

ENVIRONMENTAL DRIVERS OF NORTHERN BOBWHITE FALL AND WINTER
SURVIVAL AND RESOURCE SELECTION IN SOUTHWEST MISSOURI

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by
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SURVIVAL AND RESOURCE SELECTION IN SOUTHWEST MISSOURI
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ENVIRONMENTAL DRIVERS OF NORTHERN BOBWHITE FALL AND WINTER SURVIVAL AND RESOURCE SELECTION IN SOUTHWEST MISSOURI

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined over the last 50 years throughout the majority of their historical range, primarily due to habitat loss and degradation caused by modern farming practices, increased urbanization, succession of native grasslands to forests, decreases in native pasture acreage and increases in grazing intensity. Recent questions regarding conservation grazing and prescribed burning management regimes and extensive grassland management suggest further information on vegetation and management effects on bobwhite demographics is necessary for robust conservation planning. Information regarding the survival and resource selection through fall and winter is necessary to create a holistic management plan which benefits bobwhite at all stages of their annual cycle. Therefore, our objective was to determine the relationship of bobwhite survival and resource selection to vegetation types and management practices to fill in knowledge gaps of their annual cycle and demography.

We used known-fate, logistic exposure survival models to estimate survival of birds fitted with tracking devices. We used 2068 bobwhite locations from 1 Nov to 31 Jan, 2017–2018 and

2018–2019 to fit 7 models that represented competing hypotheses concerning the amount of native grass, intensive and extensive management, and woody cover. Variation in survival was not explained by the amount of native grass managed by prescribed burning and grazing on the landscape. However, survival was negatively related to prescribed burning. Survival was negatively related to the distance to shrubs but not related to shrub edge density or proportion of shrub cover within 50 m. Survival was also positively related to the distance from the nearest tree.

We used conditional multinomial logit discrete models to evaluate the relationship of vegetation and management types to bobwhite resource selection by comparing covariates among the used point and a set of random points that defined a choice set for each bobwhite location. We used 671 choice sets from 1 Nov 2018 to 31 Jan 2019 to fit 6 candidate models in a model selection framework which represented combinations of our hypothesized drivers of bobwhite fall and winter resource selection. We found no support for an effect of native warm season grasses or the effect of prescribed burning and grazing on resource selection. Bobwhite selected locations with greater woody stem counts and greater visual obstruction, both of which are indicative of shrub cover, and there was a weak positive relationship with woody edge density. However, bobwhite also selected locations that were closer to trees. We found weak support for negative effects of the percentages of forb and bare ground at a given location on resource selection, while there was a negative effect of grass on winter resource selection.

Woody cover was an important component of vegetation contributing to fall and winter survival and resource selection of bobwhite in Missouri. More specifically, proximity to shrubs and distance from trees were positively related to survival. Greater quantities of woody stems, indicative of shrub thickets also increased the relative probability of selection. Interestingly,

closer proximity to trees also increased the relative probability of selection, potentially indicating an ecological trap. While necessary, the utility of native grasslands for bobwhite is greatly diminished if they do not contain shrub cover. Prescribed burning is perhaps the most effective tool to manage native grasslands for bobwhite habitat as it simultaneously promotes native grass quality, removes litter, and prevents shrub cover from dominating the landscape and succeeding to trees. While prescribed fire is important for controlling woody vegetation and for the creation of breeding, nesting, and brood rearing habitat, its short-term effect was to reduce survival of bobwhite in the fall and winter. We suggest that application of prescribed fire on short intervals at large scales will likely reduce the quality of habitat available to bobwhite during the fall and winter seasons. However, the use of fire in a multiyear rotation in combination with grazing in native and restored grasslands can create the needed interspersion of shrub cover for fall and winter while meeting the other annual resource needs of bobwhite. Felling mature trees while still maintaining adequate interspersion of shrubs may also prevent an ecological trap because survival was lower nearer trees. Lastly, while our study focused on fall and winter habitat, we suggest conservation planning and management needs to consider quail needs throughout their full annual cycle.

THESIS FORMAT

This thesis is comprised of chapters written as separate manuscripts to be submitted for publication in peer-reviewed journals. Chapters may include repeated content, but have their own literature cited sections. The plural noun “we” is used in place of “I”. Additionally, format for each chapter may differ depending on target journal for each manuscript.

CHAPTER 1

ENVIRONMENTAL DRIVERS OF NORTHERN BOBWHITE SURVIVAL DURING FALL AND WINTER

ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined over the last 50 years throughout the majority of their historical range, primarily due to habitat loss and degradation caused by modern farming practices, increased urbanization, succession of native grasslands to forests, decreases in native pasture acreage and increases in grazing intensity. Recent questions regarding conservation grazing and prescribed burning management regimes and extensive grassland management suggest further information on vegetation and management effects on bobwhite demographics is necessary for robust conservation planning. We modeled bobwhite fall and winter survival as a function of environmental drivers on traditionally (intensively) managed sites and extensively managed grasslands managed with fire and grazing in southwestern Missouri using known-fate, logistic exposure models in a Bayesian framework. We captured and tracked 184 individuals, obtained 4,430 bird locations, and detected 80 mortalities November – January 2017/2018 and 2018/2019. Adults had greater survival than juveniles (Posterior Mean [PM]: 0.42, 95% Credible Interval [CRI]: -0.17, 1.02). Prescribed burning within the last 12 months had a strong negative effect on survival (PM: -1.06, 95% CRI: -1.84, -0.24). Survival increased with the distance from tree (PM: 0.18, 95% CRI: -0.15, 0.53) but decreased with the proximity to shrubs (PM: -0.16, 95% CRI: -0.35, 0.04). Bobwhite fall and winter survival benefited from being close to shrubs but distant from trees, and was lower in areas recently burned. We emphasize the importance of considering these relationships within the context of year-round habitat needs of bobwhite.

INTRODUCTION

Northern bobwhite (*Colinus virginianus*, hereafter bobwhite) are a short-lived species that have experienced consistent declines in abundance across the majority of their historical range over the last 50 years (Stoddard 1931, Brennan 1991, Sauer et al. 2011). In the early 1990s, researchers predicted that by 2005 bobwhite detectability per hour of observer effort would effectively be zero (Brennan 1991). Bobwhite are a shrub-obligate species that require early successional, woody cover interspersed throughout grasslands. Their decline, is at least in part due to the loss of more than 97% of native grasslands in the United States (NABCI 2011), primarily due to modern farming practices, increased urbanization, the planting of trees, decreases in native pasture acreage, increases in non-native vegetation throughout rangelands, and increases in grazing intensity (Roseberry et al. 1979, Roseberry and Klimstra 1984, Brennan 1991, Capel et al. 1995, Veech 2006).

Habitat loss and degradation are likely the primary cause for the decline of bobwhite but populations are also influenced by hunting, natural mortality, and predation (Guthery et al. 2000). In particular, late season hunting negatively impacts bobwhite populations (Robinette and Doerr 1993, Peterson 2001, Williams et al. 2004, Rolland et al. 2010), and predation negatively impacts bobwhite survival at all life stages (Rollins and Carroll 2001). Avian predators often perch along tree edges (Chamberlain et al. 2002, Seckinger et al. 2008) and are most abundant during migration periods. Mesomammals such as bobcats (*Felis rufus*), coyotes (*Cain latrans*), opossums (*Didelphis marsupialis*), and raccoons (*Procyon lotor*) are also known predators of bobwhite (Stoddard 1931, Rollins and Carroll 2001). Fluctuations in the harvest of furbearers due to changing social and market trends have resulted in decreased hunting and trapping for bobwhite predators (Conlee and Johnston 2018). Subsequently, predator abundance has

increased throughout bobwhite range (Peoples et al. 1995). Extreme winter weather also negatively impacts bobwhite survival (Folk et al. 2007, Gates et al. 2012, Williams et al. 2012). Remaining bobwhite habitat must be properly managed to promote persistence of bobwhite populations. However, further understanding the interactions among habitat (DeMaso et al. 2014), and natural and hunting mortality are required (Sandercock et al. 2008).

Bobwhites are a shrub-obligate species that require dense, early successional, woody cover (i.e., shrubs) interspersed throughout grasslands in a way that the woody cover is immediately accessible for escape cover from predators (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). Shrub-scrub and other early successional vegetative habitats succeed to trees without proper management. Forests may provide bobwhite escape cover and loafing sites when shrubs are limited (Lohr et al. 2011). However, forests and tree edges may also provide habitat for predators of bobwhite (Seckinger et al. 2008). Further, landscapes dominated by forests with overstory canopy cover greater than or equal to 60% have a bobwhite occupancy probability near zero (Crosby et al. 2013), likely because canopy cover greater than 60% limits the production of grass, forb, and shrub species required by bobwhite (Peitz et al. 1997, Cram et al. 2002).

Bobwhite also use bare ground, shrubs, and forbs that grow in conjunction with native warm season grass for nesting, feeding, and brood rearing habitat (Stoddard 1931, Doxon and Carroll 2010). Native warm season grasses such as big blue stem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), little blue stem (*Schizachyrium scoparium*), and switchgrass (*Panicum virgatum*), provide higher quality habitat for bobwhite than non-native grasses such as tall fescue (*Festuca arundinacea*; Washburn et al. 2000, Yeiser et al. 2015). Schroeder (1985) found that quality winter feeding areas include 25–60% bare ground. Similarly, typical roost

sites consist of loose, sparse vegetation of 30–90 cm in height that have no accumulation of litter (Klimstra and Ziccardi 1963). Native, warm season grass that is not actively managed does not provide the bare ground and vertical vegetative structure required for forage and roost cover (Stoddard 1931, Barnes et al. 1995, Yeiser et al. 2015).

Agriculture is responsible for the loss of 70% of the world's grasslands and 50% of savannahs (Foley et al. 2011, Ramankutty et al. 2008). Growing farm sizes and monocultures have replaced what was historically a highly fragmented landscape of small farms, fence rows, and pastures. Population declines in bobwhite are strongly tied to these changes in agricultural land use (Murphy 2003). Many researchers have suggested that the elimination of grass edges and fencerows have contributed to the decline of bobwhite (Brennan 1991, Warner 1994). In addition, fields that are left bare over winter create expansive unusable space for bobwhite during a critical period in their annual cycle (Sandercock et al. 2008).

Research addressing the impacts of extensive management techniques on fall and winter survival is lacking. Land managers historically adopted an intensive management system in an attempt to reconstruct historical patterns of interspersed vegetation types required for nesting, foraging, brood rearing and escape cover, generally located within 40 ac of each other. Intensive, or traditional, management mimics the formerly fragmented landscapes of the late 19th and early 20th century United States through the use of small agricultural units, native grasses, and shrub rows closely interspersed throughout the landscape to create heterogeneity. Management may include small prescribed burns (5–20 ac), in addition to mowing, disking, and herbicide use. Extensive management creates heterogeneity at a fine scale within grasslands. Prescribed burning and grazing are used to create irregular interspersed shrubs throughout grasslands. Extensive management provides forage through native grasses and forbs instead of agricultural

units. Fire and grazing provide the disturbance needed to provide a balance of grasses and forbs, and bare ground for foraging. There is debate among researchers and managers whether intensive management negatively or positively impacts survival, dispersal, and resource use of bobwhite (Sisson et al. 2000, Fies et al. 2002, Sisson et al. 2002, Cook 2004, Hughes et al. 2005). We hypothesize that the potential benefits of extensive management (e.g., increased grassland and shrub cover) are reliant on the heterogeneity created by prescribed burn and grazing rotations. Williams et al. (2004) addressed the necessity to prioritize the creation of usable bobwhite habitat at regional scales as opposed to the single farm management scales (i.e. intensive management) historically recognized by conservation practitioners and suggested that modern management should occur at broader scales such as multiple farms or physiographic regions.

The native grasslands historically inhabited by bobwhite evolved with fire and ungulate grazing (Fuhlendorf and Engle 2004). Therefore, it is intuitive that management via prescribed burning and grazing, often referred to as extensive or grassland management, would provide the disturbance necessary to maintain grassland ecosystems suitable for bobwhite. Prescribed fire is a common management tool for bobwhites which inhibits woody encroachment, creates relatively low, sparse vegetation necessary for quail roosts, and increases plant diversity (Stoddard 1931, Ellis et al. 1969, Brennan et al. 1998, Fuhlendorf and Engle 2004). Prescribed grazing can increase plant species diversity, richness, and production (Howe 1994, Hickman et al. 2004) and can also prevent succession of shrubs to forests (Penfound 1964) under certain grazing system. The fire-grazing interaction model proposed by Fuhlendorf and Engle (2004) predicts that when a patch is regularly burned and focally grazed, tall graminoid species will decrease while bare ground and forbs will increase. The importance of this interspersed of tall graminoids, bare ground, and forbs for bobwhite broods is undisputed (Lehmann 1984, De Vos

and Mueller 1993, Taylor et al. 1999). However, it is not yet well understood how the interaction of prescribed fire and grazing affect fall and winter survival.

Knowledge regarding the interactions of bobwhite with fire is limited within their western distribution (Renwald et al. 1978, Carroll et al. 2017). Prescribed fire is common during the winter season when vegetation is dormant. However, individual bobwhite may be particularly vulnerable to the effects of disturbance during late winter. Carroll et al. (2017) discovered that mean covey home range sizes decreased when prescribed fire was applied to the landscape, suggesting that habitat 25–35 months post-fire was “excellent” or “good”. However, prescribed fire also temporarily alters vegetation structure and reduces opportunities for foraging and escape cover. Kamps et al. (2017) found that adult survival was negatively associated with larger fire sizes and cautioned that prescribed fires should be planned to balance chick growth and adult survival. Research that directly examines the relationship between prescribed fire and fall and winter survival would better inform bobwhite management.

Land managers have recently expressed interest in converting from an intensive management style to a more extensive management approach that uses prescribed burning and grazing, to create vegetative structural diversity advantageous to bobwhites during the breeding season. However, more information regarding the impacts of intensive and extensive management techniques and the difference between the two on the fall and winter survival of bobwhite is necessary to make appropriate management decisions. Our objective was to estimate fall and winter survival of juvenile and adult bobwhite and determine relationships between survival and vegetation characteristics and management treatments within the context of intensive and extensive management approaches. We hypothesized that fall and winter survival (1 November–31 January) would be positively related to: 1) the proportion of managed native

warm season grass on the landscape managed by prescribed burning and grazing, both independently and combined; 2) proximity to shrubs and greater shrub edge density compared to all other vegetation types; and 3) distance from trees and less tree edge density compared to all other vegetation types.

METHODS

Study Area

We conducted our research on 5 Missouri Department of Conservation (MDC) conservation areas in southwest Missouri: Robert E. Talbot Conservation Area (Talbot), Shawnee Trail Conservation Area (Shawnee Trail), Stony Point Prairie Conservation Area (Stony), Wade and June Shelton Memorial Conservation Area (Shelton), Wah'Kon-Tah Prairie Conservation Area (Wah'Kon-Tah; Figure 1). This region has been identified as having high potential for successful bobwhite habitat management and population recovery in Missouri (The National Bobwhite Technical Committee 2011). Sites were dominated by big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*) grasses. Cool season and mixed grass pastures contained large quantities of fescue (*Festuca acundinacea*). Dominant shrubs and trees included sumac (*Rhus* spp.), blackberry (*Rubus* spp.), plum (*Prunus* spp.), dogwood (*Cornus* spp.), and oak (*Quercus* spp.). The surrounding counties (Barton, Cedar, Dade, Lawrence, and St. Clair) were largely converted to pasture, forestland, cultivated crops, and urban development (Homer et al. 2015, USDA National Agriculture Statistics Service Cropland Data Layer 2015).

Sites varied in history, size, and management strategy. Shelton (129.5 hectares), Stony (388.5 hectares), and Wah'Kon-Tah (943.3 hectares) were remnant prairies. These areas were

extensively managed using a combination of fire, grazing, brush hogging, haying, high clipping, and herbicide to maintain a grassland landscape. Grazing, mowing, and prescribed burns were used to mimic the pyric herbivory of historic disturbance and enhance the overall biological diversity of the area (Collins et al. 1998, Fuhlendorf et al. 2009). Talbot and Shawnee Trail were intensively managed sites (1764.4 and 1471 hectares, respectively) composed of agriculture, food plots, woody cover, and planted grassland managed by prescribed grazing, mowing, and prescribed burning. Agricultural practices occurred historically on Shawnee Trail and cattle grazing occurred on Talbot prior to land acquisition by MDC and before this study. Several of the agricultural units have since been restored to native grass and mixed-prairie on both Shawnee Trail and Talbot. All areas used patch burn grazing (Fuhlendorf and Engle 2004) to a degree, but varied in proportion of area this extensive management technique.

All sites were managed with prescribed burning and grazing throughout the duration of the study. Average burn unit sizes were generally larger on extensively managed sites (approximately 50–100 acres) than intensively managed sites (approximately 10–40 acres). Prescribed burning typically occurred on a 3–5-year rotation with extensively managed sites burned more frequently than intensively managed sites. Prescribed burning occurred from January to April and August to December. Prescribed burn units which are managed concurrently with prescribed grazing (i.e., patch burn grazing) were generally burned from February to April. Extensively managed sites, primarily comprised of native grasslands, were typically grazed at a stocking rate of 1 animal unit (AU) per 5.5 acres where 1 AU is 1,000 pounds of cattle with grazing durations ranging from 90 to 180 days. Intensively managed sites, primarily comprised of planted cultivar grasses with more robust growth rates, were grazed at a

higher intensity of 1 AU per 4 acres with grazing durations ranging from 90 to 120 days (personal communication, K. Hedges, Missouri Department of Conservation).

Quail Captures and Tracking Devices

We captured bobwhite using funnel traps baited with cracked corn and milo (Stoddard 1931). We located capture sites where bobwhite were observed by field staff and near locations of bobwhite radio tagged in an ongoing breeding season study. We attempted to mark individuals from as many unique coveys as possible. Capture sites were pre-baited for 4 to 10 days prior to placement of a funnel trap. Funnel traps were weighed down with bricks and covered with cedar (*Juniperus virginiana*) boughs to prevent predators from locating trapped bobwhite and to provide protection from inclement weather. We checked traps two to four hours after sunrise and no earlier than 30 min before sunset to reduce the amount of time birds spent in traps. We did not trap if severe weather (e.g., heavy rainfall) was expected that could harm trapped individuals. We removed a trap from a site if an individual was captured three times to reduce exposure to trapping. We ceased trapping and removed all evidence of trapping (i.e., bait, cedar boughs, and flagging) prior to November 1 each year, because that was the opening of the bobwhite hunting season in Missouri. All captured individuals which met weight requirements were fitted with transmitters during the first year of the study to ensure sufficient sample sizes of marked individuals while the number of individuals fitted with transmitters were restricted to ≤ 4 per covey during the second year to maximize the number of coveys with marked individuals.

We marked bobwhite with a uniquely numbered leg band (National Band & Tag Company, Newport, KY, USA) and individuals >100 grams were fitted with a pendant-style radio transmitter that weighed 5.3–5.5 grams (model AWE-QII from American Wildlife

Enterprises, Monticello, FL, USA). We recorded sex, age class (i.e., adult or juvenile; Petrides and Nestler 1943, Petrides and Nestler 1952), weight (g), and tarsus length (mm) and released individuals at their capture site. While attachment of transmitters may handicap birds using marginal habitats (Sandercock et al. 2008), studies based on large samples of marked individuals with rigorous mark-recapture methods have not detected a negative effect of tracking devices on bobwhite survival (Parry et al. 1997, Palmer and Wellendorf 2007, Terhune et al. 2007). All animal procedures were approved under University of Missouri Animal Care and Use Committee protocol #8766.

Quail Locations

We attempted to locate bobwhite three times per week from 1 November to 31 January each fall through winter by homing to within 10 m of each individual (White and Garrott 1990). We recorded this location with a Global Positioning System (GPS) unit, as well as the distance and azimuth to the bobwhite. One location was recorded for coveys and individuals were assumed to be in the same covey if they were located within 10 m of each other. We used triangulation from two or more points (White and Garrott 1990) to locate individuals on property we did not have access to. We attempted to not flush individuals.

We searched for individuals that we could not locate by radio telemetry at least once per week by intensively searching the area surrounding the last known location and by searching the larger, surrounding area using a dipole omnidirectional antenna on local roads. After 12 hours of no movement the transmitters emitted a fast pulse rate at which point we located the transmitter and classified it as either a dropped transmitter or a mortality. If a transmitter was located with no apparent damage to it and no sign of predation, it was considered dropped and included in the

analysis as alive up to that day. If a transmitter showed evidence of damage, was located with a dead bobwhite, or near sign of a predator (e.g., predator was observed with carcass, transmitter was in an animal burrow, or was located in scat), it was considered a mortality event. Individuals that were classified as a drop or mortality within the first 7 days of the tracking period (1 November–31 January) were completely eliminated from the dataset. At each location, we recorded the vegetation classification, management that had been conducted, and if the individual was in a tree edge, shrub, or both at each location.

Vegetation and Management Classifications

Maps of vegetation and management types were provided by land managers for each study site. We considered up to 13 unique vegetation types: Native Prairie (NP), Restored Prairie (RP), Mixed Grass (MG), Cool Season Grass (CS), Native Grass Planting (NG), Agriculture (AG), Idle Agriculture (ID), Food Plot (FP), Strip Crop (SC), Shrub-scrub (SS), Savanna (SA), Woodland (WD), and Timber (TI). Management was identified as grazed (GR), prescribed burn (PB), mowed (MW), hayed (HA), woody removal (WR), bullhogging (BH), and sprayed (SP).

We improved mapping of shrubs and trees by using airborne light detection and ranging (LiDAR) data from the years 2014 (Vernon and Barton counties) and 2016 (Bates, St. Clair, Cedar, Dade and Lawrence counties) that were publicly available from the Missouri Spatial Data Information Service (<http://www.msdis.missouri.edu>). Shrubs, trees/tree edges, and forests are often associated with ground cover consisting of grasses and forbs. We created separate rasters at 3.6 m resolution to represent shrubs and trees by classifying vegetation height from 0.7 to 3.5 m as shrub, and 3.5 to 40 m as trees following George et al. (2017).

Ecological factors operating at different scales influence bobwhite habitat occupancy and survival (Howell et al. 2009). At a more localized scale, herbaceous and woody cover should be interspersed such that bobwhite are not more than 30 m from either vegetation type (Hernandez and Guthery 2012) and The National Bobwhite Conservation Initiative Coordinated Implementation Plan does not consider habitat further than 50 m from woody protective cover (i.e., vegetation which provides overhead protection from predators and weather year-round) as suitable habitat (Morgan et al. 2016). At larger landscape scales, Cram et al. (2002) found a strong effect of the amount of suitable habitat (e.g., habitat managed with wildlife stand improvement and fire) within 400 m of a sampling unit on relative abundance of bobwhite. Crosby et al. (2013) determined the probability of bobwhite occupancy was negatively related to canopy cover, positively related to early successional habitat, and positively related to the amount of potential habitat within 1 km of the sampling unit. Therefore, we assessed the influence of vegetation, vegetation height, and management metrics on bobwhite locations at each of three scales surrounding bobwhite locations: 50 m, 400 m, and 1 km.

We condensed vegetation and management classifications in ArcGIS (ESRI 2018) to ecologically meaningful categories that directly addressed our hypotheses: native grass, prescribed burned, and prescribed grazed. Given that native warm season grasses provide higher quality habitat for bobwhite than non-native grasses such as tall fescue (Washburn et al. 2000, Yeiser et al. 2015), we hypothesized that bobwhite survival would increase as the proportion of native grass throughout the landscape increased. We categorized native grass as any parcels within a conservation area that were native prairie, native grass planting, and restored prairie identified as primarily native grass via field verification, regardless of associated management technique. We calculated the proportion of land surrounding an individual's location that was

native grass (NG) compared to all other available cover types to evaluate our hypothesis that survival is positively related to the proportion of native grass on the landscape. We also modeled the proportion of land that was managed via prescribed burning and grazing because unmanaged native grass quickly loses value for bobwhite. To evaluate our hypothesis that survival was positively related to the proportion of land prescribed burned and grazed on the landscape across all cover types, we calculated the proportion of parcels which were managed with either prescribed burning or grazing, or both, within two years prior surrounding an individual's location (PG). We also created a binary variable which indicated whether a bobwhite was located in an area that was prescribed burned (PB) within 12 months prior to January 31.

Bobwhite also require woody cover as refuge from predators (Davis 1964, Roseberry and Klimstra 1984, Williams et al. 2000). We hypothesized the proximity to shrubs and the density of shrub edges on the landscape positively impacts fall and winter survival while proximity to trees and increased density of tree edges negatively impacts fall and winter survival. Therefore, we created variables which quantified the distance to the nearest shrub (SD), the density (m/ha) of shrub edge (i.e. the border between shrubs and other vegetation types) surrounding an individual's location (SE), and the proportion of shrub cover surrounding an individual's location (ST). We believed that the relationship between survival and the proportion of shrub cover may not be linear, so we also considered a quadratic relationship for the proportion of shrub cover surrounding an individual's location (shrub cover + shrub cover²; SS). We calculated the distance from the nearest tree (TD) and the density (m/ha) of tree edges surrounding an individual's location (TE) to evaluate our hypothesis that survival was explained by a positive relationship with the distance from the nearest tree and negatively related to the density of tree

edges compared to all other vegetation types. Each landscape metric was quantified within a radius of 50 m, 400 m, and 1 km.

We calculated all landscape metrics (e.g., percent cover, distance to shrub or from tree) using the landscapemetrics package (Hesselbarth et al. 2019) in program R version 3.6.0 (R Core Team 2019). We standardized all covariates prior to model runs (Table 1) and assessed multicollinearity among variables by calculating variance inflation factors (VIF) using the car package (Fox and Weisberg 2019) in Program R version 3.6.0 (R Core Team 2019) and ensured all variables within candidate models had a VIF <2.5 (Allison 1995, Kutner et al. 2004). We created a final model set which directly evaluated our hypotheses comprising combinations of these variables.

Survival Analyses

Known fate, logistic exposure models (Dinsmore et al. 2002, Shaffer 2004, Shaffer and Thompson 2007) are commonly used to estimate nest survival and survival of birds fitted with tracking devices (Matthews et al. 2011, Gates et al. 2012, Matthews et al. 2012, Anich et al. 2013). We assigned a covey identification number (covey ID) to each unique combination of individuals located within 50 meters of each other at the time of resighting. We included covey identity as a random effect in all models to account for non-independence among marked individuals occurring within the same covey. We also included site as a random effect in all models to account for potential increased homogeneity of responses of individuals within a study site and account for any unmeasured effects that varied by site. We developed models in a Bayesian framework using Markov chain Monte Carlo (MCMC) algorithms in JAGS (Plummer 2003) via the package jagsUI 1.5.0 in Program R version 3.6.0 (R Core Team 2019). We used a

Bernoulli distribution and a modified logit link function to estimate daily survival as an exponential function of the number of days between locations with hypothesized covariates and random effects.

We considered a single individual from a random sample of marked individuals in a hypothetical population. We let t be the number of days (i.e., observation interval) between resightings of that individual. The probability of an individual surviving a given observation interval was $\theta = s^t$, where s was a daily survival rate that depended on the value of an explanatory variable, X . The random component of this generalized linear model was the binomial distribution with probability of survival equal to θ .

The daily survival rate was modeled in terms of X which represented our hypothesized covariates influencing fall and winter survival:

$$S \sim \text{Bernoulli}(\theta),$$

$$g(\theta) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \varepsilon^S + \varepsilon^C,$$

where θ was the binary response variable for alive or dead, β_0 was the intercept with assumed normal distribution, mean 0 and variance σ^2 , X_1 to X_3 were covariates for age (adult compared to juvenile), and the months of December (December compared to November) and January (January compared to November), respectively. The terms ε^S and ε^C were random effects for site (s) and covey (c), respectively, and both were assumed to follow normal distributions with mean 0 and variance σ^2 .

We included a logistic-exposure link function (Shaffer 2004) to calculate daily survival and account for unequal time periods between locations:

$$g(\theta) = \log_e \frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}}$$

where t was the number of days between resightings. This link function included the exponent ($1/t$) in the numerator and denominator to account for the fact that the probability an individual survived an interval was an exponential function of the length of the interval.

We predicted that survival was dependent on age and month, with adults experiencing higher survival than juveniles, and all individuals experiencing lower survival as winter progressed. Thus, we initially evaluated models consisting of: 1) no fixed effects, 2) age (juvenile or adult), 3) month, and 4) age + month to determine the most parsimonious model that accounted for these intrinsic or temporal effects. Age and month explained substantial variation in survival and were included in all additional models with vegetation and management factors. We used the most supported scale for each cover type and management effect in a final model set of combinations of effects which we hypothesized would explain variation in fall and winter survival. We constructed a model to represent each hypothesis: native grass managed with prescribed burning and grazing (m4), distance to and density of shrub edges (m1), and distance from and density of tree edges (m8); as well as ecologically-meaningful combinations of our hypotheses (m2, m3, m6, m7, m9, m10), a null model (m8), and a model (m5) which directly evaluates the impacts of intensive and extensive management (Table 2).

Our model estimates were based on 3 chains of 10,000 iterations, a burn-in of 4,000 iterations, a thinning rate of 2, and a posterior sample of 9,000, with the exception of model 5 (m5) which required 3 chains of 20,000 iterations, a burn-in of 4,000 iterations, and a thinning rate of 2 in order to achieve convergence. Diffuse normal priors were used for the regression parameters and diffuse uniform priors for the standard deviation parameters. We evaluated model convergence by visual inspection of MCMC chains and ensured the Gelman-Rubin convergence statistic was <1.1 (Brooks and Gelman 1998). We calculated the proportion of

posterior samples less than or greater than zero according to direction of posterior mean to measure relative strength of covariate relationships (Zhao et al. 2018).

We compared support among models based on the Watanabe-Akaike Information Criteria (WAIC; Watanabe 2013) because WAIC estimates expected out-of-sample-prediction error by averaging the entire posterior distribution and then corrects for the effective number of parameters within the model (Gelman et al. 2014) We present the posterior mean values as an estimate of the mean effect, 95% credible intervals for the model parameters, and the proportion of the posterior distribution with the same sign as the mean (which can be interpreted as the probability the effect is negative or positive) when the credible interval spanned zero. We present predicted fall and winter survival estimates for the period 1 November to 31 January each year for supported parameters while holding all other covariates at their means.

RESULTS

We captured 136 bobwhite from 27 unique coveys and attached transmitters to 101 individuals in 2017. After censoring, 44 and 39 individuals were used for analyses from intensively and extensively managed sites, respectively, and no individuals were captured on Shelton. We captured 158 bobwhite from 67 unique coveys and attached transmitters to 119 individuals in 2018. We captured 23, 3, 34, 14, and 31 juveniles at Shawnee Trail, Shelton, Stoney Point, Talbot, and Wah’Kon-Tah, respectively. We captured 19, 4, 21, 20, and 20 adults at Shawnee Trail, Shelton, Stoney Point, Talbot, and Wah’Kon-Tah, respectively. After censoring, 30 and 73 individuals were used in analyses from intensively and extensively managed sites, respectively. We obtained 2,068 locations of bobwhite during 2017–2018 and

2,595 locations during 2018–2019. Thirty-nine of 83 individuals survived from 1 October 2017 to 31 January 2018 and 43 of 103 survived from 1 October 2018 to 31 January 2019.

We fit ten candidate models and interpreted effects from model 1 (m1), and model 2 (m2) because they were $<2 \Delta\text{WAIC}$ of the top model (Table 2). We did not interpret model 3 (m3) because it did not include supported effects that were unique from m1 and m2 (Table 2). We found no support for our hypothesis that survival was positively related to the proportion of managed native warm season grass on the landscape managed by prescribed burning and grazing (independently and combined). Contrary to our hypothesis, survival was lower at locations that were prescribed burned within the last 12 months. Our hypotheses that survival was positively related to proximity to shrubs and distance from trees were supported, however, our hypotheses that survival was positively related to greater shrub edge density and less tree edge density were not supported. Further, the proportion of shrubs within 50 m of the locations and the associated quadratic term do not appear to describe substantial variation in survival. Effect sizes were similar among models so refer to the effect size of a covariate in the highest ranked model it occurred in (Table 3). We found no support for a difference in survival between intensively and extensively managed sites (m10; Table 2).

Age explained substantial variation in survival and adults had greater survival than juveniles (Table 3; Figure 2). Based on our top model (m1), 90-day survival was 0.68 (95% credible interval [CRI]: 0.58, 0.77) for juveniles and 0.78 (95% CRI: 0.61, 0.89) in adults (Figure 3A). Survival varied by month (Table 3, Figure 2) and was 0.75 (95% CRI: 0.68, 0.81) in November, 0.81 (95% CRI: 0.65, 0.91) in December, and 0.63 (95% CRI: 0.38, 0.80) in January (Figure 3B).

Contrary to our hypothesis, we found no support for an effect of native grasslands and vegetation managed with prescribed burning and grazing was negatively related to survival at 1 km interval, but did not in the top two models (Table 2). However, prescribed burning within the last 12 months had a strong negative effect on survival (Table 3; Figure 2). Ninety-day period survival was 0.46 (95% CRI: 0.14, 0.76) for individuals located in areas that were prescribed burned within the last 12 months and 0.76 (95% CRI: 0.64, 0.84) for individuals in land parcels that were not prescribed burned within the last 12 months (Figure 3C).

As hypothesized, survival increased with the distance from trees (Figure 2). Based on model m2, survival increased from 0.67 (95% CRI: 0.49, 0.79) to 0.89 (95% CRI: 0.40, 0.99) as distance from trees increased from 0 to 306 meters (Figure 4A). We did not find support for an effect of tree edge density. Consistent with our hypothesis, survival was positively related to proximity to shrubs (Figure 2). Period survival based on model m1 decreased from 0.77 (95% CRI: 0.64, 0.85) to 0.31 (95% CRI: 0.00, 0.82) as distance to shrubs increased from 33 to 160 meters (Figure 4B). We did not find support for an effect of shrub edge density, or the quadratic form of proportion of shrub cover within 50 m (Table 2).

DISCUSSION

The greatest contributors to fall and winter survival in our study were age, month, proximity to shrubs, distance from trees, and prescribed burning. Our survival rates were greater than those previously reported for similar seasonal intervals. Burger et al. (1995) reported fall-spring (1 Oct-31 Mar) survival rates of 0.159 in northcentral Missouri while Williams et al. (2004) estimated 0.209 survival from Nov-Jan in east-central Kansas where study sites experienced 60% harvest. Winter (15 Oct-10 Apr) survival rates were estimated to be 0.375 in

Tennessee (Seckinger et al. 2008). In Oklahoma, monthly survival estimates were 0.727, 0.544, and 0.565 in November, December, and January, respectively (Cox et al. 2004). Low fall and winter survival rates can be major contributors to the characteristically low annual survival of bobwhites (Guthery et al. 2000, Hughes et al. 2005, Folk et al. 2007, Sandercock et al. 2008, Janke et al. 2015).

Previous research has shown that survival can be explained by site management (Terhune et al. 2009) and composition (Seckinger et al. 2008). Fall and winter survival was explained by a negative relationship with the occurrence of prescribed burns in the previous 12 months in our study. Fall and winter burns can negatively impact fall and winter survival by decreasing usable space, forcing relocation to unfamiliar or less desirable territory (Folk 2006), and potentially increasing predation (Hovick et al. 2017). In Kentucky, disking, prescribed burning, and herbicide treatments negatively affected nonbreeding season bobwhite survival because burning increased cover of native warm season grasses from 49% to 77%, which resulted in a proportionally larger amount of decomposed native grass during fall and winter (Tanner 2012, Peters et al. 2015). Thus, we suggest that prescribed burning should be used at suitable burn intervals and in conjunction with other management techniques such as grazing to maintain proper forb densities, bare ground, and shrub cover.

The importance of woody cover to bobwhite during winter has been commonly reported (Seckinger et al. 2008, Gates et al. 2012, Janke et al. 2015). Janke et al. (2015) also found that early-successional woody cover was the most influential driver of survival, specifically early-successional woody cover, whereby woody-edge density with 95 m of the location was the largest contributor to winter survival. Distance to shrubs was negatively related to bobwhite survival, supporting our hypothesis that survival was positively related to the proximity of shrub

cover. However, we found no support for our hypothesis that survival was positively related to the density of shrub edges in comparison to all other available vegetation types. This may be because overall, there was an adequate amount of shrub cover, but its spatial distribution was variable so proximity to shrub cover was important.

Survival also was explained by a positive relationship with the distance from the nearest tree. Trees can provide perches for raptors, which are common predators of bobwhite (Chamberlain et al. 2002, Seckinger et al. 2008). Raccoons also are bobwhite predators and have greater movement and activity near trees and forest edges (Brown and Amadon 1968, Brown 1976, Dijak and Thompson 2000, McClain 2017). Therefore, survival of bobwhite was likely related to distance from trees because of greater predation risk near trees. Additionally, large proportions of tree cover can limit the production of grasses and forbs, reducing the amount of available forage (Peitz et al. 1997, Cram et al. 2002, Crosby et al. 2013), and potentially increasing time spent foraging and exposure to predation risk. We found no support for our hypothesis that survival was positively related to less tree edge density compared to all other vegetation types. Given that trees may harbor predators, survival is maximized when the distance from trees is also maximized. While short, early-successional shrub cover provides escape cover from predators, and tall, tree cover may harbor predators, species composition of each vegetation type may impact bobwhite decision-making and was not quantified in this analysis.

Contrary to our hypotheses, prescribed burning within the last 12 months negatively impacted bobwhite survival. The distance from trees positively impacted survival while distance to shrubs negatively impacted survival. The proportion of native grass negatively affected survival where proportions of native grass managed with prescribed burning and grazing were low (e.g., 0.34) to moderate (e.g., 0.45). While grasslands may be important for breeding season

and brood survival, if they lack adequate access to shrub cover they can have a negative impact on fall and winter survival. Thus, intensive and extensive management techniques may each benefit bobwhite during fall and winter, if management is conducted to increase the amount of heterogeneous vegetation across the landscape.

We found no support for a difference in survival between intensively and extensively managed sites. Rather, fall and winter survival was more directly related to vegetation and management characteristics such as the proximity of woody cover and if a site was recently burned. The benefits of burning and grazing in extensively managed native grasslands may be more important to other life stages, such as the brood rearing period (Sinnott 2020).

MANAGEMENT IMPLICATIONS

Woody cover was an important component of vegetation contributing to fall and winter survival of bobwhite in Missouri. More specifically, proximity to shrubs and distance from trees were positively related to survival. Native grasslands are important to the full annual cycle of bobwhite. However, the utility of grasslands for bobwhite is greatly diminished if they do not contain interspersed shrub cover; we found survival was greatest when shrub cover was within 40 m. Prescribed burning is perhaps the most effective tool to manage native grasslands for bobwhite habitat as it simultaneously promotes native grass quality, removes litter, and prevents shrub cover from dominating the landscape and succeeding to trees. While prescribed fire is important for controlling woody vegetation and for the creation of breeding, nesting, and brood rearing habitat, its short-term (12 months post-burn) effect was to reduce survival of bobwhite in the fall and winter. Therefore, we suggest prescribed burning at intervals >1 year will benefit fall-winter survival and managers consider the size and juxtaposition of burn units so units >1 -

year post-burning are available to bobwhite. The use of fire in a multiyear rotation, such as used in systems which utilize both prescribed burning and grazing in native and restored grasslands, can create the needed interspersion of shrub cover for fall and winter while meeting the other annual resource needs of bobwhite.

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TABLES

Table 1. The mean, standard deviation (SD), and minimum (min) and maximum (max) values for landscape, vegetation, and management characteristics at Northern bobwhite locations used to predict fall (Nov) and winter (Dec–Jan) survival in southwest Missouri, 2017–2019.

Variable ^a	Mean	SD	Min	Max
NG	0.38	0.25	0.02	0.87
PG	0.48	0.20	0.06	0.91
PB	0.10	0.30	0.00	1.00
TD	36.58	44.60	0.00	306.19
SD	13.86	16.14	0.00	147.99
TE	194.18	190.75	0.29	870.69
SE	298.27	137.89	17.78	692.10
ST	0.09	0.09	0.00	0.65
SS	1.63	3.34	0.00	41.78

^aNG = proportion of native grass at 1km scale, PG = proportion of land managed via both prescribed burning and grazing at 1km scale, PB = binary variable indicating if an individual was located in an area that was prescribed burned within the last 12 months, TD = distance from the nearest tree (meters), WE = density of shrubs and tree edges combined at 400m scale, SD = distance to nearest shrub (meters), WC = contagion of shrubs and tree edges combined at 400m scale, TE = density of tree edges at 400m scale, SE = density of shrub edges at 400 m scale, ST = proportion of shrub cover at 50m scale, SS = quadratic of proportion of shrub cover at 50m scale.

Table 2. Candidate models explaining fall (Nov) and winter (Dec–Jan) survival of Northern bobwhite in southwest Missouri, 2017–2019. Non-significant variables (proportion of the posterior distribution <0.85) are indicated with a “0”, and significant variables (proportion of the posterior distribution >0.85) are indicated either with a “+” if the effect was positive or a “-” if the effect was negative for fall and winter (fall/winter). Models are ranked according to the Watanabe-Akaike Information Criteria (WAIC).

Model	NG	PG	NG*PG	PB	TD	SD	SE	TE	ST	SS	MA	WAIC	ΔWAIC
m1	0			-		-	0					690.26	0.00
m2	-			-	+	-						690.39	0.13
m3	0			-		-		0				691.69	1.43
m4	0	-	+	-								692.87	2.61
m5											0	693.46	3.20
m6	0			-			0	0				693.75	3.49
m7	0			-	0		0					693.83	3.57
m8												693.91	3.65
m9	0			-	0			0				693.97	3.71
m10					0			+	0	0		701.16	10.9

^aAll models included site and covey ID as random effects and age and month as fixed effects. Model-specific fixed effects were NG = proportion of native grass at 1 km scale, PG = proportion of land managed via both prescribed burning and grazing at 1 km scale, PB = binary variable indicating if an individual was located in an area that was prescribed burned within the last 12 months, TD = distance from the nearest tree (m), SD = distance to nearest shrub (m), SE = density of shrub edges at 400 m scale, TE = density of tree edges at 400 m scale, ST = proportion of shrub cover at 50 m scale, SS = quadratic of proportion of shrub cover at 50 m scale, MA = binary variable indicating if an individual was located on an intensively or extensively managed site.

Table 3. Posterior mean (PM) and 95% credible interval (CRI) for variables in the most supported models explaining fall (Nov) and winter (Dec–Jan) survival of Northern bobwhite in southwest Missouri, 2017–2019.

Effect ^a	Model 1		Model 2	
	PM	95% CRI	PM	95% CRI
NG	-0.20	-0.77, 0.38	-0.30	-0.86, 0.28
PB	-1.06	-1.84, -0.24	-1.07	-1.84, -0.28
TD			0.18	-0.15, 0.53
SD	-0.16	-0.35, 0.04	-0.25	-0.48, -0.01
SE	-0.11	-0.35, 0.58		
AD	0.42	-0.17, 1.02	0.42	-0.14, 1.01
DE	0.34	-0.31, 1.00	0.36	-0.28, 1.02
JA	-0.47	-1.12, 0.17	-0.45	-1.12, 0.21

^aNG = proportion of native grass at 1 km scale, PB = binary variable indicating if an individual was located in an area that was prescribed burned within the last 12 months, TD = distance from the nearest tree (m), SD = distance to nearest shrub (m), SE = density of shrub edges at 400 m scale, AD = adult, DE = December, JA = January.

FIGURES

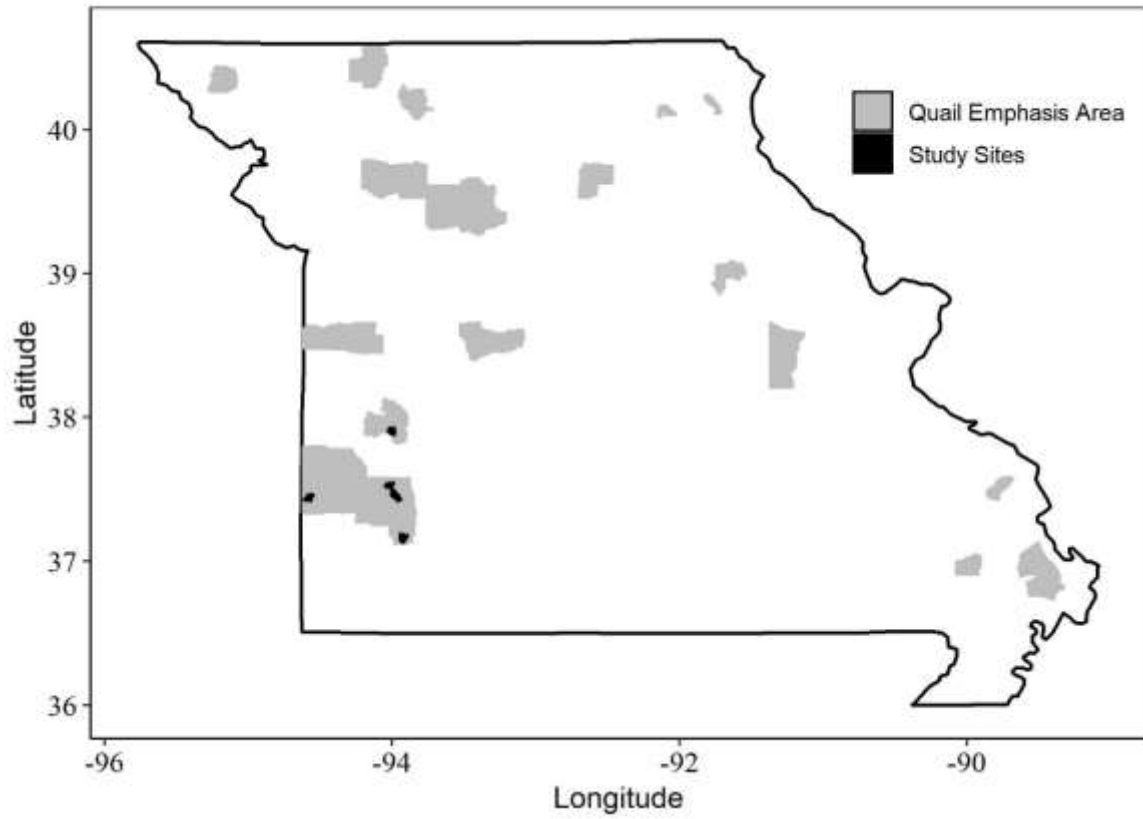


Figure 1. Quail emphasis areas (grey) and study sites (black) where we examined Northern bobwhite fall (Nov) and winter (Dec–Jan) survival.

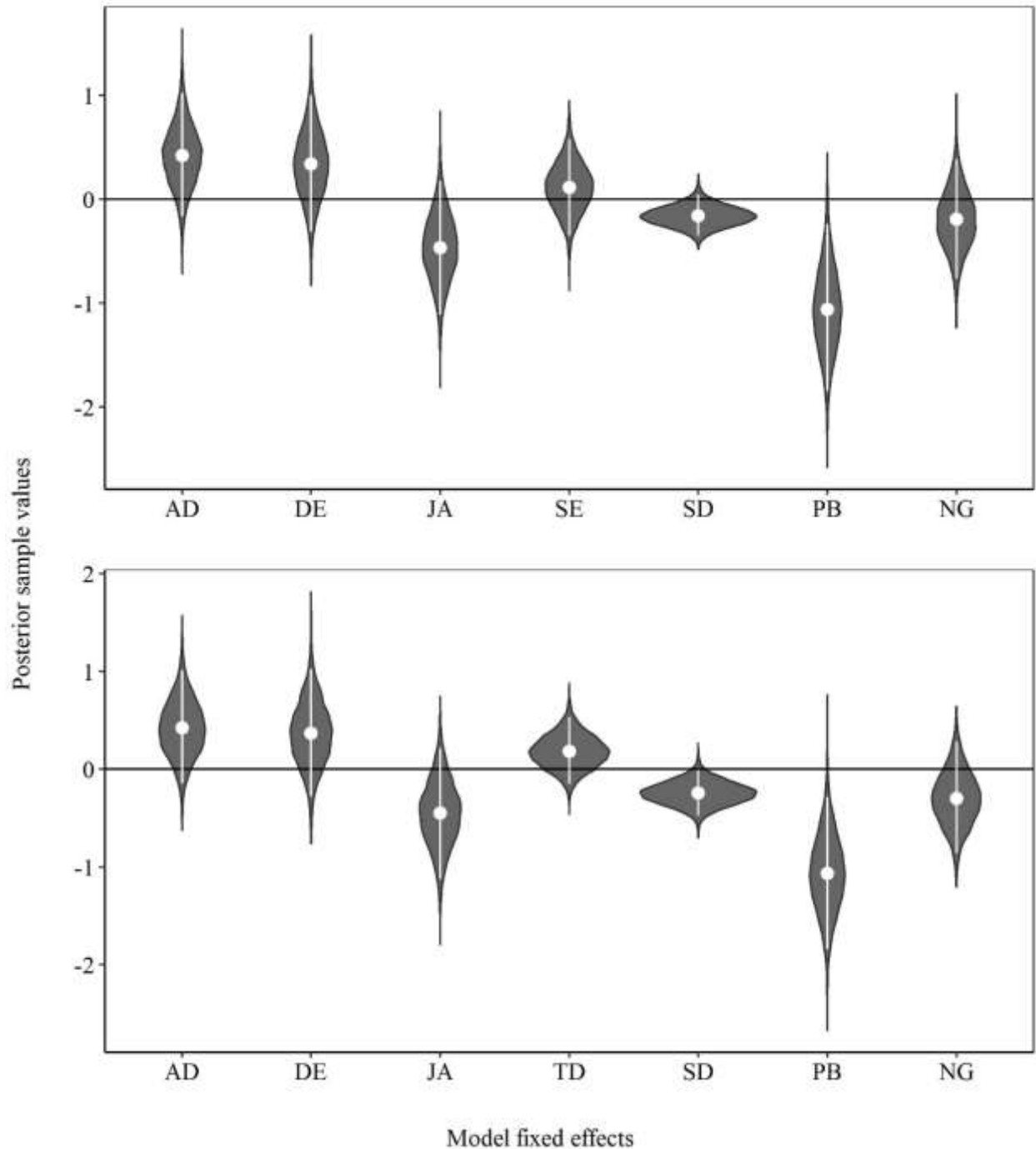


Figure 2. Posterior distributions (grey “violins”), posterior means (white dots), and 95% credible intervals (CRI; white bars) from the models m1 (top plot) and m2 (bottom plot) representing cover and management effects on fall (Nov) and winter (Dec–Jan) survival of Northern bobwhite, 2017–2019, in southwest Missouri. Model effects are AD = adult, DE = December, JA = January, SE = density of shrub edges at 400 m scale, SD = distance to nearest shrub (m), PB = binary variable indicating if an individual was located in an area that was prescribed burned within the last 12 months, NG = proportion of native grass at 1 km scale, TD = distance from the nearest tree (m).

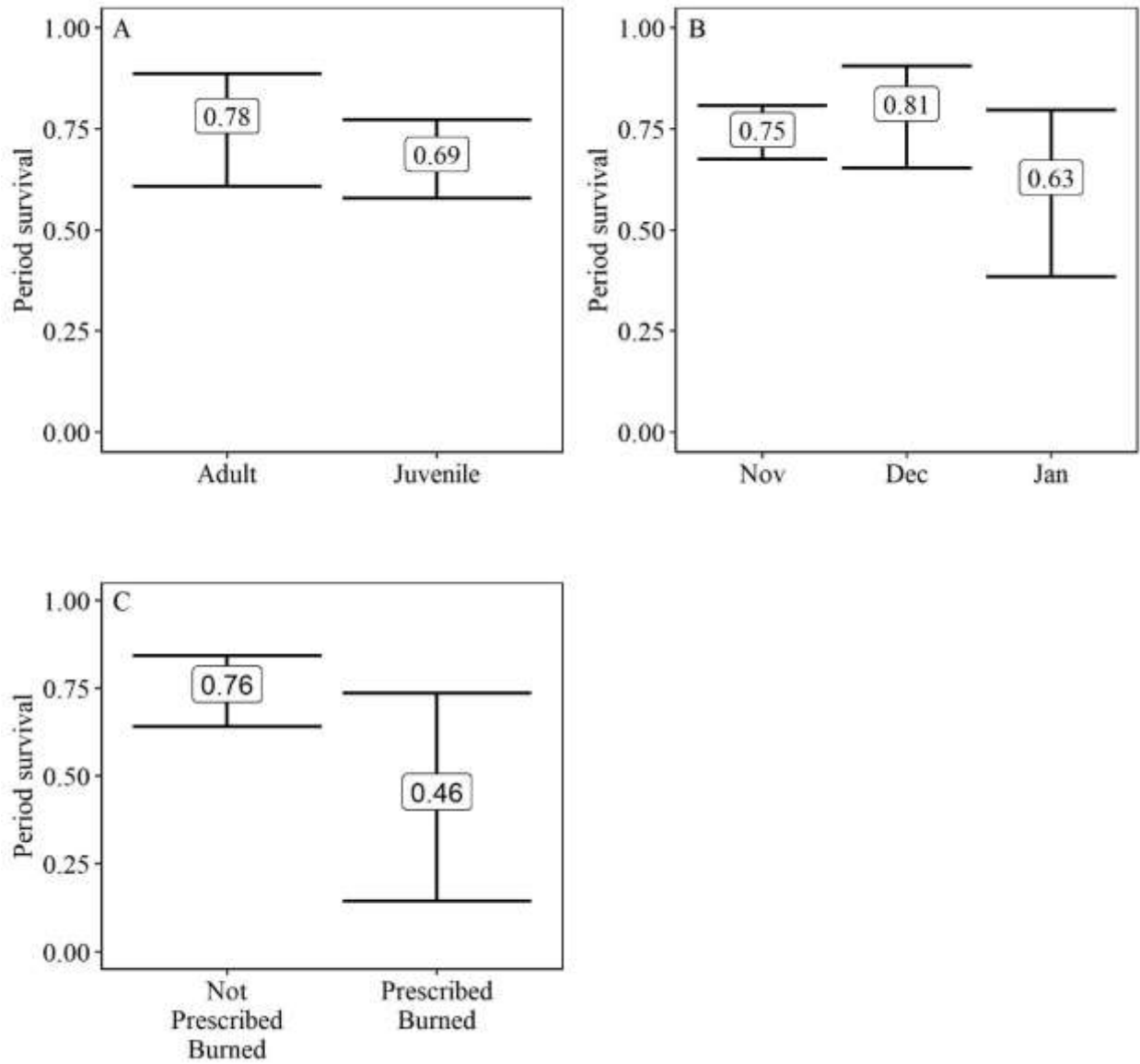


Figure 3. Northern bobwhite period survival and 95% CRI specific to age (A), month (B) and areas either prescribed burned or not (C) in fall (Nov) and winter (Dec–Jan) in southwest Missouri, 2017–2019.

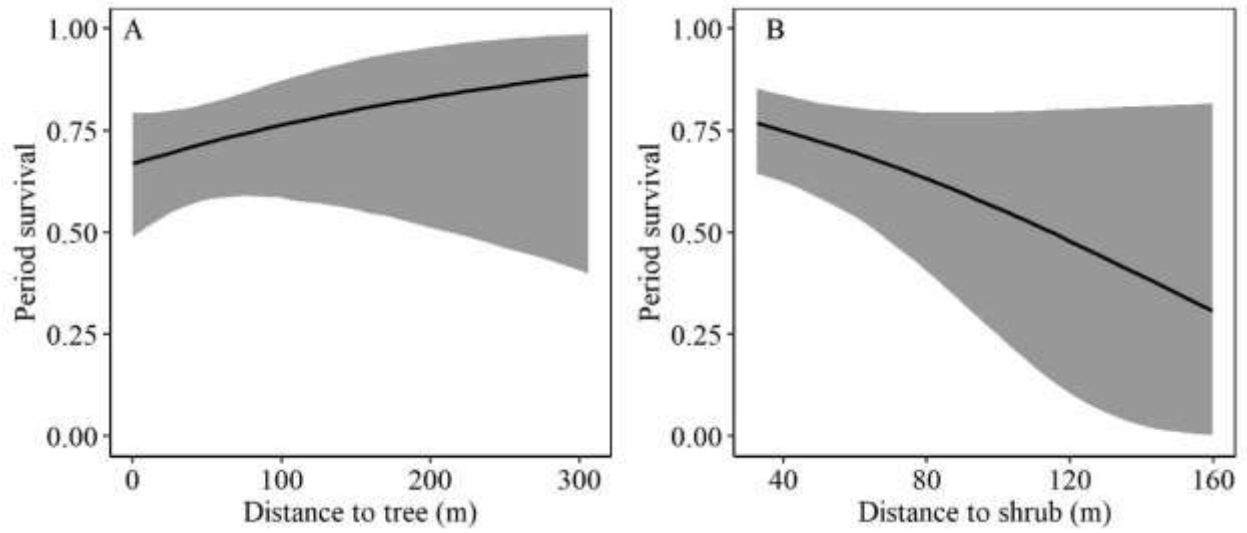


Figure 4. Northern bobwhite period survival and 95% CRI as a function of distance from tree (A) and distance to shrub (B) in fall (Nov) and winter (Dec–Jan) in southwest Missouri, 2017–2019.

CHAPTER 2

ENVIRONMENTAL DRIVERS OF NORTHERN BOBWHITE RESOURCE SELECTION DURING FALL AND WINTER

ABSTRACT

Resource selection is a key component in understanding the ecological processes underlying population dynamics, particularly for species such as northern bobwhite (*Colinus virginianus*) that are declining across their range in North America. There is a growing body of literature quantifying breeding season resource selection, however, winter information is particularly sparse, despite it being a season of substantial mortality. Information regarding winter resource selection is necessary to quantify the extent to which resource requirements are driving population change. We modeled bobwhite fall and winter resource selection as a function of vegetation structure, composition, and management from traditionally (intensively) managed and extensively managed sites in southwest Missouri using multinomial logit discrete choice models in a Bayesian framework. We captured 158 bobwhite from 67 unique coveys and attached transmitters to 119 individuals. We created 671 choice sets comprised of 1 used location and 3 available locations. Bobwhite selected for locations which were closer to trees during the winter (Posterior Mean [PM]: -3.28, 95% Credible Interval [CRI]: -8.33, -0.41) and provided more visual obstruction during both fall and winter (PM: 4.59, 95% CRI: 2.21, 8.99). Bobwhite also selected locations which had higher quantities of woody stems during both fall (PM: 2.67, 95% CRI: 0.91, 5.42) and winter (PM: 3.35, 95% CRI: 1.35, 6.97), as well as lower percentages of grass cover at the location during fall (PM: -3.77, 95% CRI: -7.72, -1.29). We suggest dense shrub cover interspersed in native grasslands is an important component of fall and winter cover

given bobwhite selection of shrub cover and its previously reported survival benefits in fall and winter.

INTRODUCTION

Resource selection is a key component in understanding the ecological processes underlying population dynamics (Morris 2003). Conservationists may gain better understanding of factors driving abundance at various spatial and temporal scales by linking the impacts of predation, foraging behavior, and availability of resources (Morris 2003). The resource requirements of species such as upland game birds may change over the course of their life cycle (e.g., from juveniles to adults) and annual cycle (e.g., from the breeding season to the non-breeding season). Conservation practitioners require an understanding of resource selection throughout the annual cycle to fully understand the trade-offs in life history events and land use. There is a growing body of literature on breeding season resource selection of upland game birds (Jones et al. 2008, Goddard et al. 2009, Carpenter et al. 2010, McNew et al. 2013), especially for northern bobwhite (*Colinus virginianus*, hereafter bobwhite; Taylor et al. 1999, Collins et al. 2009, Sands et al. 2012, Brooke et al. 2015, McGrath et al. 2017). However, many bobwhite populations are declining (Sauer et al. 2014), suggesting that current understanding and conservation plans based on resource selection during the breeding season is not enough to effectively increase bobwhite populations (Guthery 1997). Information regarding fall and winter resource selection is necessary for more complete understanding of habitat requirements in each season for trade-offs in conservation decisions throughout the annual cycle.

Grasslands and the associated bare ground, forbs, and shrubs provide foraging and loafing cover for bobwhites (Stoddard 1931, Doxon and Carroll 2010). Grasslands dominated by

native warm season grasses are particularly beneficial for bobwhite as they provide greater quality habitat than non-native grasses if they are managed by burning, grazing, herbicide, or disking to keep them from becoming rank, over-vegetated, and unsuitable for bobwhite (Barnes et al. 1995, Washburn et al. 2000, Yeiser et al. 2015, Sinnott 2020). Declines in bobwhite abundance are typically attributed to losses of grasslands that are converted to agricultural crops (Murphy 2003, Veech 2006), suggesting that landscapes with greater quantities of grasslands could increase bobwhite abundance. However, previous studies have found decreased selection for grasslands and agricultural crops as the availability of these vegetation types increases (Williams et al. 2000, Janke and Gates 2013). This likely indicates a functional response of selection relative to the abundance of either vegetation type, suggesting that the benefits of either cover type diminish as they become increasingly available (Beyer et al. 2010, Janke and Gates 2013). Neither grasslands nor agricultural crops are beneficial to bobwhite unless they are associated with other vegetation required by bobwhite, particularly early successional woody cover (Guthery and Bingham 1992).

Bobwhite are a shrub-obligate species that require dense, early successional, woody cover interspersed on the landscape in a manner that it is immediately accessible as escape cover from predators, thermal refugia, protection from extreme winter weather, and safe loafing areas (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). However, unmanaged shrub cover can quickly succeed to forest. While forests can provide escape cover and loafing sites when scrub-shrub is limited (Lohr et al. 2011), trees provide habitat for predators of bobwhite (Seckinger et al. 2008) and closed canopy forests (i.e., canopy cover $\geq 60\%$) often limit production of grasses, forbs, and shrubs (Peitz et al. 1997, Cram et al. 2002). Janke and Gates (2013) found that early successional woody vegetation was selected for over all

other vegetation types, while forests were generally not selected for. Generally, bobwhite select for habitat patches which average at least 30% early successional woody cover (Guthery et al. 2005, Hiller et al. 2007, Ransom et al. 2008).

Bobwhite management typically focuses on creating heterogeneous landscapes which maximize usable space. However, the structural attributes of the vegetation (e.g., height, density, and visual obstruction) within these landscapes are also important (Johnson and Guthery 1988, Fulbright and Guthery 1995, Kopp et al. 1998, Cram et al. 2002, Ransom et al. 2008). Winter feeding areas are most beneficial when vegetation is interspersed with 25–60% bare ground (Schroeder 1985). Roost sites in Missouri typically consist of 27% forb cover, 23% bare ground (Burger et al. 1994), 65% litter cover, and a maximum vegetation height of 94 cm (Chamberlain et al. 2002). Sites which offer high visual obstruction provide enhanced protection from predators (Ransom et al. 2008). Kopp et al. (1998) found that bobwhite used habitat with bare ground ranging from 10 to 60% and herbaceous cover ranging from 0 to 35%.

Heterogeneous landscapes are often created through disturbance, such as prescribed fire, grazing, and disking, and are often distributed non-uniformly in space and time (Turner et al. 2001). Resource selection of bobwhite is impacted by these disturbances. Previous studies have documented differences in resource selection of bobwhite on managed, publicly-owned lands and privately-owned lands dominated by agricultural production (Hughes et al. 2005, Potter et al. 2011). Activities such as the harvest of row crops may lead to the creation of unusable space in the winter months (Leopold 1931, Roseberry and Klimstra 1984). Prescribed fire applied during winter may create unusable space for several months post-burn through the removal of grass cover, but creates bare ground for improved mobility for a couple of years post-burn (Brennan et al. 1998, Glitzenstein et al. 2012) and increases forage (i.e., seeds) abundance and availability

(Brennan et al. 1997). Similarly, grazing promotes the complex vegetation structure required by bobwhite as well as the amount of litter and bare ground consistent with the habitat requirements of bobwhite (Harper et al. 2015). Historically, disturbance throughout the bobwhite range consisted of periodic, low-intensity fire (Pyne 1982) and ungulate grazing (Anderson 2006).

Effective conservation strategies require detailed knowledge of resource selection patterns of bobwhite. Managers typically adopt intensive, or traditional, management regimes for bobwhite. Intensive management regimes mimic the formerly fragmented landscapes of the United States through the use of small agricultural units, native grasses, and shrub rows closely interspersed throughout the landscape. Food plots provide forage for breeding adults and chicks during the summer, managed native grass provides bare ground and forage throughout the year, and shrub/tree rows provide woody escape cover during winter. However, extensive management regimes have been developed in large native grassland landscapes and utilize combinations of prescribed burning, grazing, brush hogging, haying, high clipping, and herbicide. Extensive management tries to mimic pre-settlement landscapes that meet the yearly resource requirements of bobwhite. The spatial configuration of these factors likely impacts resource selection of bobwhite (Riddle et al. 2008, Holt et al. 2009).

A modeling framework that allows robust evaluations of seasonal resource selection would help improve our understanding seasonal resource needs. Discrete choice models allow comparison of used and available habitats even when availability changes over time (e.g., due to harvest of row crops or prescribed burning; McDonald et al. 2006). We used discrete choice models to directly evaluate the impacts of cover type, vegetation structure, and management on bobwhite resource selection within the context of intensively and extensively managed conservation areas.

Our objectives were to quantify resource selection of bobwhite during fall and winter for vegetation characteristics and management treatments in the context of intensive and extensive management techniques. Many ecological factors, operating at different scales, may influence the resource selection of bobwhite. Hernandez and Guthery (2012) found that herbaceous and woody cover should be interspersed in such a way that an individual is never further than 30 meters from either vegetation type. Further, the National Bobwhite Conservation Initiative (NBCI) Coordinated Implementation Plan (CIP) does not consider habitat further than 50 m from woody protective cover as suitable habitat (Morgan et al. 2016). Thus, we evaluated both the structure and composition of the vegetation for selection preferences in bobwhite. We fit multinomial logit discrete choice models representing competing hypotheses within a model selection framework to compare support for hypotheses relating to native grass, managed grasslands, shrub cover, and trees. We hypothesized that bobwhite coveys would select for habitat which consisted of 1) higher proportions of native warm season grass, 2) higher proportions of grasslands which were managed via patch-burn-grazing, 3) landscapes which contained higher interspersions of shrub cover, 4) landscapes which maximized the distance from trees, and 5) habitat which provided structure with moderate amounts of forbs, grasses, and bare ground, high densities of woody cover, and high visual obstruction.

METHODS

Study Area

We conducted our research on 5 Missouri Department of Conservation (MDC) conservation areas in southwest Missouri: Robert E. Talbot Conservation Area (Talbot), Shawnee Trail Conservation Area (Shawnee Trail), Stony Point Prairie Conservation Area

(Stony), Wade and June Shelton Memorial Conservation Area (Shelton), Wah’Kon-Tah Prairie Conservation Area (Wah’Kon-Tah). This region has a high potential for successful bobwhite habitat management and population recovery in Missouri (The National Bobwhite Technical Committee 2011). Sites were dominated by big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*), little bluestem (*Schnizachyrium scoparium*), and sideoats grama (*Bouteloua curtipendula*) grasses. Cool season and mixed grass pastures contained large quantities of tall fescue (*Festuca acundinacea*). Dominant shrub and trees included sumac (*Rhus* spp.), blackberry (*Rubus* spp.), plum (*Prunus* spp.), dogwood (*Cornus* spp.), and oak (*Quercus* spp.). The surrounding counties (Barton, Cedar, Dade, Lawrence, and St. Clair) were largely converted to non-native pasture (tall fescue), forest, cultivated crops (e.g., corn, soybeans, wheat), and urban development (Homer et al. 2015, USDA National Agriculture Statistics Service Cropland Data Layer 2015).

Sites varied in history, size, and management strategy. Shelton (129.5 hectares), Stony (388.5 hectares), and Wah’Kon-Tah (943.3 hectares) were predominantly remnant prairies extensively managed with a combination of fire, grazing, brush hogging, haying, high clipping, and herbicide to maintain a grassland landscape. Grazing, mowing, and prescribed burns were used to mimic the pyric herbivory characteristic of historic disturbance and enhance the species richness of the area (Collins et al. 1998, Fuhlendorf et al. 2009). Talbot and Shawnee Trail were intensively managed sites (1764.4 and 1471 hectares, respectively) composed of row-crop agriculture, food plots, woody cover, and planted grassland managed by prescribed grazing, mowing, and prescribed burning. Agricultural practices occurred historically on Shawnee Trail and cattle grazing occurred on Talbot prior to land acquisition by the MDC. Several of the

agricultural units have since been restored to native grass and mixed-prairie on both Shawnee Trail and Talbot.

All sites were managed with prescribed burning and grazing (in combination or separately) throughout the duration of the study. Average burn unit sizes were generally larger on extensively managed sites (approximately 50–100 acres) than intensively managed sites (approximately 10–40 acres). Prescribed burning typically occurred on a 3 to 5-year rotation with extensively managed sites being burned more frequently than intensively managed sites. Prescribed burning occurred from January to April and August to December. Prescribed burn units which were managed concurrently with prescribed grazing (i.e., patch burn grazing) were generally burned February to April. Managed sites with remnant or restore prairie are typically grazed at a stocking rate of 1 animal unit (AU) per 5.5 acres where 1 AU is 1,000 pounds of cattle with grazing durations ranging from 90 to 180 days. Managed sites that were not prairie, but primarily comprised of warm season grass plantings and non-native cool season grass pastures were grazed at a higher intensity of 1 AU per 4 acres with grazing durations ranging from 90 to 120 days (personal communication, K. Hedges, Missouri Department of Conservation).

Quail Captures and Tracking Devices

We captured bobwhite using funnel traps baited with cracked corn and milo in October 2018 (Stoddard 1931). We located capture sites where bobwhite were observed by field staff and near locations of bobwhite radio tagged in an ongoing breeding season study. We attempted to mark individuals from as many unique coveys as possible. Capture sites were pre-baited for 4 to 10 days prior to placement of a funnel trap. Funnel traps were weighed down with bricks and

covered with eastern red cedar (*Juniperus virginiana*) boughs to prevent predators from locating trapped bobwhite and to provide protection from inclement weather. We checked traps 2 to 4 hours after sunrise and no earlier than 30 min before sunset to reduce the amount of time birds spent in traps. We did not trap if severe weather (e.g., heavy rainfall) was expected that could harm trapped individuals. We removed a trap from a site if any individual was captured 3 times to reduce exposure to trapping. We ceased trapping and removed all evidence of trapping (i.e., bait, cedar boughs, and flagging) prior to November 1 each year because that was the opening of the bobwhite hunting season in Missouri. Up to 4 individuals/covey were fitted with transmitters to ensure a large number of coveys were included in the study.

We marked bobwhite with a uniquely numbered leg band (National Band & Tag Company, Newport, KY, USA) and individuals >100 grams were fitted with a pendant-style radio transmitter that weighed 5.3–5.5 g (model AWE-QII from American Wildlife Enterprises, Monticello, FL, USA). We recorded sex, age class (adult/juvenile; Petrides and Nestler 1943, Petrides and Nestler 1952), weight (g), and tarsus length (mm) and released individuals at their capture site. While attachment of transmitters may handicap birds using marginal habitats (Sandercock et al. 2008), studies based on large samples of marked individuals with rigorous mark-recapture methods have not detected a negative effect of tracking devices on bobwhite survival (Parry et al. 1997, Palmer and Wellendorf 2007, Terhune et al. 2007). All animal procedures were approved under University of Missouri Animal Care and Use Committee protocol #8766.

Quail Locations

We attempted to locate bobwhite 3 times per week from 1 November 2018 to 31 January 2019 by homing to within 10 m of individual (White and Garrott 1990). We recorded our location with a Global Positioning System (GPS) unit, as well as the distance and azimuth to the bobwhite. One location was recorded for coveys and individuals were assumed to be in the same covey if they were within 10 m of each other. We used triangulation from two or more points (White and Garrott 1990) to locate individuals on property we did not have access to. We attempted to not flush individuals.

We searched for individuals that we could not locate by radio telemetry at least once per week by intensively searching the area surrounding the last known location and by searching the larger, surrounding area using a dipole omnidirectional antenna on local roads. After 12 hours of no movement the transmitters emitted a fast pulse rate at which point we would locate the transmitter and individual, and classified it as either a dropped transmitter or mortality. If a transmitter was located with no apparent damage and no sign of predation, it was considered a dropped collar and included in the analysis as alive to that day. Mortality events were ascribed when a collar showed evidence of damage, was located with a dead bobwhite, or near sign of a predator (e.g., predator was observed with carcass, transmitter was in an animal burrow, or located in scat). Individuals that were classified as a drop or mortality within the first 7 days of the tracking period were eliminated from the dataset. We recorded the vegetation classification, management that had been conducted, and if the individuals were in a tree edge, shrub, or both at each location.

Vegetation and Management Classifications

Maps of vegetation and management types were provided by land managers for each study site. We considered 13 unique vegetation types: Native Prairie (NP), Restored Prairie (RP), Mixed Grass (MG), Cool Season Grass (CS), Native Grass Planting (NG), Agriculture (AG), Idle Agriculture (ID), Food Plot (FP), Strip Crop (SC), Shrub-scrub (SS), Savanna (SA), Woodland (WD), and Timber (TI). Management was identified as: grazed (GR), prescribed burn (PB), mowed (MW), hayed (HA), woody removal (WR), bullhogging (BH), and sprayed (SP).

We improved mapping of shrubs and trees by using airborne light detection and ranging (LiDAR) data from years 2014 (Vernon and Barton county) and 2016 (Bates, St. Clair, Cedar, Dade and Lawrence counties) that were publicly available from the Missouri Spatial Data Information Service (<http://www.msdis.missouri.edu>). Shrubs, trees/tree edges, and forests are often associated with ground cover consisting of grasses and forbs. We created separate rasters at 3.6 m resolution to represent shrubs and trees by classifying vegetation height from 0.7 to 3.5 m as shrubs and 3.5 to 40 m as trees following George et al. (2017).

Ecological factors operating at different scales influence bobwhite habitat occupancy and survival (Howell et al. 2009). Herbaceous and woody cover should be interspersed such that bobwhite are not more than 30 m from either vegetation type (Hernandez and Guthery 2012) and The National Bobwhite Conservation Initiative Coordinated Implementation Plan does not consider habitat further than 50 m from woody protective cover (i.e., vegetation which provides overhead protection from predators and weather year-round) as suitable (Morgan et al. 2016). In addition, vegetation should consist of combinations of grasses, forbs, bare ground, and woody cover which maximize forage, mobility, and cover. Therefore, we assessed vegetation and management metrics both at the covey's location and within a 50 m radius of the location.

We condensed vegetation and management types in ArcGIS (ESRI 2018) to ecologically meaningful categories that directly addressed our hypotheses concerning native grass, prescribed burning, and prescribed grazing. Given that native warm season grasses provide higher quality habitat for bobwhite than non-native grasses such as fescue (*Festuca arundinacea*; Washburn et al. 2000, Yeiser et al. 2015) we hypothesized that bobwhite would select for locations with higher amounts of native grass. We categorized native grass as any parcels within a conservation area that were native prairie, native grass planting, and restored prairie identified as primarily native grass via field verification, regardless of associated management technique. To evaluate our hypothesis that bobwhite would select locations in native grass, we calculated the proportion of land an individual's location that was native grass (NG). However, unmanaged native grass quickly loses value for bobwhite, so we also modeled the proportion of land that was managed via prescribed burning and grazing (i.e., combined all land that had been prescribed burned and/or grazed at any time during the study). To evaluate our hypothesis that bobwhite would select locations managed via prescribed burning and grazing, we calculated the proportion of parcels managed with either prescribed burning or grazing, or both, surrounding an individual's location (PG). We believe the amount of woody cover (i.e., shrubs and trees) on the landscape as well as the interspersions of this woody cover throughout the landscape may impact fall and winter resource selection. To evaluate our hypothesis that bobwhite select for locations with higher interspersions of woody cover, we created a variable which quantified the amount of woody edge (i.e., shrubs and trees) within 50 m of the covey's location (WE). We also calculated the distance from the nearest tree (m; TD) to evaluate our hypothesis that bobwhite would select locations further from trees. We calculated all landscape metrics (e.g., percent cover, distance

from tree or shrub) using the landscapemetrics package (Hesselbarth et al. 2019) in program R version 3.6.0 (R Core Team 2019).

Vegetation Measurements

We measured vegetation weekly at one location per covey stratified by time of location to ensure vegetation data were representative of sites used during the entire day. One third of vegetation measurements each week were collected at roost locations (16:30–08:30), one third were collected at morning locations (08:30–12:30) and one third were collected at afternoon locations (12:30–16:30). Individuals located within 10 m of each other were considered to be in the same covey and the location was determined to be where the majority of marked individuals within the covey were located. Marked individuals further than 10-m apart were considered unique coveys and given separate locations at which a unique set of vegetation measurements were collected. Vegetation measurements also were collected at three available locations because our resource selection modeling approach required data for each used location be paired with available locations which were available for selection at the time the covey chose the used location. We randomly chose 3 available locations by distance and azimuth from the used location within 400 m of the used location. Random locations were generated using a random number generator in Microsoft Excel (2016) whereby distances were constrained between 50 and 400 m to ensure random locations did not overlap and azimuths were constrained between 1 and 365. We chose 400 m as the maximum distance because it was the 90% quantile of distance traveled between resightings and we assumed points within this radius were available to bobwhite.

Vegetation composition was quantified using a 0.50-m² quadrant (modified from Daubenmire 1959) where we estimated percent cover of forbs (FB), grasses (GS), agricultural crops (AG; e.g., corn, wheat, soybeans), woody cover (W) and bare soil (BR), in 4% cover classes within the Daubenmire frame. We estimated the percent cover of each segment of a 2-m modified robel pole (Robel et al. 1970) with 10-cm² segments from 5 m in each of the 4 cardinal directions and averaged the readings to quantifying visual obstruction 0–2 m (VO). We estimated the number of woody stems (SC) >1 m in height and within 5 m of each location.

Discrete Choice Analyses

We fit conditional multinomial logit discrete choice models in a Bayesian framework (Jenkins et al. 2017) implemented in JAGS (Plummer 2015) using program R to model the probability that an individual would select a location given a choice between 3 locations available at one time (i.e., forming a choice set; Cooper and Millspaugh 1999, Thomas et al. 2006). Discrete choice models allow for comparison of covariates within choice sets rather than comparisons of used and available locations across all locations and times. Further, the composition of a choice set is allowed to change over time and between individuals, removing the variation in factors which often influence selection (e.g., an individual's age or the availability of habitat; McDonald et al. 2006). Individual bobwhite form social groups, or coveys, during the fall and winter. We believe that an individual bobwhite's resource selection decisions may be influenced by the other individuals in the covey. A covey identification number (covey ID) was assigned to each unique combination of individuals located within 10 m of each other at the time of resighting. We assigned a single, common location representing the location of the majority of individuals within the covey to all individuals in a covey. Individuals located

further than 10 m from the covey were considered a unique covey and assigned a unique location. We standardized all covariates prior to model runs and assessed multicollinearity among variables by calculating variance inflation factors (VIF) using the car package (Fox and Weisberg 2019) in Program R version 3.6.0 (R Core Team 2019). We removed any variables with VIF indices >2.5 (Allison 1995, Kutner et al. 2004).

We considered the probability that a covey, c , would select the used or available locations if given a choice between 4 locations (i.e., 1 used, 3 available). We modeled the ‘utility’ of each used location in the i th choice set of bobwhite covey c as a linear function of covariates representing the vegetation structure and the composition of surrounding vegetation and management types, following Jenkins et al. (2017):

$$U_{ic}^{used} = \beta_{1c}FB_{ic}^{used} + \beta_{2c}GS_{ic}^{used} + \beta_{3c}BR_{ic}^{used} + \beta_{4c}VO_{ic}^{used} + \beta_{5c}SC_{ic}^{used} + \beta_{6c}NG_{ic}^{used} \\ + \beta_{7c}PG_{ic}^{used} + \beta_{8c}NG_{ic}^{used}PG_{ic}^{used} + \beta_{9c}TD_{ic}^{used} + \beta_{10c}WE_{ic}^{used}$$

where FB_{ic}^{used} is the percentage of forbs within a Daubenmire frame at the used location, GS_{ic}^{used} is the percentage of grasses within a Daubenmire frame at the used location, BR_{ic}^{used} is the percentage of bare ground within a Daubenmire frame at the used location, VO_{ic}^{used} is the averaged visual obstruction from ground level to 2 m at the used location, SC_{ic}^{used} is the amount of woody stems >1 m tall within 5 m of the used location, NG_{ic}^{used} is the percent of native grass cover type within 50 m of the used location, PG_{ic}^{used} is the percent of land managed using either or both prescribed fire and grazing within 50 m of the used location, TD_{ic}^{used} is the distance from the nearest tree edge from the used location, and WE_{ic}^{used} is the density of shrub and tree edges within 50 m of the used location, and $\beta_{1c}, \dots, \beta_{10c}$ are the covey-level coefficients corresponding to covey c ($c \in (1, 2, \dots, C)$), where C is the total number of coveys included in the model. We modeled the utility of each available location in an identical manner, substituting covariates at

used locations for covariates at available locations. We then used the utility functions defined above to model the probability of selecting the used or available locations when given a choice among the four locations (hereafter relative probability). We calculated the relative probability of selecting a location as:

$$P_n(j) = \frac{\exp(U'_j)}{\sum_{k \in j_n} \exp(U'_k)}$$

where $P_n(j)$ is the probability of location j being chosen by a given covey for its n th selection event, assuming that each selection event is independent of previous selection events (Cooper and Millspaugh 1999).

We modeled population level resource selection of bobwhite by assuming that individual-level coefficients arose from Normal population-level distributions (Thomas et al. 2006, Carter et al. 2010):

$$(\beta_k) \sim N(\mu_k, \sigma_k^2),$$

where μ_k is the population mean and σ_k^2 is the variance for the effect of covariate k ($k \in (1, 2, \dots, K)$) where k is the covariate of interest representing our hypothesized drivers of resource selection. We hereafter refer to each regression coefficient distribution by the name of the associated vegetation and management covariates.

We hypothesized that resource selection would vary across months and initially considered how resource selection varied as a function of each month during winter (i.e., November, December, January). However, models would not converge due to sparse data so we then defined November as fall (i.e., November = 0, December and January = 1) and December and January as winter (i.e., November = 0, December and January = 1) and modeled separate population-level parameter distributions for fall and winter. Preliminary analyses indicated

models including season were more supported so we included season as a fixed effect in all subsequent models.

We used Markov chain Monte Carlo (MCMC) algorithms to estimate the posterior distributions of each parameter (Plummer 2015). We ran 4 chains for 100,000 iterations after a 10,000 iteration burn-in and a thinning of 50 with vague priors and assumed normal prior distributions ($N\sim(0, 0.01)$) on all vegetation and management regression coefficients and normal prior distributions ($N\sim(0, 0.01)$) for each population-level mean hyperparameter (i.e., a parameter of the prior distribution which allowed for inclusion of a random effect for covey). We evaluated model convergence by visual inspection of MCMC chains and ensured the Gelman-Rubin convergence statistic was <1.1 (Brooks and Gelman 1998).

We compared support among models based on the Watanabe-Akaike Information Criteria (WAIC; Watanabe 2010) and removed more complex models with greater WAIC values from further consideration in favor of simpler models that shared one or more of the same terms to eliminate uninformative models (Arnold 2010). For each covariate coefficient we present the mean of the posterior distribution (PM) and 95% credible interval (CRI). We estimated and interpreted relative probability of use curves over the observed range of covariates of interest, while holding other covariates at their means (McDonald et al. 2006). Relative probability of use predictions are presented based on the mean, 2.75%, and 97.5% posterior values of the covariate of interest to show variability in the mean effect size.

RESULTS

We captured 158 bobwhite from 67 unique coveys and attached transmitters to 119 individuals in 2018. After censoring, 31 and 61 individuals were used in analyses from

intensively and extensively managed sites, respectively. We utilized locations from 9, 23, 6, and 19 adults on Shawnee Trail, Stoney, Talbot, and Wah'Kon-Tah, respectively, and 6, 3, 8, 10, and 8 juveniles on Shawnee Trail, Shelton, Stoney, Talbot and Wah'Kon-Tah, respectively. We obtained 2,595 locations during 2018. We collected vegetation data on 650 used locations and their associated 3 random locations for a total of 650 choice sets in our discrete choice analyses; 370 and 280 from extensively and intensively managed study sites, respectively.

We ranked our six candidate models based on WAIC and the most supported model was model 1 (m1) while the null model had the least support (Table 2). We based inferences on the top model (m1) and the second ranked model (m2) because the latter included additional supported variables which could not be included in model m1 because more complex models did not converge. Parameters in models m3, m4, and m5 were either not supported or appeared in models m1 and m2. In general, we found support for our hypotheses that bobwhite selected greater densities of woody edges, greater woody cover indicated by higher woody stem counts and shorter distance to nearest shrub, and greater visual obstruction. We could not evaluate our hypotheses that bobwhite selected moderate amounts of grass, forb, and bare ground cover because models with quadratic terms did not converge. We instead evaluated linear effects, finding that bobwhite selecting for lesser amounts of grass and forb cover. Bobwhite selected locations closer to trees, contrary to our hypothesis that they would select locations further from trees. We found no support for our hypothesis that bobwhite would select locations based on the amount of native grass or grass grazed and/or burned in the surrounding 50 m.

Based on our top ranked model (m1), bobwhite selected locations closer to trees in winter but not in fall (Table 3; Figure 1). The relative probability of selection decreased from 0.45 (95% Credible Interval [CRI]: 0.09, 0.83) to 0.00 (95% CRI: 0.00, 0.01) as the distance from trees

increased from 0 to 313 m (Figure 2). Bobwhite also selected locations with lower percentages of grass cover at the location during fall but not winter (Table 3; Figure 1). The relative probability of selection decreased from 0.35 (95% CRI: 0.15, 0.62) to nearly 0 (95% CRI: 0.00, 0.003) as grass cover varied from 0 to 100% (Figure 3). Bobwhite selected for locations with greater visual obstruction in winter, but not fall, and greater woody stems in fall and winter (Table 3; Figure 1). The relative probability of selection increased from near 0 (95% CRI: 0.00, 0.06) to 0.29 (95% CRI: 0.03, 0.65) as visual obstruction increased from 0 to 100% (Figure 4). The relative probability of selection increased from near 0.00 (95% CRI: 0.00, 0.01) to 0.30 (95% CRI: 0.13, 0.54) and near 0.00 (95% CRI: 0.00, 0.01) to 0.35 (95% CRI: 0.18, 0.63) as stem count ranged from 0 to 1000 stems in fall and winter, respectively (Figure 5). The credible interval for woody edge density overlapped zero; however, the proportion of the posterior distribution that was positive was 0.86 and 0.92 in fall and winter, respectively, indicating substantial support for a positive effect in each season (Table 3; Figure 1). The relative probability of selection increased from near 0.00 (95% CRI: 0.00, 0.25) to 0.27 (95% CRI: 0.00, 0.67) and from near 0.00 (95% CRI: 0.00, 0.10) to 0.19 (95% CRI: 0.00, 0.45) as woody edge density increased from 0 to 111 m/ha in fall and winter, respectively.

Results from our second ranked model (m2) also indicated bobwhite selected for locations with lower percentages of grass at the location during winter and greater visual obstruction and greater woody stems during both fall and winter (Table 3; Figure 1). The credible intervals for the percentage of forbs at the location during winter overlapped zero; however, the proportion of the posterior distribution that was negative was 0.95, indicating that there is substantial support for a negative effect of the amount of forbs at the location on the relative probability of selection (Table 3; Figure 1). The credible interval for the percentage of

bare ground at the location during winter also overlapped zero; however, the proportion of the posterior distribution that was negative was 0.96. This indicates that there is also substantial support for a negative effect of the proportion of bare ground at the location on the relative probability of selection during winter.

DISCUSSION

Bobwhite resource selection was positively related to woody edge density (i.e., both tree and shrub edges), positively related to woody stem counts, indicative of shrubs, and negatively related to distance from trees. The probability of selection was negatively related to percent bare ground, forb, and grass available at the immediate location while the proportions of native grass managed with prescribed burning and grazing did not influence the relative probability of selection. Our results support the findings of previous researchers that the structural attributes of vegetation, such as height, density, and visual obstruction, are as important as the surrounding landscape habitat features (Johnson and Guthery 1988, Fulbright and Guthery 1995, Kopp et al. 1998, Cram et al. 2002, Ransom et al. 2008).

We found no support for our hypothesis that bobwhite would select locations with greater proportions of native grasses within 50 m. Although previous research has shown that bobwhite select for locations in native grass in summer (Klimstra and Ziccardi 1963, Wiseman and Lewis 1981, Burger et al. 1994, Chamberlain et al. 2002), bobwhite in our study did not select for locations with higher percentages of native warm season grasses within 50 m of their location when compared to all other vegetation types combined. Bobwhite in Ohio selected grasslands when row crops were most abundant, and row crops where grassland cover was more abundant (Janke and Gates 2013). Brooke et al. (2015) found that in Kentucky the probability of selection

decreased 2% with every 10 m increase from the location to native warm-season grasses. While we do not dispute the importance of native grass, we believe our findings alongside other recent research suggests the importance of heterogeneous landscapes for bobwhite.

Previous research has indicated that prescribed burning and grazing manage the structure and composition of vegetation through the removal of litter (Brennan et al 1998, Glitzenstein et al. 2012) and increased forage abundance and availability (Brennan et al. 1997). In our study, the effect of management (i.e., prescribed burning or grazing) did not increase selection. In Kentucky, prescribed burning increased the density of native warm season grasses from 49% to 77%, rendering the habitat unsuitable to bobwhite due to overly dense vegetation (Unger et al. 2015). Brooke et al. (2015) also found no support for the influence of burning during the previous dormant season on resource selection of non-breeding bobwhite in Kentucky. Fuhlendorf and Engle (2004) demonstrated that fire and focal grazing promote heterogenic grasslands through increased forb abundance, diversity, and structural complexity as well as decreased litter and the decreased prevalence of tallgrasses for 2–3 years post-fire. While prescribed burning and grazing did not substantially influence fall and winter resource selection in our study directly, the disturbance created by prescribed burning and grazing promotes heterogeneous vegetation structure on the landscape. We suggest that conservation practitioners should consider utilizing prescribed burning and grazing at intervals and intensities that promote the creation and maintenance of early successional woody cover for bobwhite.

Bobwhite selected locations with greater quantities of woody stems, supporting our hypothesis that they would select locations with high densities of woody cover. High densities of woody stems can be indicative of the presence of woody cover such as shrub thickets. Brooke et al. (2015) found that the number of woody stems per hectare was not a strong predictor of non-

breeding resource selection; however, their analysis included woody stems >1.37 m in height whereas our analysis included woody stems >1 m in height. High woody stem densities may be created through re-sprouting of stems after brush hogging, mowing, or fire and maintained through the periodic disturbance at a frequency great enough to prevent woody cover from getting too tall or succeeding to trees, while not too frequent to maintain adequate interspersion of woody stems.

The amount and interspersion of woody cover is a major contributor to resource selection of bobwhite during the fall and winter (Janke and Gates 2013). Woody cover, and especially shrub cover, provides escape cover from predators and weather conditions (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). We found weak support for the effect of woody edge density on resource selection. The use of areas characterized by higher woody edge density is consistent with findings in Illinois (Roseberry and Sudkamp 1998), Kansas (Williams et al. 2004), Kentucky (Brooke et al. 2015), and Ohio (Janke and Gates 2013). Unger et al. (2015) hypothesized that bobwhite selected for locations near woody edges as the mixed vegetation at these locations maximized the resources available for forage and protective cover. An increase in the amount and interspersion of woody cover may lead to an increase in the probability of selection of that location by bobwhite and create more usable space across the landscape. However, care should be taken to prevent succession of early successional woody cover into trees.

Contrary to our hypothesis, bobwhite selected locations closer to trees. In Ohio, bobwhite selected for woodlots at the home-range order of selection (Janke and Gates 2013). Similarly, bobwhite selected woodlots over shrubland in New Jersey (Lohr et al. 2011). Bobwhites may use woodlands when the understory provides early successional woody cover (Roseberry and

Klimstra 1984, Yoho and Dimmick 1972, Seckinger et al. 2008, Unger et al. 2015), likely because the early successional woody cover is functionally similar to shrub cover (Janke and Gates 2013). However, trees are known as important habitat for predators of bobwhite such as opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*; Dijak and Thompson 2000, Bryne and Chamberlain 2011). Our research on fall and winter bobwhite survival showed that bobwhite survival increased with distance from trees (Chapter 1). Paradoxically, bobwhites selected locations closer to trees, contrary to our hypothesis and the potential fitness benefit of being further from trees. We suggest bobwhites often used shrub cover that was in close proximity to trees in areas of more permanent woody cover such as fence rows and riparian areas. Alternatively, bobwhites may have selected resources which did not maximize fitness. The strong selection for locations near trees exhibited by bobwhite may indicate trees function as an ecological trap (Patten and Kelly 2010), given the negative fitness consequences associated with locations near trees (Chapter 1).

Local heterogeneity provided by forbs, grasses, and bare ground is important for bobwhites (Klimstra and Ziccardi 1963, Schroeder 1985, Kopp et al. 1998). In Texas, average percent forb cover of used locations during the winter was 16.9% and 18.3% where management regimes were atypical and consisted of short duration grazing and 2-pasture deferred-rotation grazing, respectively, while percent bare ground was 26.3% and 20.0% (Wilkins and Swank 1992). We found no support for our hypothesis that bobwhite would select locations with moderate amounts of forb and bare ground. Mean forb percentage at used sites was 8.95% while mean forb percentage at available sites was 7.78% (Table 1). Mean bare ground at used sites was 7.14% and 9.96% at available sites (Table 1). Given the relatively similar distribution of forbs and bare ground across used and available locations, it seems appropriate that there was no

selection against forb and bare ground. Bobwhite also selected locations with minimal percentages of grass at the location during the winter, contrary to our hypothesis. Previous research has noted the negative impacts of dense grass cover on movement and feeding (Scott and Klimstra 1954, Kiel 1976, Jackson 1969) and roosting sites (Klimstra and Ziccardi 1963). While grass cover is a requirement of bobwhite for nesting cover, the value of grass cover for breeding bobwhite can be replaced by the importance of woody cover for non-breeding bobwhite.

Visual obstruction is a measure of cover provided by all vegetation types that may be indicative of protection and concealment from the weather and predators. Bobwhite in Missouri selected winter roost locations which provided greater visual obstruction (early successional vegetation VOR = 21 cm; native warm season grass VOR = 29 cm) than random sites perhaps due to the increased thermal values of locations composed of taller vegetation (Chamberlain et al. 2002). Brooke et al. (2015) found coveys selected locations with denser vegetation structure from 1.75 to 2 m above ground. We similarly found that bobwhite selected locations with greater visual obstruction, which supported our hypothesis and previous research.

The amount and interspersed of permanent, early successional woody cover was the most important contributor to the fall and winter resource selection of bobwhite. While prescribed burning and grazing were not supported, these management techniques offer the disturbance necessary to prevent the succession of shrubs to trees. However, management techniques such as mowing and brush-hogging may also be utilized to prevent this succession. Bobwhite populations may be stabilized, or increased, if the amount of usable space available to bobwhite is increased. We suggest that the creation and maintenance of early successional

woody cover is an important aspect to increasing the amount of usable space for bobwhite throughout the fall and winter.

MANAGEMENT IMPLICATIONS

Woody cover was an important characteristic of locations selected by bobwhite during the fall and winter in Missouri. Specifically, greater quantities of woody stems, indicative of shrub thickets, and closer proximity to trees increased the relative probability of selection. However, fall and winter survival of bobwhite was lower when bobwhite were located near trees (Chapter 1), potentially indicating an ecological trap. We suggest that managing disturbance, whether mowing, fire, or grazing, at a return interval and spatial scale that provides high interspersions of shrub cover while preventing succession to trees, will provide quality fall and winter habitat. Felling mature trees while still maintaining adequate interspersions of shrubs may also prevent an ecological trap. Lastly, while our study focused on fall and winter habitat, managers should also be cognizant of quail needs throughout their full annual cycle.

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TABLES

Table 1. Minimum, mean, and maximum for all covariates used in discrete choice resource selection models for Northern bobwhite during fall (Nov) and winter (Dec–Jan) in southwest Missouri, 2018–2019.

Variable ^a	Used			Available		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
GS	24.01	0.00	100.00	34.29	0.00	100.00
FB	8.95	0.00	90.00	7.78	0.00	100.00
BR	7.14	0.00	95.00	9.96	0.00	100.00
VO	47.87	1.00	100.00	29.39	0.00	100.00
SC	71.84	0.00	800.00	20.20	0.00	1000.00
NG	0.43	0.00	1.00	0.48	0.00	1.00
PG	0.44	0.00	1.00	0.46	0.00	1.00
TD	46.48	0.00	295.10	67.68	0.00	312.99
WE	455.80	0.00	1692.20	348.53	0.00	2099.27

^aGS = Percent grass within the 0.50 m² quadrat at the given location, FB = Percent forb within the 0.50 m² quadrat at the given location, BR = Percent bare ground within the 0.50 m² quadrat at the given location, VO = Visual obstruction measured by a modified Robel pole, SC = Number of woody stems greater than 1 m in height and within 5 m of the given location, NG = Percent of native grass within 50 m of the given location, PG = Percent land managed with prescribed burning and/or grazing within 50 m of the given location, TD = Distance (m) from nearest tree edge or individual tree, WE = Density (m/ha) of shrub and tree edges within 50 m of the given location.

Table 2. Variables included in candidate models explaining fall (Nov) and winter (Dec–Jan) resource selection of Northern bobwhite in southwest Missouri, 2018–2019 (fall/winter). Variables with the proportion of the posterior distribution <0.85 are indicated with a “0”, and variables with a proportion of the posterior distribution >0.85 are indicated with + if the effect was positive or - if the effect was negative. Model support is indicated by the Watanabe-Akaike Information Criteria (WAIC).

Model ^a	FB	GS	BR	VO	SC	NG	PG	NG*PG	TD	WE	WAIC	ΔWAIC
m1		-/0		+/+	+/+	0/0			0/-	+/+	565.14	0.00
m2	0/-	-/-	0/-	+/+	+/+						834.79	269.65
m3					+/+				-/-	0/+	1119.35	554.21
m4						0/0	-/0	0/0	-/-	0/+	1377.78	812.64
m5						-/-	0/0	0/-			1657.70	1092.56
m6											1860.41	1295.27

^aAll models included covey ID as a random effect and season as a fixed effect with additional fixed effects: FB = Percent forb within the 0.50 m² quadrat at the given location, GS = Percent grass within the 0.50 m² quadrat at the given location, BR = Percent bare ground within the 0.50 m² quadrat at the given location, VO = Visual obstruction measured by a modified Robel pole, SC = Quantity of woody stems greater than 1 m in height and within 5 m of the given location, NG = Percent of native grass within 50 m of the given location, PG = Percent land managed with prescribed burning and grazing within 50 m of the given location, TD = Distance (m) from nearest tree edge or individual tree, WE = Density (m/ha) of shrub and tree edges within 50 m of the given location.

Table 3. Posterior means and 95% credible intervals (CRI) for landscape, vegetation, and management effects from discrete choice models for fall (Nov) and winter (Dec–Jan) resource selection of Northern bobwhite in southwest Missouri, 2018–2019.

Effect ^a	Season	Model 1		Model 2	
		PM	95% CRI	PM	95% CRI
FB	Fall			-0.20	-1.28, 0.84
	Winter			-0.95	-2.30, 0.22
GS	Fall	-3.77	-7.72, -1.29	-1.44	-2.82, -0.35
	Winter	-0.25	-1.75, 1.01	-0.48	-1.31, 0.26
BR	Fall			-0.14	-0.90, 0.57
	Winter			-0.73	-1.89, 0.09
VO	Fall	2.48	-0.19, 6.09	1.08	0.20, 2.06
	Winter	4.59	2.21, 8.94	2.67	1.79, 3.90
SC	Fall	2.67	0.91, 5.42	1.03	0.32, 1.95
	Winter	3.35	1.35, 6.97	1.67	0.87, 2.77
NG	Fall	0.21	-3.99, 4.81		
	Winter	-0.29	-3.96, 3.03		
TD	Fall	-0.92	-4.43, 1.88		
	Winter	-3.28	-8.33, -0.41		
WE	Fall	1.37	-1.17, 4.46		
	Winter	0.87	-0.36, 2.42		

^aFB = Percent forb within the 0.50-m² quadrat at the given location, GS = Percent grass within the 0.50-m² quadrat at the given location, BR = Percent bare ground within the 0.50-m² quadrat at the given location, VO = Visual obstruction measured by a modified Robel pole, SC = Quantity of woody stems greater than 1 m in height and within 5 m of the covey’s used location, NG = Percent of native grass within 50 m of the given location, TD = Distance (m) from nearest tree edge or individual tree, WE = Density (m/ha) of shrub and tree edges within 50 m of the given location.

FIGURES

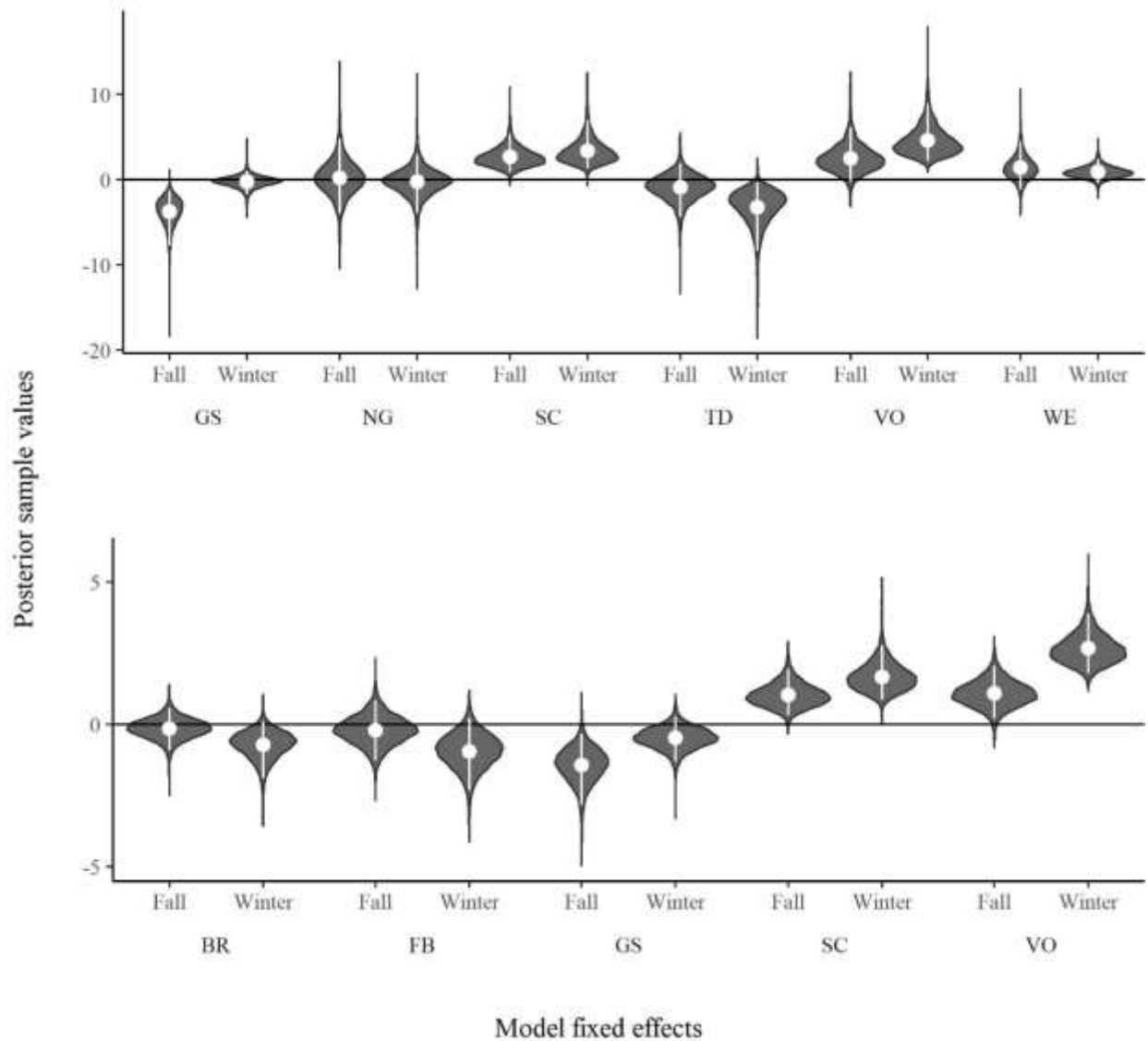


Figure 1. Posterior distributions (grey “violins”), means (white dots), and 95% credible intervals (CRI; white bars) for effects in the top two discrete choice models (m1, top; m2, bottom) for fall (Nov) and winter (Dec–Jan) resource selection of Northern bobwhite in southwest Missouri, 2018–2019. Model effects are GS = Percent grass within the Daubenmire frame at the given location, NG = Percent of native grass within 50 m of the given location, SC = Quantity of woody stems greater than 1 m in height and within 5 m of the covey’s used location, TD = Distance from nearest tree edge or individual tree, VO = Visual obstruction measured by robel pole, WE = Density of shrub and tree edges within 50 m of the given location, BR = Percent bare ground within the Daubenmire frame at the given location, FB = Percent forb within the Daubenmire frame at the given location.

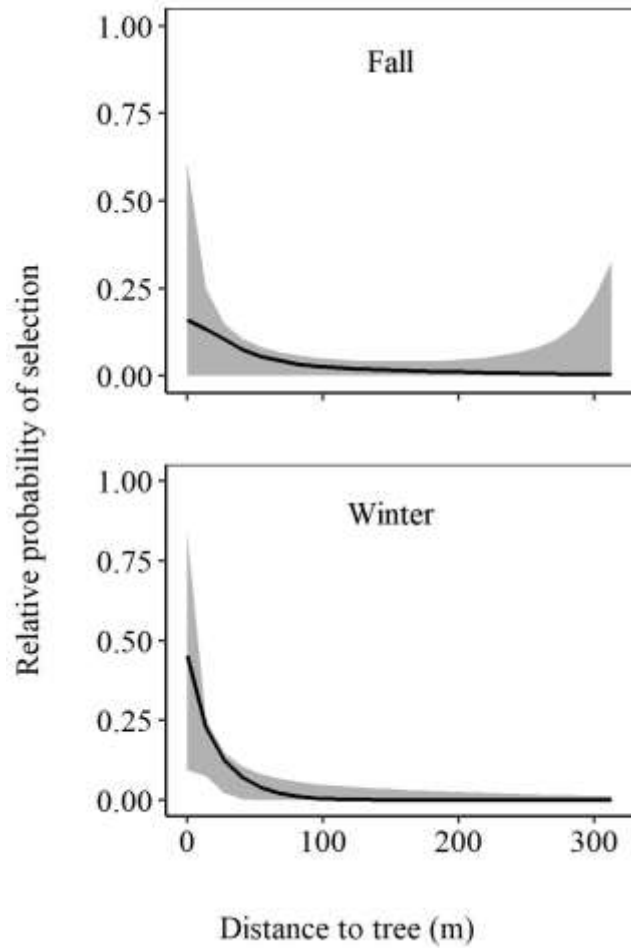


Figure 2. Mean relative probability of selection and 95% CRI for Northern bobwhite in fall and winter as function of the distance from the nearest tree (m) in southwest Missouri, 2018–2019.

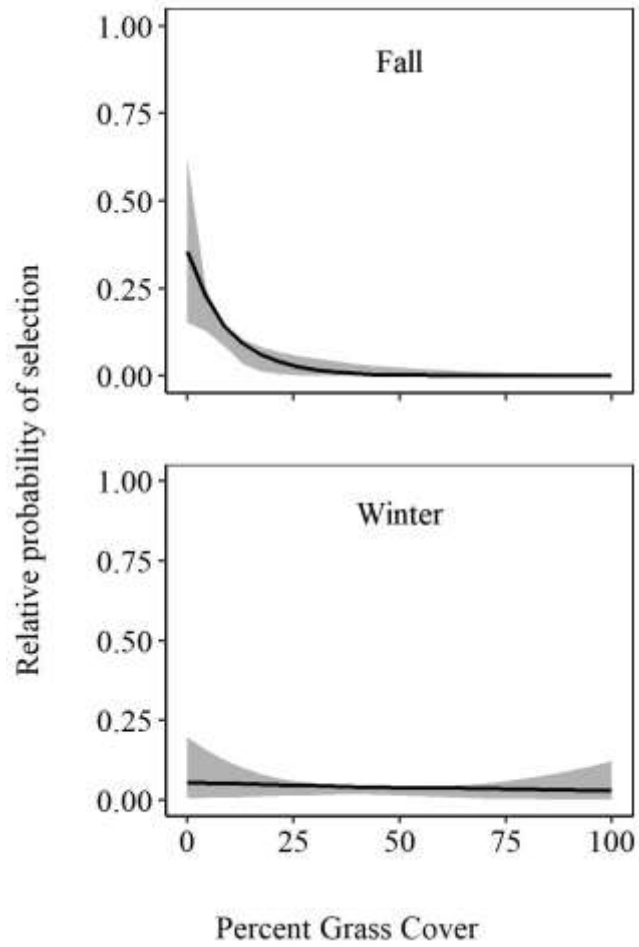


Figure 3. Mean relative probability of selection and 95% CRI for Northern bobwhite in fall and winter as a function of the percent grass cover at the given location in southwest Missouri, 2018–2019.

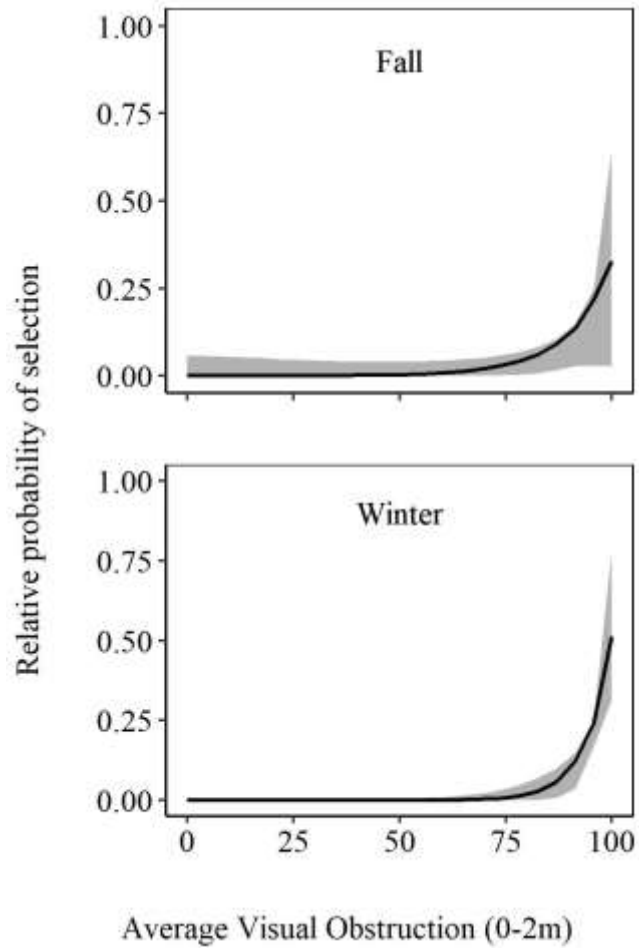


Figure 4. Mean relative probability of selection and 95% CRI for Northern bobwhite in fall and winter as a function of the average visual obstruction at a given location in southwest Missouri, 2018–2019.

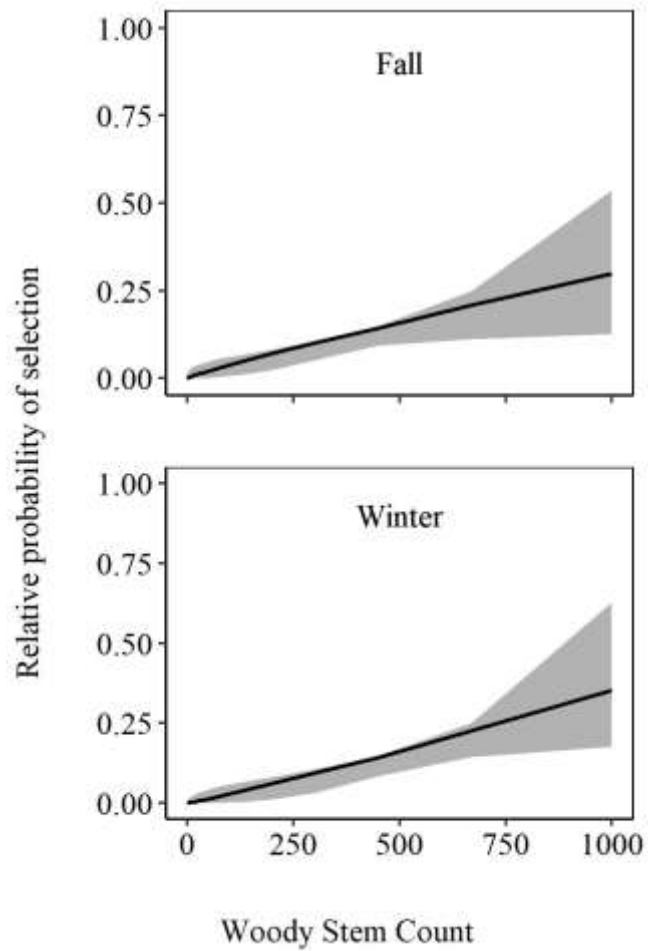


Figure 5. Mean relative probability of selection and 95% CRI for Northern bobwhite in fall and winter as a function of the number of woody stems greater than 1 m in height and within a 5 m radius of the given location in southwest Missouri, 2018–2019.