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NORTHERN BOBWHITE DEMOGRAPHICS AND RESOURCE SELECTION ARE EXPLAINED BY PRESCRIBED FIRE WITH GRAZING AND WOODY COVER IN SOUTHWEST MISSOURI

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ABSTRACT

Understanding the effects of landscape management on northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) population growth requires information about seasonal- and stage-specific demographic parameters linked across the annual cycle. We review results to date from 3 years (2016–2018) of an intensive field study evaluating drivers of bobwhite population dynamics and resource selection during the breeding and non-breeding season in southwest Missouri, USA using data from adult and juvenile bobwhite fitted with radio-transmitters. Land cover of our study sites ranged from large blocks of native grasslands maintained with prescribed fire and grazing to more traditional management resulting in small patches of grasslands interspersed with food plots, disked idle areas, and woody cover. During the breeding season, relative probability of selection by broods increased in relation to proportion of native grass managed by grazing and burning and proportion of cropland. Brood survival was also greatest on native grasslands burned and grazed within the past 2 growing seasons. During the fall and winter,

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relative probability of selection by adults increased as woody edge density increased. Fall and winter survival increased as distance from trees increased and decreased as distance to shrubs increased. Our integrated population model indicated that the number of young hatched per female and adult breeding season survival were greatest on sites with the most native grassland managed by prescribed fire with grazing. However, non-breeding season survival was greater on sites with more agriculture or food plots and woody cover. Abundance declined across all sites from 2016 to 2019. Our work suggests that native grasslands managed by prescribed fire with grazing can provide quail habitat superior to traditional management that strived for a mixture of agriculture, woody cover, and grassland. The combination of conservation grazing and fire in native grasslands interspersed with shrubs may provide the greatest chance for bobwhite populations to persist in southwest Missouri and similar landscapes.

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Key words: *Colinus virginianus*, full annual cycle, grazing, habitat management, integrated population model, native grasslands, northern bobwhite, prescribed fire, resource selection, survival

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) have declined in abundance across their range largely due to habitat loss, fragmentation, and degradation (Brennan 1991, Williams et al. 2004, Veech 2006, Hernández et al. 2013). Bobwhite declined 80% in Missouri, USA since 1967 and the rate of decline accelerated over the past 15 years (Sauer et al. 2017). Exceptions to these declines have occurred where landscapes are purposely managed for bobwhite (McConnell et al. 2018). Declines have raised concern and generated interest in the efficacy of alternative bobwhite management strategies among conservation agencies and the public in Missouri and elsewhere. Yet in many areas of the bobwhite's range the influence of management practices on specific vital rates, and the relative influence of seasonal vital rates on changes in abundance are not well understood (Sandercock et al. 2008). This is especially true in the grassland-dominated landscapes of southwest Missouri. The National Bobwhite Conservation Initiative (NBCI 2.0; Palmer et al. 2012) and the Missouri Department of Conservation (MDC) identified this region of Missouri as having high quail restoration potential, yet bobwhite populations are declining there.

Since the 1970s, quail management in Missouri has focused on providing an interspersion of grass, food plots or cropland, disked idle areas, old fields, and woody cover with the goal of providing all essential habitat components within a 16.2-ha area; we refer to this as traditional management. Traditional management can produce usable quail habitat in agriculture-dominated landscapes (Klimstra and Roseberry 1975, Burger et al. 1995*a*) but may not be the most effective or efficient approach in expansive grassland-dominated landscapes, such as those in southwest Missouri. MDC managers historically implemented traditional management in these grass-dominated landscapes. However, in the early 2000s, managers recognized that large native grasslands maintained with prescribed burning and conservation grazing were supporting stable quail populations. Prescribed burns with grazing and mowing produce a patchy grassland mosaic which enhances species richness and structural diversity on native tallgrass prairies, mimicking fire and herbivory characteristic of historical disturbance regimes (Collins et al. 1998, Fuhlendorf et al. 2008). Heterogeneity in cover created by burning and grazing in large native grasslands is in contrast to purposeful interspersion of food plots, grass plantings, shrub, and tree cover that is more common under traditional management. We refer to these 2 different combinations of management practices and resulting land cover as grassland management and traditional management. We acknowledge grassland management and traditional management share some common management practices, but the amount of each practice and resulting land covers can vary greatly and they provide useful concepts for defining 2 ends of a gradient across sites in southwest Missouri.

Wildlife biologists began surveying for quail on selected conservation areas in southwest Missouri in 2005 and detected greater densities of quail on some grassland managed sites compared to traditionally managed sites. MDC conducted a pilot study in 2012 and radio-tagged 30 birds on Robert E. Talbot Conservation Area, which is a more traditionally managed site, and 30 birds on Stony Point Prairie, which is a grassland management area. Biologists found that birds on Stony Point Prairie (the grassland site) nested earlier and earlier nests were more successful, resulting in greater production compared to Robert E. Talbot Conservation Area (K. Hedges and F. Loncarich, MDC, personal communication).

Recent studies of bobwhite demographics using a meta-analysis (Sandercock et al. 2008), local or regional models (Gates et al. 2012, Williams et al. 2012, McConnell et al. 2018), or population viability models (Guthery et al. 2000, DeMaso et al. 2014, Rosenblatt et al. 2021) have highlighted the influence of fecundity and adult survival on population growth and viability. However, key demographic components, such as chick survival and recruitment, and their relationships to habitat management and landscape context remain largely unknown. In particular, bobwhite chick survival remains the least studied demographic rate in wild bobwhite populations, although in several recent population models (Sandercock

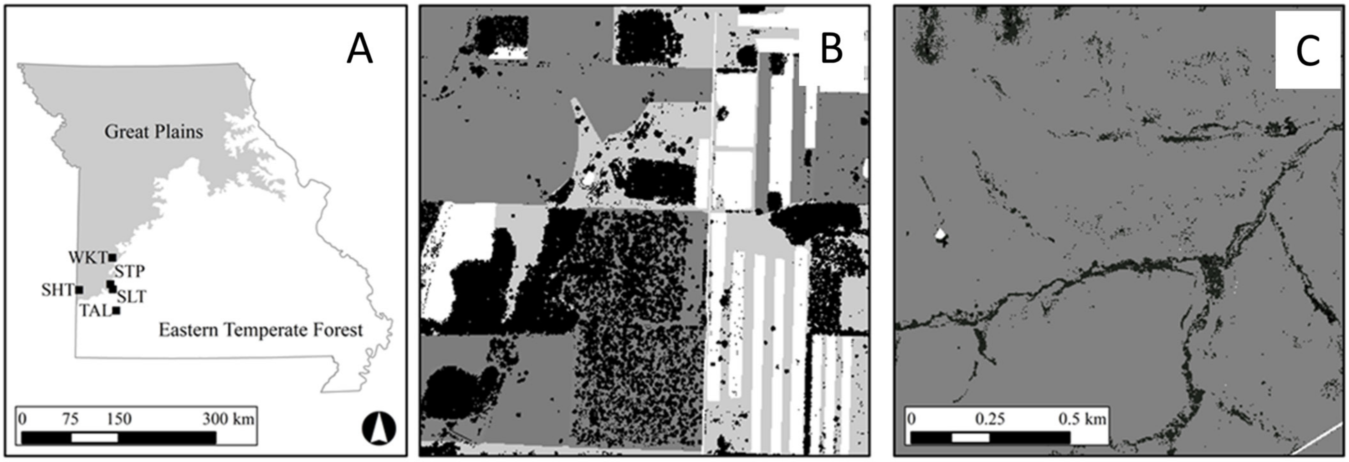

Fig. 1. A) Location of 5 study sites in southwest Missouri, USA: Shawnee Trail (SHT), Shelton (SLT), Stony Point (STP), and Talbot (TAL) Conservation Areas and Wah'Kon-Tah Prairie (WKT); B) portion of a traditionally managed site that includes food plots (white) and nonnative grass plantings (light gray), woody cover (black), and native grassland (dark gray); C) grassland managed sites were mostly native grassland with limited woody cover.

et al. 2008, Gates et al. 2012, Williams et al. 2012, Peters 2014) chick and brood survival and their contribution to annual fecundity have been identified as key demographic parameters in determining the finite rate of growth (λ) in bobwhite populations. Additionally, estimates used in these population models varied and were not necessarily based on direct estimates of survival (only 2 out of 9 were based on telemetry; Suchy and Munkel 2000, Lusk et al. 2005), but instead were based on brood counts conducted at 7 days, 14 days, and 21 days post-hatch (DeVos and Mueller 1993, Pucket et al. 1995, DeMaso et al. 1997, Mueller et al. 1999).

Based on knowledge gaps in bobwhite demographics and observations of potentially greater abundance and production under grassland management, MDC initiated a 5-year research project in 2014 to compare spring and summer adult survival, production, and resource use among sites managed by traditional management and grassland management. The study was expanded in 2016 to include juvenile survival from hatch to 100 days old and resource use across these sites. It was expanded again in 2017 to include evaluation of fall and winter juvenile and adult survival and resource use. Results from these studies have described resource selection by these cohorts (Mosloff et al. 2021, Sinnott et al. 2021*b*), survival and its relationship to management, local vegetation, and landscape factors (Mosloff 2020, Sinnott 2020, Sinnott et al. 2021*a*), and relationships between seasonal vital rates and full annual cycle population dynamics (Sinnott 2020). Our objective in this paper is to synthesize how management and land cover affect bobwhite demography and resource selection throughout the annual cycle in southwest Missouri based on these studies. While we focus on reviewing results of these studies, we also provide short descriptions of methods and analyses, and refer readers to the original publications for more details. We refer to these projects collectively as the Southwest Missouri Quail Study.

STUDY AREA

The Southwest Missouri Quail Study occurred in southwest Missouri from February 2014 to May 2019. We studied 5 sites: Shawnee Trail Conservation Area (1,471 ha; hereafter, Shawnee Trail), Robert E. Talbot Conservation Area (1,764 ha; hereafter, Talbot), Wade and June Shelton Memorial Conservation Area (130 ha; hereafter, Shelton Memorial), Stony Point Prairie Conservation Area (516 ha including 169 ha of adjacent private land; hereafter, Stony Point Prairie), and Wah'Kon-Tah Prairie (1,226 ha; Figure 1A). Shawnee Trail and Talbot Conservation Areas are at the traditional end of the management spectrum, where management focused on small units (<1–24 ha) of food plots, woody vegetation, grassland, and some larger cropland and grassland units. Management 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 (Figures 1B, 2A, 3). Shelton Memorial and Stony Point Prairie Conservation Areas and Wah'Kon-Tah Prairie are at the grassland end of the management spectrum. They had no food plots or cropland and were >80% native grassland managed by fire, grazing, and brush hogging, which created heterogeneity in grassland composition and structure and varying amounts of scattered shrub cover (Figures 1C, 2B, 3). Prescribed burning and conservation grazing used low-intensity grazing of 1 animal unit (454 kg of cattle)/1.6–2 ha for 90–120 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 or after each burn in a burning cycle. Prescribed burns occurred September–April. For additional details on study site composition and management see Mosloff et al. (2021), and Sinnott et al. (2021*a*).

Fig. 2. A) Example of traditional management on Talbot Conservation Area, Missouri, USA, including agricultural strip crops and linear wooded edges among grassland units; B) example of grassland management on Stony Point Prairie, Missouri, consisting of continuous remnant or reconstructed prairies managed with fire, grazing, and mowing (photo by David Stonner, Missouri Department of Conservation, used with permission).

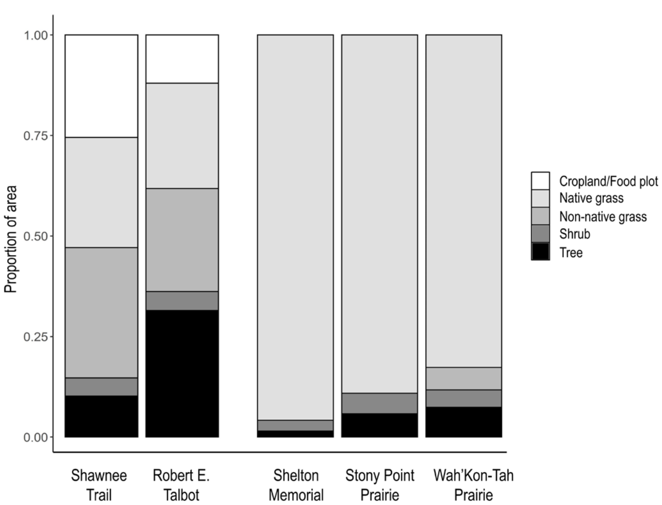

Fig. 3. Proportion of study sites in southwest Missouri, USA in different land cover types, 2016–2018.

METHODS

We conducted bobwhite spring whistle counts 15 May–1 July during 2016–2018 on Shawnee Trail (*n* = 16 listening stations), Shelton Memorial (*n* = 2), Stony Point Prairie (*n* = 8), Talbot (*n* = 16), and Wah'Kon-Tah Prairie (*n* = 18). We recorded the number of birds calling within 500 m during a 10-minute period between sunrise and 0900 during 1–3 visits annually to each station.

We captured and radio-tagged bobwhite to measure survival, fecundity, and resource use. Bobwhite were captured using funnel traps in February and March 2014–2018 and fitted with uniquely numbered leg bands and 6-g necklace style radio-transmitters (model AWE-QII, American Wildlife Enterprises, Monticello, FL, USA). We located birds at least 3 times/week by homing in on birds and recorded locations on a hand-held Global Positioning System to monitor adult breeding season survival and locate nests. Success of nests incubated by radio-collared birds was monitored to estimate the number of eggs hatched/adult as a measure of fecundity.

We captured broods of radio-tagged adults at approximately 20 days old and fitted them with backpack transmitters (model AWE-QC-0.8 and AWE-QC-0.65, American Wildlife Enterprises, Monticello, FL, USA) using the suture technique to estimate juvenile breeding season survival in 2016–2018 (Terhune et al. 2020). Broods were tracked on average 6 days/week and at each location we collected data on cover type, management, and woody vegetation composition using maps derived from field observations, remotely sensed land cover data, and LiDAR data (Sinnott et al. 2021*a*, *b*).

We captured bobwhite using funnel traps in September and October 2017–2018 and radio-tagged adults and juveniles for non-breeding season survival estimates and resource selection. We located birds approximately 3 times/week from 1 November to 31 January. Similar to brood locations, we collected data on cover type, management, and woody vegetation composition using maps derived from field observations, remotely sensed land cover data, and LiDAR data (see Mosloff 2020, Mosloff et al. 2021 for details).

Data Analysis

Brood resource selection.—We evaluated population-level, age-specific patterns in bobwhite brood resource selection during the juvenile development period using integrated step selection analysis within a Bayesian hierarchical modeling framework. This approach evaluated resource selection and daily movement decisions in a conditional logistic regression that included both a habitat utilization kernel and a movement kernel (Avgar et al. 2016). We sampled 10 available locations for every one used location by projecting 10 empirically sampled step lengths and randomly selected turning angles based on observed consecutive daily locations. Vegetation characteristics at end points of each used step were then compared to projected end points of each available step (Sinnott et al. 2021*b*).

Fall and winter resource selection.—We modeled bobwhite fall and winter resource selection as a function of vegetation structure, composition, and management with a multinomial logit discrete choice model in a Bayesian framework. We fit conditional multinomial logit discrete choice models to model the probability that an individual selected a location given a choice among 3 locations available at one time (i.e., forming a choice set; Cooper and Millspaugh 1999, Thomas et al. 2006, Mosloff et al. 2021).

Brood survival.—We estimated juvenile survival from hatch to 90 days and related it to cover type composition and grassland management (i.e., conservation grazing, prescribed burns, mowing and haying) at the local (50 m) and landscape (1 km) scale with a Bayesian known-fate logistic exposure model (Sinnott et al. 2021*a*).

Fall and winter survival.—We estimated fall and winter survival and its relationship with hypothesized drivers using a known-fate logistic exposure model (Shaffer 2004, Shaffer and Thompson 2007). We included covey identity and site as random effects and age (juvenile, adult) and month as fixed effects. We then examined support for various combinations of local (50 m)- and landscape (1 km)-scale cover type composition and grassland management (i.e., conservation grazing, prescribed burns, mowing and haying; Mosloff 2020).

Integrated population model.—We developed an integrated population model (IPM) that linked spring whistle counts with nest monitoring and telemetry data to estimate abundance, fecundity, and survival, in order to model population change for each site (Schaub et al. 2007, Schaub and Abadi 2011, Kéry and Schaub 2012, Zipkin and Saunders 2018). We used a 2-stage, 2-sex periodic matrix design comprising the breeding season (1 May–31 Oct) and non-breeding season (1 Nov–30 Apr) to account for differences in survival and productivity among adults and juveniles, and males and females among our sites (Burger et al. 1995*a*, Sandercock et al. 2008). We included sex-specific productivity rates because bobwhite are polygamous and both females and males contribute to fecundity (Curtis et al. 1993; Burger et al. 1995*a*, *b*). We fit our IPM in a Bayesian framework with a joint likelihood and prior probability distributions for estimates of abundance, survival, and productivity. Details on each of the component likelihoods are described further in Sinnott (2020).

RESULTS

Brood Resource Selection

Sinnott et al. (2021*b*) reported on resource selection behavior of 101 bobwhite broods for a total of 2,790 step choice-sets from 2016 to 2018. These data contained 627 steps (movements) by 80 broods ≤14 days old, 1,092 steps by 91 broods 15–35 days old, and 1,071 steps by 45 broods 36–114 days old. A model that included all proposed habitat drivers and brood age class had strong support compared to other models, including a null model. Relative probability of selection increased in relation to proportion of native grass managed by grazing and burning and proportion of cropland for all brood age classes (Figure 4). Relative probability of selection increased greatly with

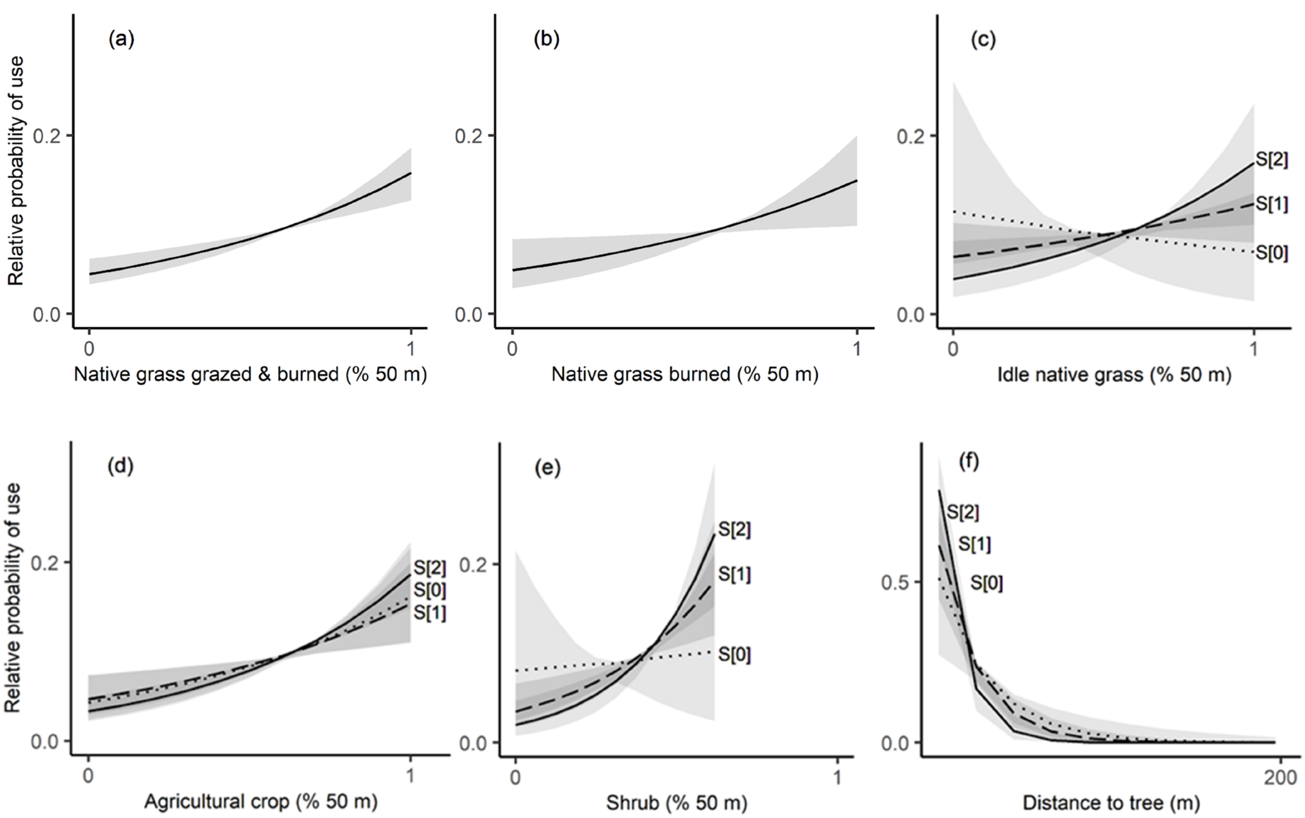

Fig. 4. Predicted relative probability of use of sites by northern bobwhite (*Colinus virginianus*) broods in southwest Missouri, 2016–2018, as a function of percent cover within 50 m of native grassland that was A) burned and grazed, or B) only burned and not grazed within the past 2 years; and stage-dependent predicted relative probability of use as a function of percent cover within 50 m of C) idle native grassland, D) agricultural crop, E) shrub cover; F) predicted relative probability of use as a function of distance to nearest tree for young flightless broods ≤14 days old (S[0]; dotted line), dependent broods 14 to 35 days old (S[1]; dashed line), and independent broods >35 days old (S[2]; solid line). Adapted from Sinnott et al. (2021*b).*

proportion of idle native grass for the older 2 age classes, but less so for the youngest broods. Relative probability of selection increased with proportion of shrub cover for the oldest 2 age classes. Counter to predictions, relative probability of selection decreased as distance to trees increased (Figure 4; Sinnott et al. 2021*b*). Broods that survived to 35 days showed stronger selection for shrub cover than broods that failed.

Fall and Winter Resource Selection

Mosloff et al. (2021) reported on resource selection based on 119 bobwhite tracked in the fall–winter of 2018–2019 and vegetation data on 650 used locations and 3 associated random locations for a total of 650 choice sets in their discrete choice analyses. We ranked competing models based on the Watanabe-Akaike Information Criterion and their null model had the least support. We summarized effects based on their top supported model and effects for which >0.85 of the posterior distribution indicated a positive or negative effect. Bobwhite selected locations closer to trees in winter but not in fall. Bobwhite also selected locations with lower percentage of grass cover at the location during fall but not winter. Bobwhite selected for locations with greater visual obstruction in winter, but not fall, and more woody stems in fall and winter. The relative probability of selection increased as woody edge density increased in fall and winter, respectively (Figure 5).

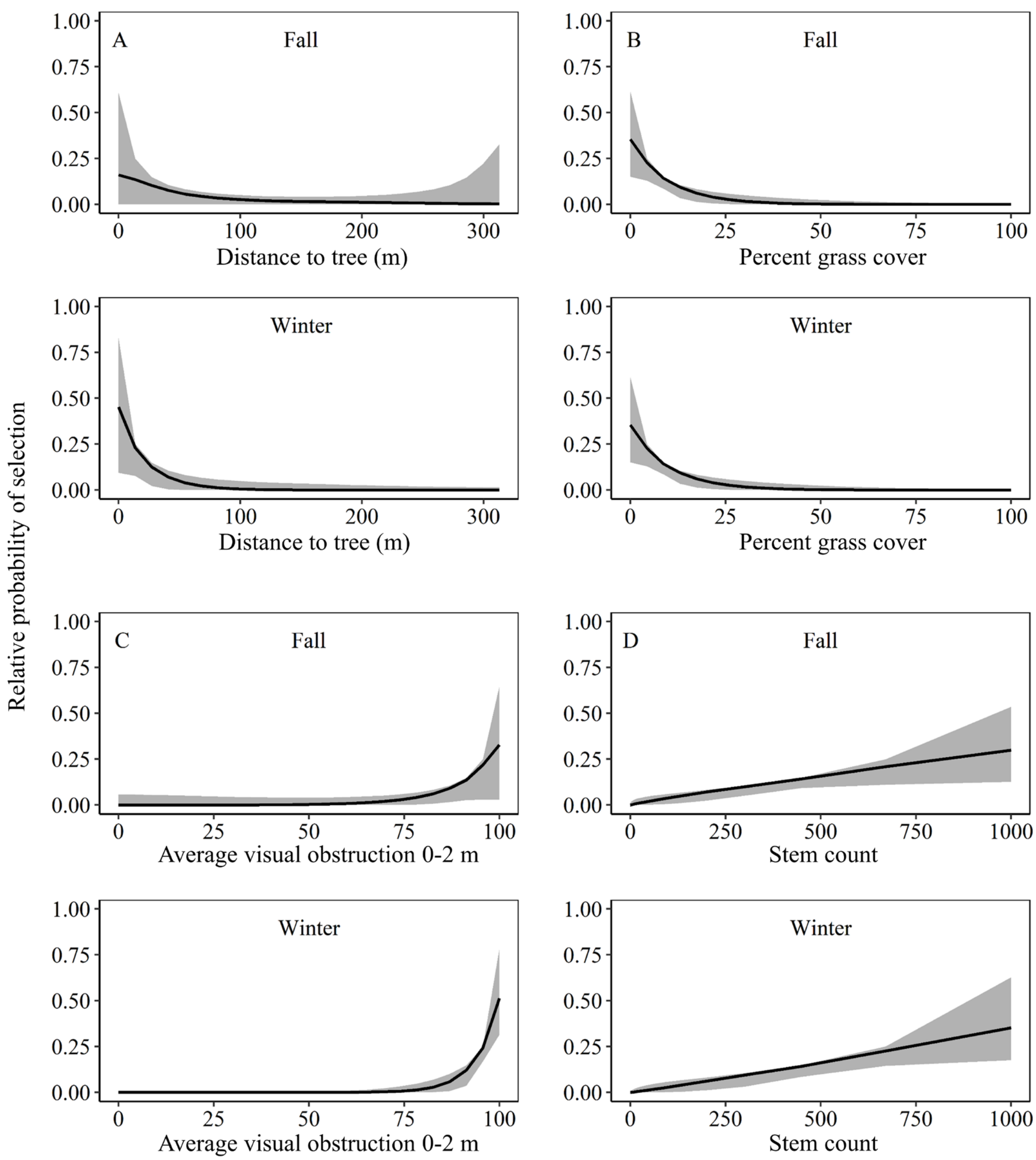

Fig. 5. Predicted relative probability of use of sites by northern bobwhite (*Colinus virginianus*) in fall and winter in southwest Missouri, USA, 2018–2019, as a function of A) distance to the nearest tree (m), B) percent grass cover measured by Daubenmire frame, C) average visual obstruction (0–2 m), and D) woody stem count in a 5-m radius. Adapter from Mosloff et al. (2021).

Brood Survival

Sinnott et al. (2021a) monitored survival of 705 individuals from 75 broods from hatch to up to 114 days old for 14,904 exposure days. Daily survival was a quadratic function of age and increased from 0.96 (95% credible interval [CrI]: 0.91–0.99) post-hatch to 1.00 (95% CrI: 0.99– 1.00) at 114 days old, for 90-day period survival of 0.33 (95% CrI: 0.18–0.46). We drew inferences on survival from the top 2 supported models which evaluated local habitat management effects and interactive effects of landscape-scale agriculture and local-scale native grassland, as well as agricultural cover on juvenile survival. Consistent with predictions, local native grasslands burned and grazed in the past 2 growing seasons had the largest positive effect on daily juvenile survival. Period survival increased from 0.21 to 0.84 as native grasslands burned and grazed within 50 m increased from 0% to 100% (Figure 6). Effects of grazed mixed grasslands were also positive and period survival increased from 0.32 to 0.81 over 0% to 100% cover. Period survival increased from 0.27 to 0.75 as percent shrub cover increased from 0% to 53%. Contrary to predictions, percent agriculture cover had a positive effect, and percent mixed grass burned had a negative effect on survival (Figure 6; see Sinnott et al. 2021a for additional details).

Fall and Winter Survival

Mosloff (2020) analyzed observations from 2,068 locations of 186 radio-tagged bobwhite from 1 November–31 January 2017–2019. She fit 10 candidate models and interpreted effects from the top 2 supported models. Based on her top model, 90-day period survival was 0.68 (95% CrI: 0.58–0.77) for juveniles and 0.78 (95% CrI: 0.61–0.89) for adults. As predicted, period survival increased from 0.67 to 0.89 as distance to trees increased from 0 m to 306 m. Period survival also decreased from 0.77 to 0.31 as distance to shrubs increased from 33 m to 160 m (Figure 7). Contrary to predictions, there was no support for a positive effect of native grasslands and vegetation managed with prescribed burning and grazing.

Integrated Population Model

Three rounds of bobwhite spring whistle counts were conducted annually on Shawnee Trail, Shelton Memorial, and Stony Point Prairie 2016–2018. Two rounds were conducted on Talbot in 2017; 3 rounds were conducted in 2016 and 2 rounds in 2017 and 2018 on Wah'Kon-Tah Prairie. We tracked 766 juveniles and 618 adults during the breeding season and monitored success of 276 nests incubated among 576 adults active on 1 May at the start of the breeding season across all years. We monitored 772 juveniles and 349 adults to estimate non-breeding season survival probabilities (see Sinnott 2020 for details).

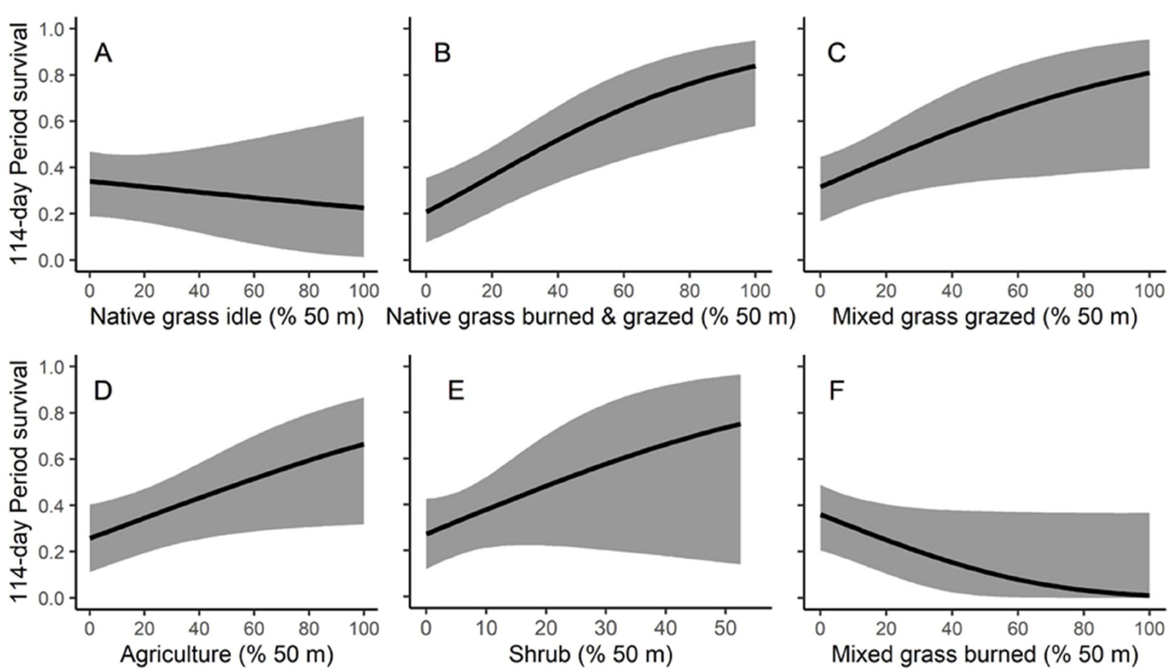

Fig. 6. Period survival estimates increased as B) proportion of native grasslands managed with fire and grazing, C) grazed mixed grasslands, D) agriculture, and E) shrub cover within 50 m of northern bobwhite (*Colinus virginianus*) juveniles increase in southwest Missouri, USA, 2016–2018. Period survival estimates decreased as (F) proportion of burned mixed grasslands within 50 m of daily locations increased and estimates did not vary with A) proportion of native grasslands left idle for at least 2 years. Mean (line) and 95% credible interval (ribbon) 90-day period survival of juvenile northern bobwhite were based on selected effects from the top-ranking cover type and management model describing percent cover composition within 50 m of daily locations.

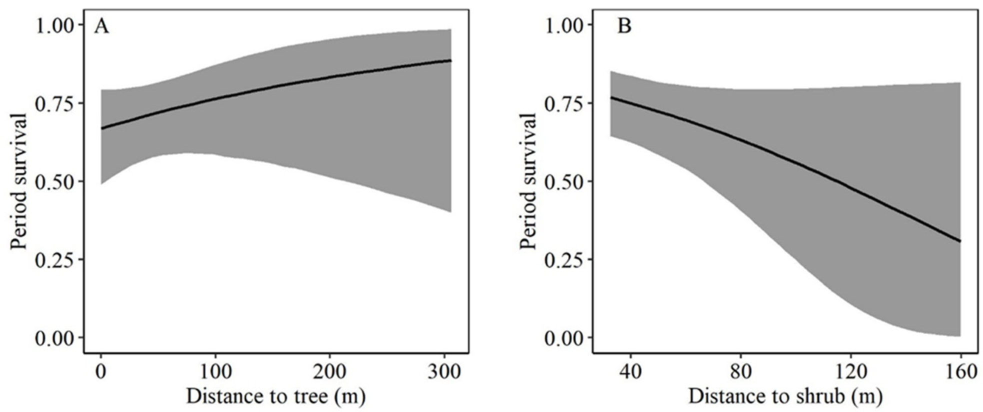

Fig. 7. Bobwhite fall and winter 90-day period survival and 95% credible interval as a function of A) distance to tree (m) and B) distance to shrub (m) in southwest Missouri, USA, November–January 2017–2019.

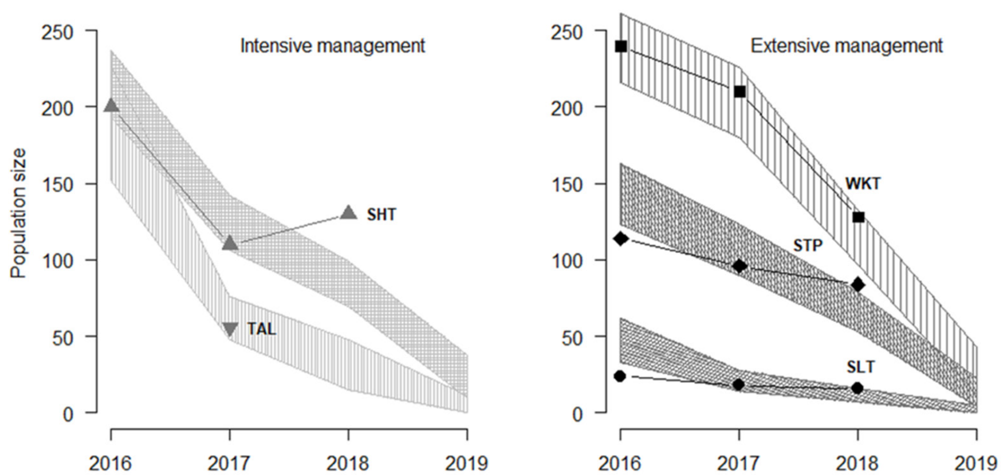

Fig. 8. Northern bobwhite (*Colinus virginianus*) population counts (points) and estimated abundances (ribbons) for (on left) 2 traditionally managed sites, Shawnee Trail (SHT) and Talbot (TAL), and (on right) 3 grassland managed sites, Shelton Memorial (SLT), Stony Point Prairie (STP), and Wah'Kon-Tah (WKT), in southwest Missouri, USA, 1 May 2016–2018.

Spring whistle counts showed declining trends for all sites with 3 consecutive years of survey data 2016–2018 (Figure 8). All spring counts were within the 95% CrI of male abundance estimates except for Shawnee Trail 2018, which was estimated low (Figure 8). Across all years, mean population growth was greater on grassland management sites ($\lambda = 0.48$, 95% CrI: 0.00–0.90) compared to traditionally managed sites ($\lambda = 0.41$, 95% CrI: 0.05–0.75) though both estimates indicated that declines had large credible intervals. Population growth was highest on the largest grassland managed site, Wah'Kon-Tah Prairie ($\lambda = 0.55$, 95% CrI: 0.13–0.94) and lowest on a traditionally managed site, Talbot ($\lambda = 0.31$, 95% CrI: 0.03–0.65).

Female fecundity was greater on grassland managed sites (4.07, 95% CrI: 2.34–6.09) than traditionally managed sites (2.38, 95% CrI: 1.11–5.62; Figure 9). Female breeding season adult survival was also greater on grassland managed sites (0.48, 95% CrI: 0.32–0.64) than traditionally managed sites (0.33, 95% CrI: 0.18–0.50; Figure 9). However, counter to expectations, non-breeding season survival was not greater on grassland managed sites (0.36, 95% CrI: 0.11–0.59) compared to traditionally managed sites (0.42, 95% CrI: 0.16–0.64; Figure 9). Non-breeding season survival varied across sites and Talbot, a traditionally managed site, had the highest mean non-breeding season survival, followed by Wah'Kon-Tah Prairie, the largest grassland managed site. The 2 smaller grassland managed sites, Stony Point Prairie and Shelton Memorial, had the lowest non-breeding season survival (Figure 9).

We compared site-level vital rate estimates to the subset of posterior samples that resulted in a population growth rate ≥ 1.0 to identify which seasonal vital rates most limited population growth at each site. Female fecundity and adult breeding season survival at traditionally managed sites were lower than rates that resulted in a stable population growth rate (Figure 8). Non-breeding season survival probability at 2 grassland managed sites, Shelton Memorial and Stony Point Prairie, were also lower than rates that resulted in stable population size (Figure 9).

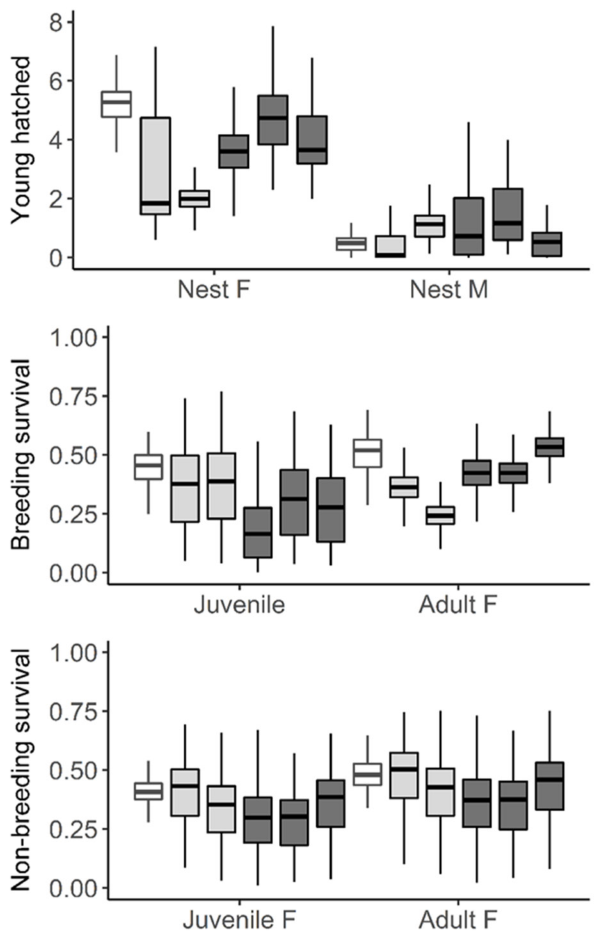

Fig. 9. Boxplots of posterior distributions of northern bobwhite (*Colinus virginianus*) seasonal vital rates in southwest Missouri, USA, 2016–2018. The first box plot for each vital rate represents a subset of posterior samples that resulted in a stable population growth rate (white; $\lambda \geq 1.00$). Observed site-level vital rates are then given in the following order for each vital rate: Shawnee Trail and Talbot (light gray, traditionally managed sites), then Shelton Memorial, Stony Point Prairie, and Wah'Kon-Tah Prairie (dark gray, grassland managed sites). Fecundity was estimated as the number of young hatched per female-incubated nest (Nest F) and male-incubated nest (Nest M). Posterior distributions of breeding and non-breeding season survival were estimated as 6-month period survival probabilities for juveniles (Juv) and adult females (Adult F). Posterior distributions of non-breeding season survival were estimated as survival probabilities for juvenile females (Juv F) and adult females (Adult F).

DISCUSSION

We synthesized 6 years of research on northern bobwhite demography and resource selection in southwest Missouri and generally found support for the idea that prescribed fire with grazing on native grasslands can provide quail habitat superior to more traditional management. Bobwhite preferred conditions created by grassland management or had greater vital rates there and these findings held among different stages of their life history. However, grassland management was not better for all stages or components of bobwhite demography. For example, bobwhite broods selected for agricultural fields and non-breeding season survival was greater on traditionally managed sites.

Resource selection by broods was strongest for native grasslands that were both burned and grazed at least once within the previous 2 years and also positive but weaker for native grasslands that were just burned or grazed the previous 2 years. Broods likely selected for burned and grazed native grasslands because these management practices provided adequate cover, open bare ground, and high invertebrate abundance for juvenile foraging, growth, mobility, and survival (Hurst 1972, Taylor et al. 1999*a*, Engle et al. 2008, Doxon and Carroll 2010, Kamps et al. 2017). Contrary to our predictions, broods also selected for row crop and idle agricultural fields. We expected row crops to provide suboptimal foraging habitat (Puckett et al. 1995, Palmer et al. 2001, Doxon and Carroll 2010, Lohr et al. 2011), but instead we found that row crops enabled broods to move easily and potentially allowed better sight of approaching ground predators, while likely providing adequate overhead cover from aerial predators. Though young broods did not select for shrub cover, older broods did. Shrubs provide protection from warm daytime temperatures and escape cover from predators (Carroll et al. 2015).

Woody cover was the primary driver of resource selection during fall and winter. As we predicted, bobwhite selected areas with greater woody edge density and more woody stems (indicative of shrub cover). Bobwhite also used areas with high woody edge density in Illinois, USA (Roseberry and Sudkamp 1998), Kansas, USA (Williams et al. 2004), Kentucky, USA (Brooke et al. 2015), and Ohio, USA (Janke and Gates 2013). Shrubs provide escape cover from predators and shelter from extreme weather (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). Contrary to our predictions, selection was negatively related to distance from trees. Trees can harbor predators such as opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), and raptors (Dijak and Thompson 2000, Byrne and Chamberlain 2011), and as discussed later, we found fall-winter survival was lower closer to trees. Bobwhite also select woodlots in other parts of their range (Lohr et al. 2011, Janke and Gates 2013). We suggest bobwhites often used shrub cover on our sites that was in close proximity to trees in more permanent woody cover such as riparian areas and fencerows, and that trees have the potential to be ecological traps.

Brood survival was greater on native grasslands managed with fire and grazing and areas with available shrub cover than in other management and vegetation types. Burning and grazing expose bare ground and allow movement and escape from predators while maintaining overhead cover (Taylor et al. 1999*a*, Harper et al. 2015, Kamps et al. 2017). These practices also can improve foraging efficiency 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. 2021*a*). Contrary to predictions, survival was not greater on landscapes with more native grassland cover nor did mowing, local agriculture, or proximity to trees decrease survival.

As predicted, fall-winter survival was greater closer to shrub cover and farther from trees. Woody cover is often reported as an important component of winter cover (Seckinger et al. 2008, Gates et al. 2012, Janke et al. 2015). Trees, however, provide perches for raptors, and raccoons and other mammalian predators have greater movement and activity near trees and forest edges (Brown and Amadon 1968, Brown 1976, Dijak and Thompson 2000, Chamberlain et al. 2002, Seckinger et al. 2008, McClain 2017).

Results from our IPM suggest changes in bobwhite abundance were related to site-level variation and differences in seasonal vital rates between grassland and traditional management. Female fecundity and breeding season adult survival were greatest on grassland managed sites and were likely the reason population growth rate was also greater on grassland managed sites. Age- and sex-specific differences in seasonal survival and male contributions to fecundity emphasized the importance of accounting for population structure and composition in the full annual cycle demography of bobwhite. Contrary to our prediction, non-breeding season survival was not greater on grassland managed sites. Indeed, non-breeding survival was highest on a traditionally managed site and lowest on 2 small (<400 ha) grassland managed sites (Sinnott 2020). Traditionally managed sites included food plots while grassland managed sites did not, and perhaps this was a factor in winter survival. We also speculate that other contributing factors, such as hunting pressure (Roseberry 1979, Williams et al. 2000), predator community composition (Lohr et al. 2011, Atuo and O'Connell 2017), and habitat in the surrounding landscape also impacted site-level variation in bobwhite non-breeding season survival. We recommend that future research further explore these drivers to improve conservation planning and management on grassland and traditionally managed areas.

MANAGEMENT IMPLICATIONS

We suggest that overall, grassland management has provided better bobwhite habitat than traditional management in these grassland landscapes in southwest Missouri. Prescribed burning with conservation grazing was implemented on the southwest Missouri sites to promote a shifting mosaic that facilitates brood use since at least one-third to one-half of each area was disturbed each year. Coupling grazing and fire on tallgrass prairies and grasslands promotes heterogeneity in vegetation structure and composition (Fuhlendorf and Engle 2004, Veen et al. 2008), and provides fine-scale grass, forb, and shrub cover in native grasslands, which positively influences breeding season survival and fecundity. Disturbance from fire and grazing also creates more suitable structure by removing litter and reducing vegetation density. While fire is clearly beneficial to birds during the breeding and non-breeding seasons, burning at intervals >1 year may promote greater non-breeding season survival. Our work consistently showed negative effects of tree cover on bobwhite survival so reducing tree cover could result in greater survival. We believe that a management combination of fire and grazing, and landscape composition of grassland with interspersed shrubs, will provide the greatest chance for bobwhite populations to persist in southwest Missouri and similar landscapes.

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