et al. 2017, Tanner et al. 2019, Terhune et al. 2019).

Juvenile survival tends to be lower and more variable than adult survival, making it an important life stage to address for conservation management (Sandercock et al. 2008, Wilson et al. 2016, Terhune et al. 2019). Our objectives were to estimate bobwhite juvenile survival from hatch through the development period and determine the relationship of daily survival to local cover type, management practices, and landscape composition. We developed a suite of predictions based on decades of research on bobwhite population dynamics and relationships with habitat. We predicted that:

(1) Juvenile survival would be positively related to native grasslands managed with fire and low-intensity grazing. Fire and grazing promote heterogeneity in plant community structure and composition, which may have improved mobility and invertebrate prey availability and abundance for young (Taylor et al. 1999, Fuhlendorf and Engle 2004, Engle et al. 2008, Kamps et al. 2017).
(2) Juvenile survival would be negatively related to mowing. Equipment results in direct mortality of young while reduced vegetation cover increases vulnerability of young to predators (Bollinger et al. 1990, Perlut et al. 2006).
(3) Juvenile survival would be negatively related to idle grasslands. Thick vegetation reduces juvenile mobility, foraging success, and may impede predator escape (Doxon and Carroll 2010).
(4) Juvenile survival would be negatively related to cool-season pastures, hayfields, and cultivated croplands. Invertebrate availability and foraging success may be low or depredation may be greater in these production fields (Palmer et al. 2001, Kentie et al. 2013).
(5) Juvenile survival would be positively related to shrub cover and negatively to tree cover. Shrub cover provides broods visual obstruction from predators and refugia from extreme temperatures (Perkins et al. 2014, Carroll et al. 2015). Trees provide nearby habitat for mesocarnivores and perches for aerial predators (Gehring and Swihart 2003, Dinkins et al. 2012, Ellison et al. 2013).
(6) Juvenile survival would be positively related to the proportion of native grasslands and negatively related to proportions of agricultural fields and cool-season pastures at the landscape scale. Increased predator abundance or harvest equipment may reduce survival in agricultural landscapes (Dijak and Thompson 2000, Giuliano and Daves 2002, Perlut et al. 2006). Additionally, loss of vegetation cover in pastures and hayfields, and the reduction of usable space, may contribute to observed declines in abundance and underlying vital rates in these landscapes (Murphy 2003, Williams et al. 2004, Perlut et al. 2006).
(7) Finally, landscape-scale cover composition would modify relationships between local cover type and juvenile survival. Landscape context can modify survival responses to local environmental conditions by affecting stress responses or influencing local predator community composition and predator–prey dynamics (Donovan et al. 1997, Latimer et al. 2020).

METHODS

Study Sites

Northern Bobwhites have declined by an average of 2.4% per year in Missouri, for a cumulative loss of 71.7% from 1967 to 2019 (Sauer et al. 2020). We studied bobwhite juvenile survival in southwest Missouri, USA, from 2016 to 2018 on 5 state conservation areas and surrounding private lands (Figure 1A). This region is within the ancestral lands of the Osage Nation and was historically tallgrass prairie. While it has been largely converted for agricultural use, there is relatively high potential for successful bobwhite population recovery with conservation actions (Morgan et al. 2016). Three sites were extensively managed remnant prairies: Wade and June Shelton Memorial Conservation Area (SLT; 129 ha), Stony Point Prairie Conservation Area (STP; 389 ha), and Wah'Kon-Tah Prairie (WKT; 1,226 ha). Combinations of prescribed fire, grazing, and haying (10–52 ha) have been used at these sites to maintain grassland landscapes with limited woodland habitat (<6%; Figure 1B), enhance species richness of herbaceous plants, and mimic historic disturbance regimes (Fuhlendorf and

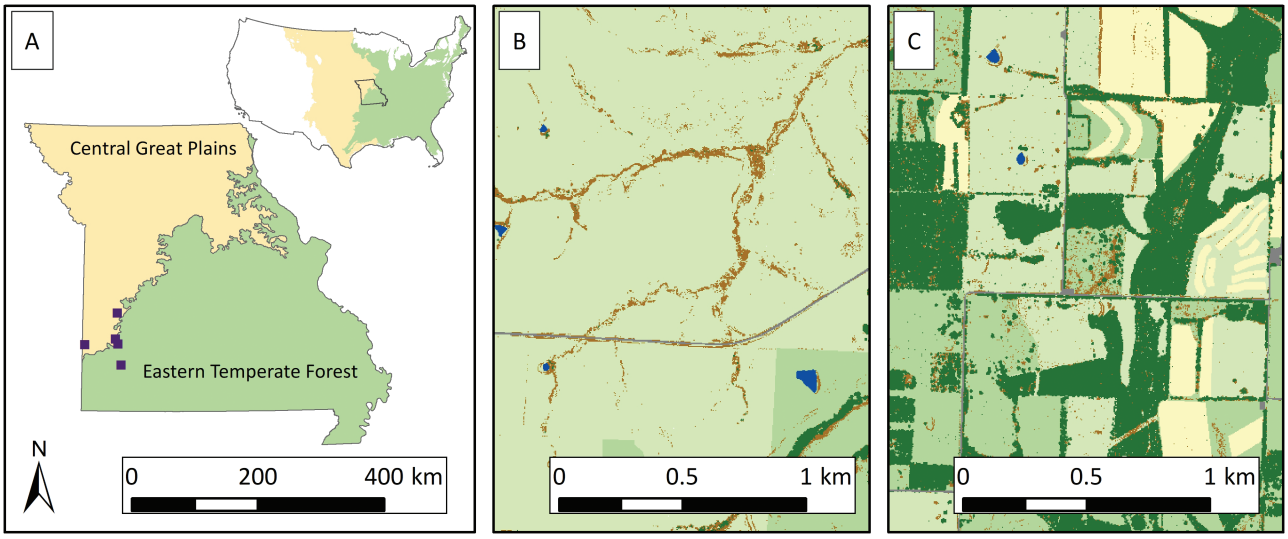

FIGURE 1. Maps (A) of our 5 study sites located in southwest Missouri, USA: Shawnee Trail, Shelton Memorial, Stony Point Prairie, and Talbot Conservation Areas and Wah'Kon-Tah Prairie. (B) Extensively managed sites consisted of grasslands (light green), shrub (brown), and tree cover (dark green). (C) Intensively managed sites also incorporated agricultural food plots (yellow) among grassland units.

Engle 2004). By contrast, 2 of our study sites were intensively managed: Shawnee Trail Conservation Area (SHT; 1,471 ha) and Robert E. Talbot Conservation Area (TAL; 1,764 ha). These sites incorporated traditional, fine-scale habitat improvement practices such as planted strip crops, food plots, and woodland habitats (1–24 ha) for wildlife use among grassland units managed with prescribed fire, grazing, and mowing (4–28 ha; Figure 1C). Surrounding private lands were mainly cool-season grass pastures as well as cultivated crop fields.

Juvenile Capture, Marking, and Tracking

We estimated bobwhite juvenile survival from hatch to 90 days by monitoring nests, capturing broods, and radio-tracking brood-attending adults and juveniles. Missouri Department of Conservation funnel trapped adults and fit them with radio collars in February and March each year. Nests of incubating radio-tagged adults were monitored, and the number of eggs hatched from successful nests was recorded. We then tracked brood-attending adults until we could capture the brood and radio-tag juveniles at approximately 3 weeks old.

We captured broods to mark young with patagial tags and fit individuals with radio transmitters using the corral technique (Smith et al. 2003; Supplementary Material Appendix S1). Juveniles captured at ≤2 weeks old were uniquely marked with colored permanent marker on their throat, axillaries, and underwing coverts. Juveniles ≥2 weeks old were marked with numbered aluminum patagial tags (Style 4-1005, Size 1, National Band and Tag Company, Louisville, KY, USA; Carver et al. 1999) and 1–6 individuals within each brood weighing >20 g received 0.6- to 0.8-g radio transmitters using the suture technique (Terhune et al. 2020; Supplementary Material Appendix S2). Transmitter weight was <4% of body mass; 0.6-g transmitters had a 45-day expected battery life and 0.8-g transmitters had a 60-day expected battery life, although some transmitters were active over 80 days (AWE-QC-0.8 and AWE-QC-0.65, American Wildlife Enterprises, Monticello, FL, USA). Capture and handling protocols were approved by the University of Missouri Animal Care and Use Committee (protocol 8766).

We tracked brood-attending adults from hatch to brood capture and then attending adults and radio-tagged juveniles through the life of the bird or transmitter. We recorded observations of survival status, location, and vegetation cover type and management history of brood locations daily. We tracked broods to roost locations before the first light at least once per week and rotated daytime tracking order. We homed in on a bird signal, circled within 10 m of their location, and avoided flushing the group (Orange et al. 2016). If birds were on privately owned lands that we did not have permission to access, we triangulated locations based on azimuths, signal strength, topography, and vegetation.

Landscape and Habitat Covariates

We measured ecologically meaningful habitat covariates to test our predictions. We quantified local cover type composition as percent cover within a 50-m radius of each daily juvenile location. Young broods <14 days old traveled an average of 129 m day^{-1}, and 50 m reasonably captured an area of cover and resources available at locations of daily survival observations (Sinnott et al. 2021c). We quantified

landscape-scale cover type composition as percent cover within 1 km of each daily juvenile location (Supplementary Material Table S1). This radius is based on research that found weakly negative effects of agricultural land cover on Dickcissel nest survival probabilities (Nelson et al. 2018). It also encompasses the maximum daily distance traveled among observed broods at our study sites (800 m; Sinnott et al. 2021c). Land managers mapped management activities and cover types of management units within and surrounding each study site. We supplemented their classifications with field observations of cover types and management on surrounding private lands. We also used Light Detection and Ranging data (LiDAR; USACE 2015, 2016) and Cropland Data (USDA National Agricultural Statistics Service Cropland Data Layer 2018) to map cover type and management practices across our study extent.

We classified herbaceous cover types as native-, mixed-, or cool-season grasslands, agricultural crop, or idle agriculture. Native grassland cover types included remnant and reconstructed prairies as well as native warm-season grass plantings (Supplementary Material Appendix S3). Native grassland units were dominated by grasses, such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*), and had a high diversity and abundance of forbs such as prairie blazing star (*Liatris pycnostachya*), pale purple coneflower (*Echinacea pallida*), and goldenrod (*Solidago* spp.). Most native grassland management units were 10 to 30 ha but could be as large as 55 ha. Cool-season grasses on surrounding private lands were dominated by non-native species such as tall fescue (*Festuca arundinacea*), orchard grass (*Dactylis glomerata*), or timothy grass (*Phleum pratense*). Mixed grassland units occurred on both public and private lands and included old fields, grasslands composed of both native and non-native grasses listed above, and grasslands with significant sericea lespedeza (*Lespedeza cuneata*) or ragweed (*Ambrosia* spp.). Agricultural crop units were planted soybean (*Glycine max*), corn (*Zea mays*), sunflower (*Helianthus* spp.), and winter wheat (*Triticum* spp.). Idle agricultural units were unplanted and had weedy areas with residual crops. Agricultural units on intensively managed sites ranged in size from <1 to 25 ha, but area of crop fields on surrounding private lands could exceed 120 ha.

We identified woody cover types by height using LiDAR at 3.6-m resolution. Vegetation of 0.7- to 3.5-m tall and 3.5- to 40-m tall was classified as shrubs and trees, respectively (Supplementary Material Appendix S3). We measured Euclidean distance (m) from daily juvenile locations to the nearest tree in ArcMap10.4.1 using the *Near* proximity analysis tool (ESRI 2019). Common shrub species included plum (*Prunus* spp.) and sumac (*Rhus* spp.), and dominant tree species included oaks (*Quercus* spp.).

We characterized management practices for each field or management unit as mowed (including haying) if vegetation was cut during the current year's growing season; burned, grazed, or burned and grazed if these practices occurred within the previous 2 years; and idle if not mowed in the current year, or grazed or burned in the previous 2 years (Supplementary Material Appendix S3).

For young broods tracked between hatch and capture without radio-tagged juveniles, cover type and management data for the early exposure period were assigned based on averages of daily locations of brood-attending adults. For survival observations with exposure periods of >1 day, cover type and management data were assigned based on the location of the brood or radio-tagged individual when located, which represented the last day of each exposure period.

Survival Analysis

We used nest monitoring, brood capture, and radio-telemetry tracking data to estimate daily juvenile survival and period survival from hatch to 90 days old within a single known-fate logistic exposure model (Shaffer 2004, Shaffer and Thompson 2007; see Supplementary Material Appendix S4). The logistic exposure model is similar to other known fate approaches used for nest survival and telemetry data (Dinsmore et al. 2002, Rotella et al. 2004); it uses a modified link function to estimate daily survival for observation intervals where time between survival observations varies (Equation 1). Accounting for variable interval length t, between individual observations i of survival y_i, allowed for a streamlined estimation of individual survival probability P_i, across observation intervals defined by hatching to first brood capture, between brood captures, and daily tracking observations of radio-tagged young (Equation 1). Models evaluated a set of fixed effects that included brood age, year, and a set of predicted cover type, management, and landscape drivers (X; Equation 2). Models also included a common intercept and random effects for brood identity m and site k (e.g., $\gamma = (\gamma_m, \gamma_k)'$) (Equation 2):

$$\begin{aligned} y_i &\sim \text{Bernoulli}\,(P_i) \\ P_i &= s^{t_i} \end{aligned} \tag{1}$$

$$\text{logit}\,(s) = \beta\, X + \gamma \tag{2}$$

Early period survival estimates for bobwhite young from hatch to approximately 3 weeks old are only possible through the use of nest hatch and brood count data from captures at roost locations (DeVos and Mueller 1993, Dahlgren et al. 2010, Schreiber et al. 2016, Kamps et al. 2017). We determined individual fates from hatch to ~3 weeks old based on the number of eggs hatched and the

number of young recaptured at roost locations. For example, if 10 eggs hatched and 8 individuals were captured at a roost location 12 days later, this represented 8 individuals surviving an interval of t = 12 and 2 individuals dying. Interval lengths for this early brood period averaged 12 days and ranged from 1 to 23 days. If broods were discovered with a radio-tagged attending adult and no nest information was available, initial brood sizes were counted from number of chicks on first capture (approximately 4- to 12-days old). Brood counts from captures at roost locations are the most reliable method for estimating chick survival for gallinaceous birds (DeVos and Mueller 1993, Dahlgren et al. 2010, Schreiber et al. 2016, Kamps et al. 2017). Observation error in the number of hatched eggs counted and brood amalgamation are 2 potential sources of uncertainty in our early period survival estimates that we did not account for. We do not believe that brood amalgamation substantially influenced average daily survival estimates because rates of brood mixing are low in the first few weeks of life (Faircloth et al. 2005). Among 75 captures of broods included in this survival analysis, we suspected 7 broods of having adopted young. Among the 543 captures of individuals, we suspected that 21 individuals were adopted based on differences in body size. We removed adopted individuals from the analysis but could not account for emigration of chicks out of broods; hence, early period estimates may be biased slightly low.

We monitored survival of juveniles fitted with radio transmitters at ~3 weeks old through direct daily observation. Individuals that died within 3 days of capture were excluded from the analysis under the assumption capture and handling influenced their death (Larson et al. 2001). We right-censored observations for individuals due to transmitter signal loss or unknown fate but included observations up to the last observation of known fate (Tanner et al. 2019). Interval lengths between survival observations from radio-tagged young were on average 1 day and ranged from 1 to 13 days.

The logistic exposure model and similar nest survival model in Program MARK (Dinsmore et al. 2002) have been widely used to estimate daily survival of nests and radio-tagged birds, and, to a lesser extent, young birds based on brood captures and flushes. We are not aware of any studies that combined 2 data types into a single daily survival analysis. However, Anders et al. (1997) calculated cumulative survival beginning with eggs in nest through the early fledgling period with radio-tagged individuals for Wood Thrush (*Hylocichla mustelina*) using a known fate Kaplan–Meier model. Given our early brood observations and telemetry-based observations can both be expressed in the required structure for this model, we combined these observations for the increased power of a larger dataset and a more comprehensive analysis of survival of young through their full development period during this vulnerable life stage. We believe that the advantages of using a single model to span this developmental period outweigh potential uncertainties that could result from longer intervals and brood mixing during the hatch to brood capture period.

Overall, we estimated multiple effects of cover type, management, and woody composition on daily juvenile survival in a Bayesian framework to test our predictions. We standardized values of age as well as local and landscape composition data 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. All survival models included a fixed age effect as juvenile survival improves with age (Lusk et al. 2005). All models included a random effect for brood identity, to account for nonindependence of individual fates within a brood. We also included a random site effect and a fixed year effect in all models to account for nonindependence associated with spatial and temporal variation (Darrah et al. 2018, Terhune et al. 2019).

We developed 13 candidate models based on our predictions including a null model that contained random effects for site, year, and brood and a fixed age effect (Supplementary Material Table S2). We formulated multiple models for some predictions to evaluate sets of habitat parameters or represent multiple levels of complexity. We fit survival models in a Bayesian framework in program R version 3.6.1 (R Core Development Team 2019) using JAGS (Plummer 2003) via the JagsUI package (Kellner 2019). We specified vague priors for normally distributed year, age, and vegetation parameters with mean 0 and precision 0.001. We also specified vague hyper priors for standard deviation of random effect parameters, using a uniform distribution from 0 to 10 (see model code in Supplementary Material Appendix S5). We ran models using 3 chains, each contained 50,000 iterations including a burn-in of 20,000, and a thin rate of 4, yielding 22,500 samples for each parameter. We evaluated model convergence by checking for R-hat <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 evaluated support for our predictions using leave-one-out (LOO) cross-validation by estimating pointwise out-of-sample prediction accuracy and ranking models based on differences in the information criterion (ΔLOOIC; Veharti et al. 2017, 2020). We also compared expected predictive accuracy of our competing models to the top model by estimating the difference in their expected log pointwise predictive density (elpd diff) and the standard error (SE) of that difference (Veharti et al. 2017, 2020). 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 posterior support for a negative or positive relationship. We

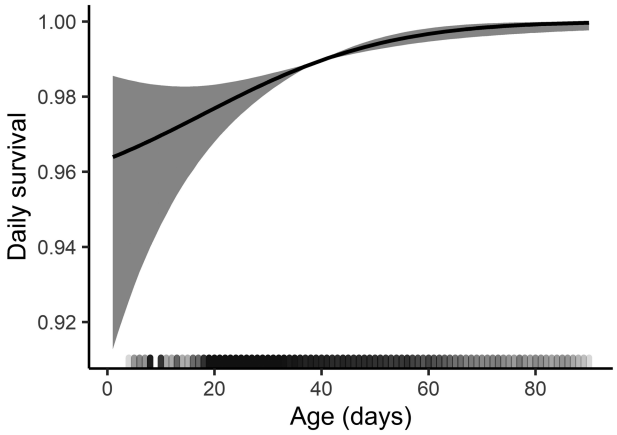

FIGURE 2. Predicted daily survival of Northern Bobwhite juveniles from hatch to 90 days old increases nonlinearly with age (days) in southwest Missouri, 2016–2018. Mean (line) and 95% CI (ribbon) depict estimated daily survival rates. The band along the *x*-axis illustrates the density of survival observations of individuals 1- to 90-day old.

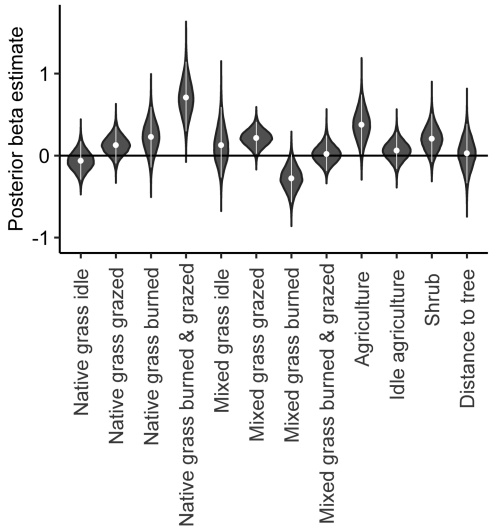

FIGURE 3. Native grasslands that were burned and grazed at least once in the previous 2 years had the greatest positive relationship with Northern Bobwhite juvenile survival, followed by agricultural crops in southwest Missouri, 2016–2018. Mean (point), 95% CI (bar), and posterior distribution (shaded area) of effect sizes of local cover type and management (% within 50 m) on daily survival from our most supported model. All covariates were standardized.

presented credible intervals (CIs) as a measure of uncertainty around parameter estimates. We estimated the effect of variables on 90-day period survival predictions by varying the variable of interest across its range of observed values and exponentiating estimates for individuals aged 1- to 90-days old while holding other variables in the model at their mean.

RESULTS

We monitored survival of 705 individuals from 75 broods across 5 sites (SHT = 10, SLT = 10, STP = 17, TAL = 15, and WKT = 23), from 2016 to 2018, totaling 14,904 exposure days (see Supplementary Material Appendix S6). One-hundred forty-four radio-tagged individuals contributed to survival estimates of juveniles greater than 30 days old, 63 radio-tagged individuals contributed to survival estimates of juveniles over 60 days old, and 15 individuals contributed to survival estimates of juveniles over 90 days old. While cause of mortality could not always be reliably determined, depredation appeared to be the most frequent source of mortality based on damage to transmitters, such as bite marks or bent antennae. We found marginally greater support for a model with a quadratic vs. linear age effect (elpd diff = 1.8, SE = 1.5). Therefore, all competing cover type, management, and landscape models included this quadratic age effect. Several transmitters lasted longer than the expected 60-day battery life, and our oldest individual observed was 114 days old. We estimated bobwhite juvenile survival from hatch to 90 days old.

Our top model estimated a nonlinear increase in daily survival from 0.964 (95% CI: 0.913, 0.986) post-hatch to 1.000 (95% CI: 0.999, 1.000) at 90 days old (Figure 2), and 90-day period survival of 0.333 (95% CI: 0.186, 0.458). Seven candidate models had lower LOOIC values than the null model (Supplementary Material Table S3). We present results from the top 2 models that evaluated local habitat management effects and interactive effects of landscape agriculture and local native grassland and agricultural cover on juvenile survival (elpd diff = –1.4, SE = 4.8).

Our top model evaluated the relationship between bobwhite juvenile survival and local cover type, management, and woody vegetation. It provided support for our prediction that native grasslands managed with fire and grazing are positively related to survival (Supplementary Material Table S3). Percent cover of idle native grasslands within 50 m of juvenile locations was not related to daily survival probability (Figures 3 and 4A; Table 1). Native grasslands burned and grazed in the past 2 growing seasons had the largest positive relationship with daily juvenile survival ($\beta_{native\ grass\ burned\ \&\ grazed}$ = 0.71, 95% CI: 0.30, 1.15, f = 1.00; Figure 3; Table 1). Period survival increased from 0.21 (95% CI: 0.08, 0.36) to 0.84 (95% CI: 0.58, 0.95) as percent cover of native grasslands burned and grazed within 50 m increased from 0% to 100% at daily locations (Figure 4B). Relationships between survival and cover type were weakly positive for native grasslands that were burned only and grazed only in the previous 2 years (Figure 3; Table 1). Survival was also positively related to grazed mixed grasslands (Figure 3; Table 1), and period survival increased from 0.32 (95% CI: 0.17, 0.45) to 0.81

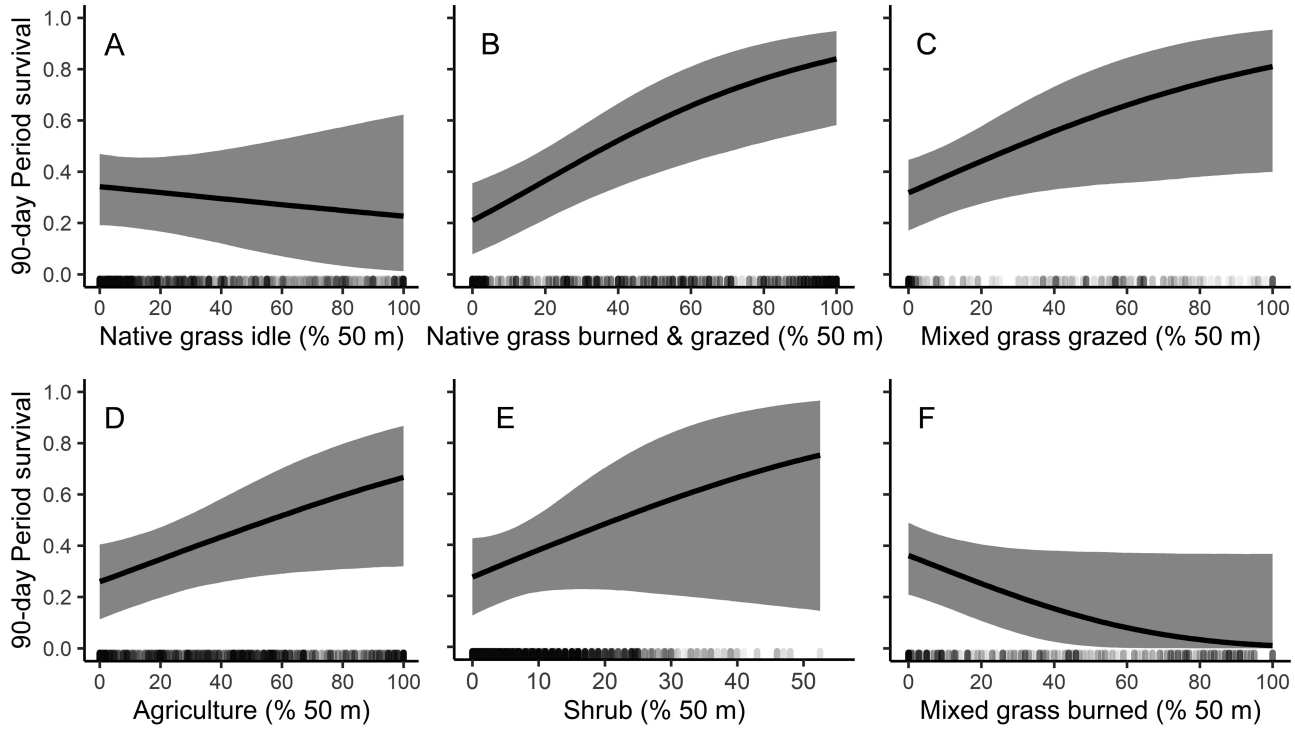

FIGURE 4. Period survival estimates increased as proportion of native grasslands managed with fire and grazing (B), grazed mixed grasslands (C), agriculture (D), and shrub cover (E) within 50 m of Northern Bobwhite juveniles increased in southwest Missouri, 2016–2018. Period survival estimates decreased as proportion of burned mixed grasslands within 50 m of daily locations increased (F) and estimates did not vary with proportion of native grasslands left idle for at least 2 years (A). Mean (line) and 95% CI (ribbon) estimates of 90-day period survival of juvenile Northern Bobwhite based on selected effects from the top-ranking cover type and management model describing percent cover composition within 50 m of daily locations. The band along the *x*-axis illustrates the density of survival observations of individuals across the range of values of percent local cover type.

TABLE 1. Parameter estimates from the top-ranked model of local and landscape cover type, management, woody structure, and age on juvenile Northern Bobwhite survival in southwest Missouri 2016–2018 including mean, 95% CI, and proportion with the same sign as mean (*f*) of posterior distribution for the intercept, fixed effects, and standard deviation of brood and site random effects.

		95% CI		
	Mean	0.025	0.975	*f*
Intercept	4.797	3.730	5.880	1.000
Native grass idle	–0.064	–0.293	0.175	0.711
Native grass grazed	0.126	–0.095	0.353	0.871
Native grass burned	0.227	–0.144	0.596	0.886
Native grass burned & grazed	0.707	0.295	1.145	1.000
Mixed grass idle	0.126	–0.268	0.592	0.701
Mixed grass grazed	0.214	0.021	0.410	0.986
Mixed grass burned	–0.279	–0.570	0.011	0.971
Mixed grass burned & grazed	0.019	–0.186	0.244	0.558
Agriculture	0.376	0.016	0.743	0.980
Idle agriculture	0.060	–0.162	0.284	0.703
Shrub cover	0.205	–0.078	0.510	0.916
Distance to tree	0.027	–0.338	0.387	0.560
Age	0.970	0.637	1.341	1.000
Age^2	0.171	–0.077	0.445	0.904
Year.2016	0.000	0.000	0.000	1.000
Year.2017	–0.488	–1.551	0.544	0.823
Year.2018	–0.344	–1.479	0.794	0.728
Brood	1.506	1.140	1.976	1.000
Site	0.627	0.025	2.236	1.000

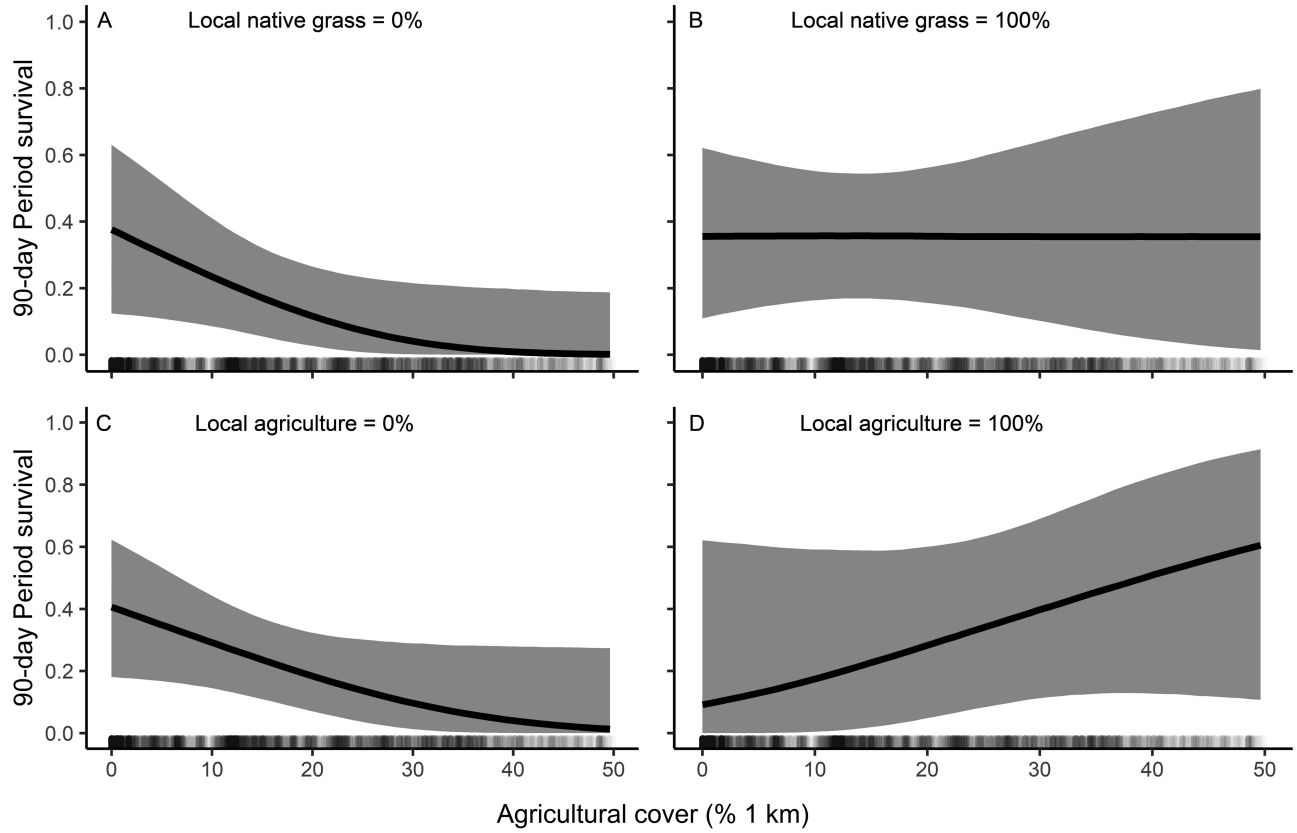

FIGURE 5. The relationship between Northern Bobwhite juvenile survival and agricultural cover within 1 km varied depending on local cover type within 50 m of individuals. Within non-native grassland cover (A) and nonagricultural cover (C), survival decreased with increasing landscape agriculture. Within local native grassland cover, survival did not vary with increasing landscape agriculture (B). Within agricultural cover, survival increased with increasing landscape agriculture (D). Mean (line) and 95% CI (ribbon) estimates of 90-day period survival of juveniles as landscape-level agricultural composition increases in southwest Missouri, 2016–2018. The band along the *x*-axis illustrates the density of survival observations of individuals across the range of values of percent landscape agricultural cover.

(95% CI: 0.40, 0.95) over 0% to 100% cover (Figure 4C). Contrary to our prediction, survival was positively related to agriculture ($\beta_{agriculture}$ = 0.38, 95% CI: 0.02, 0.74, f = 0.98; Figure 3D; Table 1), and period survival increased from 0.26 (95% CI: 0.11, 0.40) to 0.67 (95% CI: 0.32, 0.87) as local agricultural cover increased 0% to 100% (Figure 4D). Survival was negatively related to percent cover of local mixed grass that was burned (Figure 3; Table 1); period survival decreased from 0.36 (95% CI: 0.21, 0.49) to 0.01 (95% CI: 0.00, 0.37) as local burned mixed grassland cover increased 0% to 100% (Figure 4F). As predicted, survival was positively related to shrub cover ($\beta_{shrub\ cover}$ = 0.21, 95% CI: –0.08, 0.51, f = 0.92; Figure 3; Table 1); 90-day period survival increased 0.27 (95% CI: 0.12, 0.43) to 0.75 (95% CI: 0.14, 0.97) as shrub cover within 50 m of daily locations increased 0% to 52.5% (Table 1; Figures 3 and 4E). We considered several post hoc models that consisted of interactions between age (greater or less than 28 days) and idle native grassland, agriculture, shrub cover, and distance to tree but none were supported more than the model without the interaction so we did not consider them further.

Our second-ranked model evaluated interactions between effects of local native grassland and agricultural cover within 50 m of daily juvenile locations and agricultural land cover composition within 1 km of broods (Figure 5; Table 2). As predicted, survival was positively related to percent cover of local native grass ($\beta_{native\ grass\ 50\ m}$ = 0.25, 95% CI = –0.07, 0.59, f = 0.94). There was weak support for a negative relationship between survival and landscape agriculture ($\beta_{agriculture\ 1\ km}$ = –0.31, 95% CI = –0.84, 0.22, f = 0.88). Interactions between agricultural land cover composition within 1 km of juveniles and local native grassland and agricultural composition within 50 m supported our prediction that landscape context influenced the relationship between survival and local cover type (Table 2). While landscape-level agriculture in our data ranged from 0% to 92.7% cover within 1 km (mean = 16%; Supplementary Material Table S1), we reported period survival from 0%

TABLE 2. Parameter estimates from the second-ranked model (elpd diff = –1.4, SE = 4.8) of local native grassland (NatGrass) and agricultural cover (Ag) within 50 m and their interactive effects (NatGrass Ag1k, AgAg1k) with agricultural land cover composition within 1 km (Ag1k) on juvenile Northern Bobwhite survival in southwest Missouri 2016–2018 including mean, 95% CI, and proportion with the same sign as mean (*f*) of posterior distribution for the intercept, fixed effects, and standard deviation of brood and site random effects.

		95% CI		
	Mean	0.025	0.975	*f*
Intercept	4.200	3.197	5.197	1.000
NatGrass	0.254	–0.068	0.585	0.939
Ag	0.083	–0.290	0.472	0.662
Ag1k	–0.310	–0.839	0.222	0.875
NatGrass Ag1k	0.403	0.020	0.807	0.980
AgAg1k	0.476	0.112	0.856	0.995
Age	0.817	0.512	1.171	1.000
Age^2	0.210	–0.032	0.479	0.951
Year.2016	0.000	0.000	0.000	1.000
Year.2017	–0.214	–1.198	0.781	0.663
Year.2018	–0.085	–1.107	0.990	0.570
Brood	1.542	1.173	1.997	1.000
Site	0.528	0.018	2.069	1.000

to 46.8% cover because 95% of our observations were within this range. In areas with no local native grassland cover, juvenile period survival decreased with increasing landscape-level agricultural cover from 0.38 (95% CI: 0.12, 0.63; Figure 6C) to 0.00 (95% CI: 0.00, 0.19; Figures 5A and 6F). When local native grassland cover equaled 100% and local agriculture equaled 0%, landscape-level agricultural composition did not explain substantial variation in juvenile survival; period estimates remained stable from 0.36 (95% CI: 0.11, 0.62; Figure 6A) at 0% agriculture within 1 km to 0.35 (95% CI: 0.02, 0.78; Figures 5B and 6D) at 46.8% agriculture within 1 km. In areas with no local agriculture, when native grass was held at its mean, survival decreased from 0.41 (95% CI: 0.18, 0.62) to 0.02 (95% CI: 0.00, 0.28) as landscape agriculture increased from 0% to 46.8% (Figure 5C). When local agricultural cover equaled 100% and local native grass cover equaled 0%, juvenile period survival increased with increasing landscape-level agriculture from 0.09 (95% CI: 0.00, 0.62; Figure 6B) at 0% agriculture within 1 km to 0.58 (95% CI: 0.11, 0.89; Figures 5D and 6E) at 100% agriculture within 1 km.

DISCUSSION

The early development period for precocial young is often a critical influence on population growth characterized by low survival probabilities that are variable and sensitive to environmental conditions (Taylor et al. 2012, Terhune et al. 2019). In upland pine forests of Florida in the southeastern USA, 90-day-old bobwhite juvenile survival was estimated to be 0.36 (95% CI: 0.22, 0.48) and negatively related to precipitation early in the brood stage (Terhune et al. 2019). We estimated a similar 90-day-old survival probability of 0.33 (95% CI: 0.19, 0.46), although variation in survival may be influenced by different environmental factors in these distinct landscapes. We found support for our predictions that survival was greater on native grasslands managed locally with fire and grazing and areas with available shrub cover. We also discovered agricultural cover at the landscape scale modified local effects of agricultural and native grassland cover. Juvenile survival was relatively high in row crop fields within agricultural landscapes, but lower in small plots of agriculture, such as strip crop fields surrounded by grassland landscapes. Juvenile survival was similar in native grasslands in grassland and agricultural landscapes. Juvenile survival was high in non-native grasslands in grassland landscapes but low when surrounded by agricultural, such as field borders.

Juvenile survival was likely high on native grasslands that were burned and grazed as these disturbances expose bare ground, allowing movement and facilitating escape from predators, while also maintaining vegetation height for cover (Taylor et al. 1999, Harper et al. 2015, Kamps et al. 2017). These disturbances may have improved foraging efficiency, body condition, and growth of young by removing accumulated litter and increasing insect abundance (Engle et al. 2008, Doxon and Carroll 2010, Gruchy and Harper 2014, Sinnott et al. 2021a). Most burning occurred in winter and spring, and no management units were burned during the summer brood-rearing period, ensuring herbaceous cover was available for broods. Although intensive grazing may reduce productivity by removing herbaceous cover and exposing nests and young to predators, light to moderate rotational grazing practices can increase suitable breeding habitat for bobwhite and other grassland birds (Sutter and Ritchison 2005, Perlut et al. 2006, Harper et al. 2015, Behney 2021).

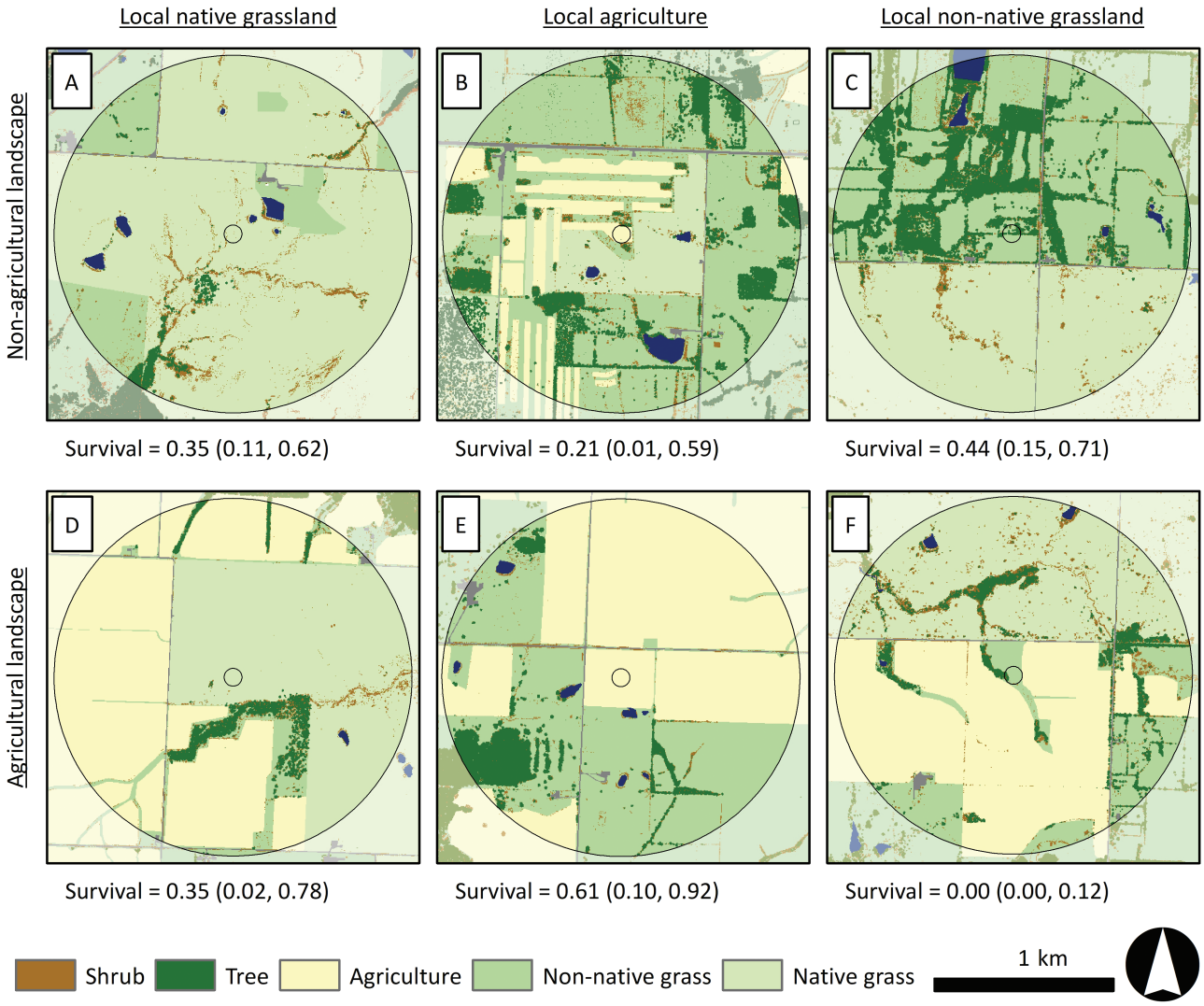

FIGURE 6. Interactive relationships of landscape agriculture (% Ag 1 km; large circle) and local habitat composition (% 50 m; small circle) with predicted 90-day period survival rates of Northern Bobwhite juveniles in southwest Missouri, 2016–2018. For each local habitat cover type—native grassland (C, D), agriculture (B, E), and non-native grassland (C, F)—predicted 90-day period survival rates at observed brood locations are given for nonagricultural landscapes (% Ag within 1 km = 0, 0.13, and 0 for A, B, and C, respectively) and agricultural landscapes (% Ag within 1 km = 0.47, 0.50, and 0.43 for D, E, and F, respectively).

We found a weak positive relationship between juvenile survival and percent shrub cover within 50 m of an individual. Broods that survived to 35 days old showed stronger selection for habitat with greater shrub cover than broods that failed (Sinnott et al. 2021c). Shrubs provide bobwhite broods important thermal refugia during peak daytime summer temperatures (Carroll et al. 2015, Tanner et al. 2017). Shrubs also provide cover for predator escape and bobwhite survival improves with proximity to shrubs throughout the full annual cycle (Perkins et al. 2014, Mosloff 2020).

We expected agriculture to negatively influence bobwhite juvenile survival as cropland monocultures may provide poor foraging habitat, reduce juvenile body condition, expose young to rainfall and temperature extremes, and increase harvest-related mortality risk (Palmer et al. 2001, Wilson et al. 2005, Sinnott et al. 2021a). Yet, we found that juvenile survival was positively related to local agricultural row crop cover, and broods readily occupied fields of soybeans, corn, wheat, and sunflower on strip crop units of public lands and surrounding private croplands. While survival was high within agricultural fields, no broods were raised exclusively in croplands; broods also used field borders and neighboring grassland habitats. Additionally, agriculture made up a smaller proportion of habitat observed at daily locations compared with native grassland habitats.

We found weak support for a negative relationship between juvenile survival and landscape agricultural

cover. There was support for an interactive effect between landscape-level agricultural cover and local native grassland and agricultural cover that suggested broods occupying local non-native grassland in landscapes with large amounts of agriculture, such as agricultural field borders, may experience greater predator pressure (Loman 1991, Pedlar et al. 1997, Dijak and Thompson 2000). However, broods in small native grasslands within agricultural landscapes had relatively high survival, suggesting that these remnant habitats may provide important islands for brood success. Wide credible intervals reflecting uncertainty in period survival estimates suggest either our data were sparse for combinations of local and landscape cover types or individual fate is highly variable in these mixed landscapes due to other unmeasured environmental factors, or both.

Population dynamics are influenced by processes acting at multiple spatial scales. Landscape context can modify local dynamics as species differentially move in response to resources and perceive barriers affecting local community composition and interactions (Tscharntke et al. 2012). We evaluated northern bobwhite juvenile survival responses to cover type and management attributes of habitat within 50 m and 1 km of daily locations. We did not identify the optimal scale of cover type and management influencing juvenile survival. It is possible scales intermediate to or outside of our 2 scales of interest have stronger impacts on juvenile survival. Other studies have found local bobwhite abundance responds positively to conservation management practices within up to 3 to 5 km of the surrounding landscape (Yeiser et al. 2018). Future research into the optimum scale of demographic responses to local habitat and landscape attributes would add insight into conservation management decisions.

Survival in small agricultural patches surrounded by nonagriculture was relatively low, suggesting that agricultural plantings for wildlife such as strip crops or food plots established as a management strategy may provide poor brood habitat. Surprisingly, brood survival was high within large agricultural fields. Crops may afford broods better visibility of oncoming predators, easier movement across bare ground, overhead cover from crop plants, and distance from predators that may occupy field edges and avoid agricultural fields (Gehring and Swihart 2003). Broods may occupy agricultural fields as a predator avoidance strategy (Gehring and Swihart 2003, Dinkins et al. 2012, Ringleman et al. 2018). These predator–prey dynamics may partially explain interactive effects of landscape-scale agricultural composition and local habitat cover on bobwhite juvenile survival.

Landscape structure can influence the effectiveness of local conservation and management practices (Tscharntke et al. 2012). While grassland bird demographic responses to fragmented habitats are unique to each species, bobwhite may be among birds that benefit from conservation practices in agricultural landscapes (Prevedello and Vieira 2010, Shahan et al. 2017, Yeiser et al. 2018, McConnell 2019). These results provide a demographic explanation for bobwhite persistence on mixed agricultural landscapes (Roseberry and Sudkamp 1998, Veech 2006; Supplementary Material Appendix S7). Local management of native grasslands with low-intensity conservation grazing and prescribed fire may achieve recruitment objectives within working agricultural landscapes. Our results further emphasize the importance of disturbance by grazing and fire to create suitable structure in native grasslands and that grasslands managed in this way may provide more suitable habitat than traditional or intensive management approaches based on food plots and strip cover. Evaluating demographic responses to both local management practices and landcover composition on heavily altered landscapes is critical for revising conservation plans to more effectively address grassland bird population declines.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Author contributions: F.R.T. and T.R.T. conceived the idea, design, and experiment (supervised research, formulated question or hypothesis). E.A.S. performed the experiments (collected data, conducted the research). E.A.S., F.R.T., T.R.T., and M.D.W. wrote the paper (or substantially edited the paper). E.A.S., F.R.T., M.D.W., and T.R.T. developed or designed methods. E.A.S. analyzed the data. F.R.T., T.R.T., and M.D.W. contributed substantial materials, resources, or funding.

Data availability: Analyses reported in this article can be reproduced using the data provided by Sinnott et al. (2021b).

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