



Research Article

Impact of Experimental Habitat Manipulation on Northern Bobwhite Survival

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ABSTRACT Habitat management for northern bobwhite (*Colinus virginianus*) should affect vital rates, but direct linkages with survival are not well documented; therefore, we implemented an experiment to evaluate those responses. We conducted our experiment on a reclaimed surface mine, a novel landscape where conditions were considered sub-optimal because of the dominance of non-native vegetation, such as sericea lespedeza (*Lespedeza cuneata*), which has been reported to provide marginal habitat for northern bobwhite and may negatively affect survival. Nonetheless, these areas have great potential for contributing to bobwhite conservation because of the amount of early successional cover they provide. Our study site, a 3,330-ha reclaimed surface mine in western Kentucky, consisted of 2 tracts (Sinclair and Ken, 1,471 ha and 1,853 ha, respectively) that served as replicates with each randomly divided into a treatment (i.e., habitat manipulation through a combination of disking, burning, and herbicide application) and an undisturbed control ($n = 4$ experimental units). Habitat treatments were applied October 2009 to September 2013. We used radio telemetry to monitor northern bobwhite ($n = 1,198$) during summer (1 Apr–30 Sep) and winter (1 Oct–31 Mar), 2009–2013. We used the known-fate model in Program MARK to evaluate treatment effects on seasonal survival rates. We included biological, home-range, landscape, and microhabitat metrics as covariates to help improve model sensitivity and further elucidate experimental impacts. Survival varied annually, ranging from 0.139 (SE = 0.031) to 0.301 (SE = 0.032), and seasonally (summer, 0.148 [SE = 0.015]; winter, 0.281 [SE = 0.022]). We found a treatment effect ($\beta = 0.256$, 95% CI = 0.057–0.456) with a seasonal interaction ($\beta = -0.598$, 95% CI = -0.898 to -0.298) with survival being higher in summer (0.179 [SE = 0.022] vs. 0.109 [SE = 0.019]) and lower in winter (0.233 [SE = 0.025] vs. 0.355 [SE = 0.035]) on treatment than control units. Among habitat covariates, litter depth ($\beta = -0.387$, 95% CI = -0.5809 to -0.1930) was the most influential effect (negative) on survival. Additional experiments across a wider range of habitat conditions may be required to determine management intensity or duration thresholds required to elicit greater changes in survival for northern bobwhite populations. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Colinus virginianus*, habitat management, northern bobwhite, Peabody WMA, Program MARK, reclaimed surface mine, survival.

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The northern bobwhite quail (*Colinus virginianus*; hereafter, bobwhite) is a recreationally and economically important game bird that has been declining by 3.8% annually across the United States for the last 40 years (Brennan 1991, Sauer et al. 2011). Similar local declines have also been reported in the Central Hardwood Bird Conservation Region (CHBCR; Sauer et al. 2011). Among the many hypotheses

thought to explain this decline are land use change (Brennan 1991), extreme weather (Lusk et al. 2001, Hernández et al. 2005), predation (Mueller et al. 1999, Palmer et al. 2005, Staller et al. 2005), hunting pressure (Madison et al. 2002, Guthery et al. 2004), and loss and fragmentation of habitat (Fleming and Giuliano 2001). All of these factors may influence such declines, but it has become clear that the major causative factor is habitat loss (Guthery 1997, Brady et al. 1998, Veech 2006).

Numerous studies have assessed the impact of management practices on habitat for bobwhite (Greenfield et al. 2003, Gruchy et al. 2009, Gruchy and Harper 2014), but few have assessed the direct effects of such manipulations on bobwhite survival. Survival has been determined to be a stronger determinant of population fitness for bobwhite than fecundity in a meta-analysis of demographic data collected throughout the range of this species (Sandercock et al. 2008), stressing the importance of understanding this parameter when evaluating habitat manipulations and conservation strategies. In one of the few studies to assess effects of habitat manipulations on survival, Seckinger et al. (2008) evaluated winter survival in Tennessee. They reported that treatments, which included converting 33% of closed-canopy forests into early successional cover, resulted in 12% greater survival on treatment versus control areas. Other researchers have assessed habitat influences on bobwhite survival (Taylor et al. 1999, Holt et al. 2009, Janke 2011, Lohr et al. 2011), but these studies were correlative rather than experimental.

Furthermore, the relationship between habitat and survival should be assessed at different spatial scales (Brady et al. 1993, Roseberry 1993), especially in the context of fragmented landscapes. This contention was confirmed in studies conducted by Seckinger et al. (2008) and Janke (2011), both of which showed evidence of multi-scale habitat influence on survival. Studies that have related multi-scale habitat metrics to survival typically have focused on a single season (Taylor et al. 1999, Seckinger et al. 2008, Holt et al. 2009) rather than multiple seasons (Lohr et al. 2011). Because bobwhite survival has been shown to vary by season (Curtis et al. 1988, Burger et al. 1995), both summer and winter should be assessed when relating survival to multi-scale habitat attributes. Understanding these broader-scale influences on survival may provide insight on how to best allocate resources for local-scale habitat improvement efforts.

In the face of continued bobwhite population declines, one opportunity to manage large tracts of land for bobwhite is reclaimed surface mines because of the scale that land can be managed and the potential to serve as source populations for surrounding properties. More than 600,000 ha have been reclaimed throughout the eastern United States under the Surface Mining Control and Reclamation Act of 1977 (SMCRA). However, the main focus of such reclamation has been to prevent erosion and this has led to the establishment of non-native species, such as sericea lespedeza (*Lespedeza cuneata*; Fitzgerald et al. 2005), which provides poor structure for bobwhite and limited food resources (i.e., small, low nutritional value seeds, marginal invertebrate substrate) while out-competing more desirable native species

that do provide good structure and food resources (Davison 1958, Bugg and Dutcher 1989, Wade 1989). Furthermore, few studies have addressed the potential of reclaimed mine lands for bobwhite (Beckerle 2004, Stauffer 2011, Tanner 2012), and no research has been conducted in the context of habitat manipulation on these areas. Therefore, efforts are needed to understand how best to manage reclaimed mine lands dominated by non-native species and considered to provide poor habitat for bobwhite (Stauffer 2011). Surface mines provide an opportunity to understand bobwhite habitat relationships and to explore these relationships in an experimental setting because of the consistent (i.e., homogeneous) nature of habitat and the scale at which it occurs. These 2 factors make manipulations of consistent experimental units possible at large scales without the limited inferences smaller or fragmented landscapes would impose.

We implemented an experiment on a reclaimed surface mine from 2009 to 2013 to assess the effects of habitat manipulation and to further our understanding of how vegetation on reclaimed mine lands affect bobwhite survival. Our primary objective was to determine if habitat management increased seasonal survival rates. Additionally, we sought to determine which vegetation attributes contributed to survival at landscape (i.e., context in which home range occurs), home-range, and microhabitat (i.e., patches within home ranges) scales. Finally, we sought to document overall survival of bobwhite on a reclaimed surface mine. We hypothesized that our habitat manipulations, which were focused on suppression of non-native herbaceous cover through burning, disking, and herbicide application, would enhance habitat and lead to improved survival. Specifically, we predicted summer survival would improve more than winter survival because habitat manipulations disproportionately affected summer habitat conditions for bobwhite; altering winter cover was less likely because of the time frame of our experiment (i.e., 4 years) and the time required to establish and develop shrub cover on a mine site. We also expected to find multi-scale habitat effects on bobwhite survival, with those at the microhabitat scale, where management activities would have the greatest impact, being particularly influential.

STUDY AREA

We conducted our study on 2 tracts of the Peabody Wildlife Management Area (PWMA) separated by 18 km, Sinclair (1,471 ha; 37°14'N, 87°15'W) and Ken (1,853 ha; 37°17'N, 86°54'W), and located in Muhlenberg and Ohio counties, Kentucky, USA. Both tracts were reclaimed surface mine sites dominated by early-successional vegetation communities. Soils on both tracts consisted primarily of udorthents, which are characteristic of reclaimed mine sites. Mean annual precipitation was 125.1 cm (National Oceanic and Atmospheric Administration 2014). Trees on the study area were established both pre- and post-SMCRA (1977), whereas all early successional cover was established post-SMCRA. Sericea lespedeza, established during reclamation, constituted much of the vegetation on both tracts. Native warm-season grasses (NWSG), including mixtures of big

bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), were established throughout both tracts from 2000 to 2004. Soil compaction during reclamation led to the slow growth of American sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), oaks (*Quercus* spp.), and maples (*Acer* spp.), which were the dominant tree species planted during reclamation throughout both tracts. Shrubs occurred throughout both sites and included patches of sawtooth blackberry (*Rubus argutus*), winged sumac (*Rhus copallina*), black locust (*Robinia pseudoacacia*), autumn olive (*Elaeagnus umbellata*), and coralberry (*Symphoricarpos orbiculatus*). Annual food plots were maintained on both tracts, and consisted primarily of a mixture of grain sorghum (*Sorghum bicolor*), corn (*Zea mays*), pearl millet (*Pennisetum glaucum*), browntop millet (*Urochloa ramosa*), soybeans (*Glycine max*), and annual sunflower (*Helianthus annuus*).

METHODS

Study Design

We used an experimental approach to test our research hypotheses. We designated Ken and Sinclair tracts as replicates, a choice that was subsequently validated by the fact that we never documented movement of any birds between sites. Each replicate was divided into approximately equal halves (experimental units; $n=4$) with similar proportions of vegetation types (Table 1). One experimental unit within each replicate was randomly assigned to receive habitat manipulation (i.e., a combination of disking, burning, and herbicide application that was implemented across the entire unit) during 2009–2013, whereas the other unit was not disturbed and served as a control (2 replicates of treatment and control; Fig. 1). Our study was not designed to evaluate the influence of individual management practices (i.e., disking, burning, or herbicide application) but rather to evaluate the net effect of the combined application of these practices in an operational manner versus undisturbed sites. Habitat manipulations were focused on decreasing cover of invasive non-native plants that were previously established, increasing plant diversity, especially native species, and increasing woody cover density. The Sinclair control and treatment units were 673 ha and 798 ha, respectively, whereas the Ken control and treatments units were 1,043 ha and 810 ha, respectively (Table 1). The manipulations we applied varied by year and season because of weather and logistical constraints. Disking (337 ha, 21% of combined treatment units' total area), which typically was applied on 0.5–2.0-ha patches, occurred throughout the year; burning (432 ha, 27% of combined treatment units' total area) occurred primarily from February–April with burns typically encompassing 5–30 ha each; and herbicide application (aerial, metsulfuron methyl; 160 ha, 10% of combined treatment units' total area) occurred during August–September. We applied 963 ha of habitat manipulations (Sinclair = 543 ha, Ken = 420 ha) during the 4 years; some areas received multiple disturbances during the experiment.

Until 2008, small game hunting was governed by prevailing statewide regulations established by the Kentucky Department of Fish and Wildlife Resources (KDFWR). From 2009 to 2013, regulated quota hunts for bobwhite were established on both units to reduce hunting pressure and gather data on harvested birds (i.e., age, sex, and crop contents).

Land Cover

Ninety-one percent of the total land cover consisted of 4 vegetation types (Table 1) and were delineated based on aerial imagery in ArcGIS 9.3 (Environmental Systems Research Institute, Inc., [ESRI], Redlands, CA). To delineate between forest, shrub, and herbaceous vegetation, we used 1-m resolution aerial imagery (2010) from the National Agriculture Inventory Program, United States Department of Agriculture, Farm Service Agency. We selected representative woody cover on our study site as a template for reclassifying all 1×1 -m cells as either woody or open with the Image Analyst tool in ArcGIS. We then used the Aggregate Tool (means procedure) to create unique polygons of woody or open vegetation with a minimum size of 0.2 ha, which was the average size of the smallest habitat management activity (disking) implemented on the site. To delineate between open vegetation, shrub vegetation, and forest, we used percentage breaks (visually) within our individual raster cells based on the percent of woody vegetation present within each 0.2-ha polygon. We classified polygons with <10% woody cover as open vegetation (open), those with 11–55% woody cover as shrub (shrub), and those with >56% woody cover as forest (forest). Forest vegetation (stems >10 cm DBH) had a mean basal area of 20.9 m²/ha (SE = 1.77) and shrub (stems typically 10–20 cm DBH) was 9.6 m²/ha (SE = 1.23). We delineated our fourth vegetation type, NWSG, by mapping areas comprised of $\geq 51\%$ native grass using ArcPad 8.0 (ESRI) on handheld global positioning system (GPS) units (Trimble Navigation Limited, Inc., Sunnyvale, CA); areas dominated by herbaceous vegetation that consisted of <51% native grass remained in the open classification. We confirmed all classifications by visual inspection of representative sites to validate GIS-based assignments of vegetation types.

Trapping and Radio Telemetry

We captured bobwhites during all months of the year using funnel traps (Stoddard 1931, Palmer et al. 2002) baited with cracked corn and grain sorghum placed throughout the study area at known covey locations and locations with suitable cover for bobwhite. Additionally, we netted coveys at night during winter and radiomarked additional birds (Truitt and Dailey 2000). We defined a biological year as 1 October–30 September and seasons as winter (1 Oct–31 Mar) and summer (1 Apr–30 Sep) based on Burger et al. (1995). We covered traps with burlap and surrounding vegetation to reduce stress and predation on captured individuals. We set traps ≥ 5 days per week and checked them once daily in the evening. We banded bobwhites with a body mass of ≥ 90 g with aluminum bands (both legs), and fitted birds with body mass ≥ 120 g with ≤ 6.5 -g necklace-style radio transmitters (crystal-controlled, 2-stage design, pulsed by a CMOS

Table 1. Delineated vegetation types and total cover (ha) on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013.

Site	Unit	Vegetation	Hectares	Total by unit	Total
Ken	Treatment	Annual grain	21.0	810.2	1,853.1
		Forest deciduous	216.6		
		Native warm-season grass	93.7		
		Open herbaceous	244.7		
		Shrub	175.4		
		Water	52.6		
		Wetland emergent	6.2		
	Control	Annual grain	4.8	1,042.8	
		Forest deciduous	189.0		
		Native warm-season grass	112.0		
		Open herbaceous	279.7		
		Shrub	344.0		
		Water	112.7		
		Wetland emergent	0.6		
Sinclair	Treatment	Forest deciduous	162.0	798.2	
		Native warm-season grass	24.1		
		Open herbaceous	367.8		
		Shrub	194.9		
		Water	44.1		
		Wetland emergent	5.3		
		Control	Annual grain		6.5
	Forest deciduous		165.3		
	Native warm-season grass		33.8		
	Open herbaceous		303.8		
	Shrub		126.8		
	Water		25.5		
	Wetland emergent		10.7		

multivibrator; American Wildlife Enterprise, Monticello, FL). Corteville (1998) reported that radiotransmitters may slightly reduce annual survival, but we assumed the magnitude of bias was consistent between treatment and control sites on our study area (Palmer and Wellendorf 2007, Terhune et al. 2007, Tanner et al. 2012). We also recorded sex, age, mass (g), and overall condition of captured birds. We determined sex by plumage and age by the presence or absence of buff-tipped primary coverts (Leopold 1933). We sought to maintain a sex ratio of radiomarked birds favoring females to help adjust for typical male-biased populations (Roseberry and Klimstra 1984) and to increase the sample size of nests. Our trapping and handling methods complied with protocols of University of Tennessee Institutional Animal Care and Use Committee Permit 2042-0911.

We located radiomarked birds ≥ 3 times/week using a scanning receiver and a handheld Yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). We used the homing method (White and Garrot 1990) to locate bobwhites by walking toward the bird, but stopped 30–50 m from the bird to avoid flushing it. We recorded the distance and azimuth to the bird by assessing the strength and direction of the telemetry signal. We then recorded the Universal Transverse Mercator (UTM) coordinates of the observer on a GPS unit (Garmin GPSMAP 60CSx, Garmin International, Inc. Olathe, KS) and used the distance and azimuth to estimate the actual location of each bird. We recorded locations of

birds at different times on subsequent days to capture the variability of diurnal patterns and classified bobwhites as being in the treatment, control, or off the study area according to the study area boundary. We also recorded the vegetation type in which the bird was located. Upon detection of a mortality signal (12-hr signal), we located the collar and confirmed mortality.

Microhabitat Variables

We collected data on microhabitat vegetation based on bird-centered locations (Block and Brennan 1993) during summer 2012, winter 2012–2013, and summer 2013. We collected these data on a subset of 20 birds from each experimental unit during each season of sampling; we added additional birds throughout the season to compensate for mortalities. We sampled vegetation at known locations within 7 days of obtaining the location for each bird in the subset throughout the season to minimize any temporal bias. Birds had to have been radiotagged for ≥ 4 weeks to be included in the analysis.

For microhabitat vegetation, we selected 12 metrics potentially influential on bobwhite survival: litter depth (cm), woody stem density (stems/ha; midstory), the structure of vegetation representing overhead herbaceous cover (Nudds board cover for 1.25–1.5 m strata; canopy), ground sighting distance (cm; sight), distance to edge (m), distance to woody cover (m), maximum herbaceous vegetation height (cm; height), and 5 composition metrics (proportion; warm-

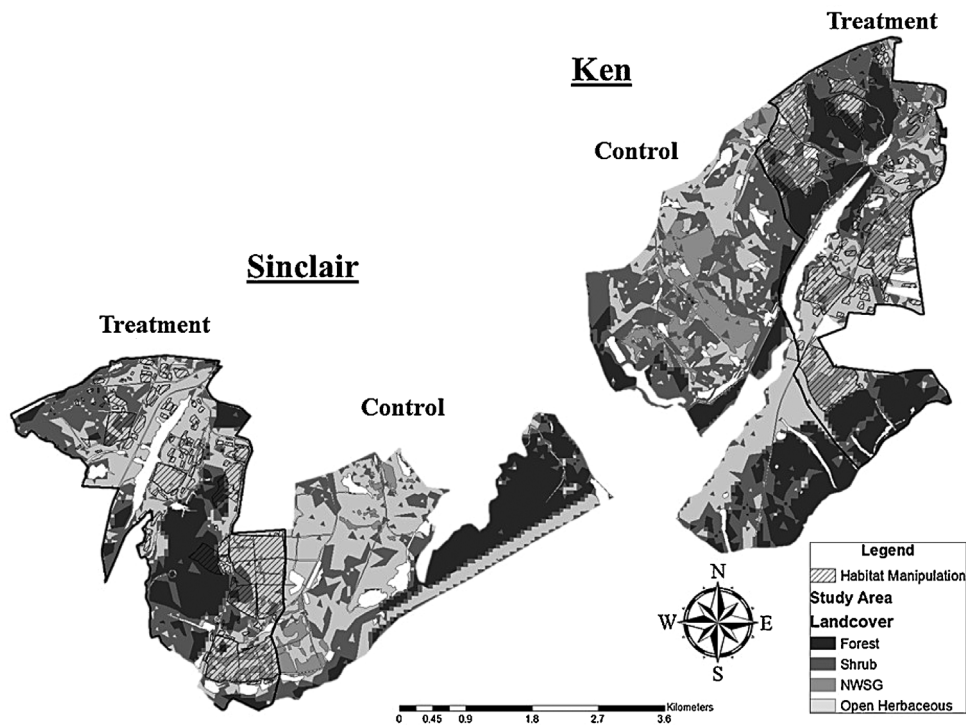


Figure 1. Map of manipulations applied on Sinclair and Ken units, Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013. NWSG stands for native warm-season grasses.

season grass, forbs, ragweed, brambles, and cool-season grass). We collected 2 metrics (height and distance to woody cover) exclusively during winter (Dec–Mar), 7 (sight, distance to edge, warm-season grass, forbs, ragweed, brambles, cool-season grass) exclusively during summer (May–Aug), and 3 (canopy, litter depth, and midstory) during both seasons.

We collected microhabitat vegetation composition, sight, and litter depth metrics from a 30-m transect centered on known bird locations. We collected plant species composition at every meter along the 30-m transect generating 30 subsamples per transect. We calculated proportion of vegetation cover as the number of points with a plant species present belonging in a given composition category divided by the total number of sampling points along each transect. We based species composition categories on their relative dominance within the vegetation community (i.e., high percent cover ratings) and their biological importance (i.e., providing food and/or cover). Species within the warm-season grass category were sideoats grama (*Bouteloua curtipendula*), big bluestem, broomsedge (*Andropogon* spp.), indiagrass, switchgrass, and little bluestem. Native grasses had been planted on the study area because of their perceived value for providing nesting and brood cover and, therefore, have been considered an important habitat management practice on the site. Forbs were considered important with respect to providing food and as a substrate for insects. Species in the forb category were musk thistle (*Carduus nutans*), horseweed (*Conyza canadensis*), daisy fleabane (*Erigeron annuus*), Maximilian sunflower (*Helianthus maximiliani*), prickly lettuce (*Lactuca serriola*), sumpweed (*Iva*

annua), sweetclover (*Melilotus officinalis*), Canada goldenrod (*Solidago canadensis*), old-field aster (*Symphotrichum pilosum*), Carolina geranium (*Geranium carolinianum*), birdsfoot trefoil (*Lotus corniculatus*), and yellow woodsorrel (*Oxalis stricta*). The single species category, ragweed, was common ragweed (*Ambrosia artemisiifolia*) and we chose it because it was a dominant plant on disked areas and was representative of an uncommon cover type on our sites (i.e., annual plant communities). We chose brambles as a category because they are known to provide escape cover for bobwhite; species were pasture rose (*Rosa carolina*), multiflora rose (*Rosa multiflora*), prairie rose (*Rosa setigera*), sawtooth blackberry (*Rubus argutus*), southern dewberry (*Rubus trivialis*), black raspberry (*Rubus occidentalis*), coralberry, and Japanese honeysuckle. Cool-season grasses were tall fescue (*Schendornorus arundinacea*), Kentucky bluegrass (*Poa pratensis*), and orchardgrass (*Dactylis glomerata*). We included cool-season grass because many of these species occur as dense stands of sod and provide structure not typically beneficial to bobwhite (Barnes et al. 1995, Harper and Gruchy 2009); therefore, they have been considered detrimental to habitat quality.

We defined litter as dead vegetative material on the soil surface (McCoy et al. 2001). We took litter depth measurements at 0, 6, 12, 18, 24, and 30 m along each transect by placing a ruler perpendicular to the ground and measuring to the nearest 0.5 cm. We averaged the 6 measurements to provide each bird location with 1 litter depth value. We measured ground sighting distance (sight), which was an index of openness at ground level, at 0, 10, 20, and 30 m along the transect by kneeling and looking

perpendicularly to the transect through a polyvinyl chloride (PVC) tube 3.2 cm in diameter and 15.2 cm long, mounted horizontally on a metal stake 20.3 cm above ground (Gruchy and Harper 2014). We recorded the distance (cm) at which vegetation obscured a ruler viewed through the tube. We averaged the 4 sighting distances to give each bird location 1 sight-tube value. We estimated midstory based on stems <11.4-cm diameter at breast height within a 5-m radius plot during summer and a 10-m radius plot during winter centered, in both cases, at each known bird location. We assessed vegetation structure using a modified Nudds board (Nudds 1977), which was 2 m tall and consisted of 8, 0.25-m strata. We took Nudds board (visual obstruction) readings at 0, 10, 20, and 30 m along each transect during summer, whereby an observer determined the amount of vegetation covering each stratum (0 = no vegetation, 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, and 5 = 81–100%) 5 m from the board from a kneeling position. During winter, we read the Nudds board from a distance of 10 m in each cardinal direction. Based on the 4 visual obstruction readings at each location, we estimated an average cover for each stratum for each sampled bird. We calculated canopy as the average vegetative cover of stratum 3 (1.25–1.5 m). We measured the average height of the tallest herbaceous vegetation 10 m from plot center in each cardinal direction during winter. We estimated distance to edge and distance to woody cover using a rangefinder. We considered edge to be where 2 different delineated vegetation types met and woody cover to be the nearest woody cover offering acceptable escape from predators.

Home Range and Landscape Variables

We used the home range tools (HRT; Rodgers et al. 2007) extension in ArcGIS 9.3 (ESRI) and Geospatial Modelling Environment (GME; Spatial Ecology LLC, <http://www.spatialecology.com/gme/>, Accessed 15 Jan 2013) to calculate 95% fixed-kernel home ranges (Worton 1989, Seaman et al. 1999) for each individual within each season. We calculated home ranges only for individual birds with ≥ 20 locations (DeVos and Mueller 1993, Taylor et al. 1999). During winter, we estimated home ranges for individuals rather than coveys because our subsequent analyses were focused on survival estimates derived for individual birds.

At the landscape scale, we calculated metrics associated with a buffer placed around each home range. We created buffers using a radius equal to double the average daily movement observed during our study within each season (summer, 127 m; winter, 133 m). We calculated average daily movement as the mean distance between consecutive daily locations for an individual. Similar studies have used a buffer equal to the mean daily movement observed during the study (Holt et al. 2009). We doubled the average daily movement because we wanted to ensure that the scale of our landscape was large enough to capture substantive features around the home range and to ensure that the landscape scale had the potential to reflect meaningful differences from the home range, something a smaller buffer would be less likely to achieve.

Home range covariates included the proportion of each vegetation type and seasonal home range size for each bird. We selected 7 landscape-level metrics based on previous research (Taylor et al. 1999, Holt et al. 2009, Janke 2011) that identified bobwhite habitat needs and population responses to habitat at different spatial scales: forest-open vegetation (both NWSG and open) edge density, shrub-open vegetation edge density, core area of all 4 major vegetation types (using a 30-m edge effect), and a contagion index. The contagion index is a measure of patch-type interspersions and overall patch dispersion (i.e., 1.0 = no interspersions, 0 = max. interspersions; O'Neill et al. 1988), and has been shown to have a relationship with bobwhite presence (Roseberry and Sudkamp 1998). We calculated the mean of these metrics for each buffered home range using FRAGSTATS (McGarigal and Marks 1994) based on a 150-m moving window.

Survival Analysis

We estimated seasonal survival rates using the known-fate model with a logit link function in Program MARK (White and Burnham 1999). We estimated survival rates separately for summer and winter. We censored the first 7 days after a bird was released in our analysis to control for potential capture myopathy (Guthery and Lusk 2004). We used a staggered-entry method to analyze survival with the known-fate model (Pollock et al. 1989), which left-censors encounter histories for individuals until they are captured and enter the monitored population. We right-censored individuals because of emigration from the study area, radio failure or loss, or unknown fate. We assumed birds were randomly sampled, survival times for individuals were independent, and censoring mechanisms were independent of animal fate. Some coveys contained >1 radiotagged bird, which may have violated the assumption of independence. However, the number of radiotagged birds within the coveys was relatively evenly distributed (70% of our coveys had multiple birds telemetered at some point during the winter, typically 2–4 birds/covey), there was interchange of individual birds among coveys, and our expectation was that any bias would be consistent between treatment and control sites. Within each of our sites, some birds moved between treatment and control units throughout the season. Thus, we determined whether a bird was a treatment or control bird for the purposes of analysis by the preponderance of locations (>70%) on each unit. The cutoff of 70% was arbitrary but represented a good break point in our data and resulted in the vast majority of our birds being included in the analyses. Each survival period (summer and winter) consisted of 183 days. We encoded encounter histories as weekly survival periods, whereby each survival period had 26 encounter history occasions. If individual birds survived from one season to the next, we considered them to be new individuals and independent at the start of the next season.

Habitat metrics associated with home range and landscape scales were calculated only for birds with estimated home ranges (i.e., >20 locations) to establish a reliable, explicit spatial context for these individuals that could then be geo-

referenced to our vegetation layers. For birds without estimated home ranges or associated microhabitat data, we used null (average) values for missing covariates (Cooch and White 2008). Though the missing covariates provided no information on treatment effects and may negatively bias the variances for the covariates, we were able to include all birds in our analysis, thus reducing bias associated with excluding short-lived birds for which home range estimates were unavailable. We determined this to be preferable to systematically eliminating birds that may have had low survival rates.

Our survival analysis consisted of 5 suites of covariates that were sequentially combined into a single analysis to assess the value of all covariates on survival (Doherty et al. 2012). These 5 suites of covariates represented biological metrics, experiment covariates, and habitat metrics measured at 3 different spatial scales: home range, landscape, and microhabitat. To minimize inclusion of extraneous models and keep model sets to a reasonable size, we used a 3-stage modeling process whereby we found the best biological, experiment, and habitat (at all 3 scales) models (in that order) from our 5 suites of covariates. That is, we used the best single model in all subsequent stages of analysis.

We based the selection of covariates and development of candidate models on published studies and our assessment of relative biological importance. The first stage of analysis (biological) included biological metrics: sex, age, mass, condition index, season, linear time, and weekly time effects. Linear time was variation in survival from week 1 to week 26 during a season and weekly time was variation in survival among weeks during a season. We selected the top model from the biological stage based on the corrected Akaike's Information Criterion (AIC_c) value and used this model as the baseline model in the second stage of analysis (experiment). We then combined covariates explicitly associated with the implementation of the experiment (site, year, and treatment status) with the top biological model as additive and interaction terms. We considered year an experimental covariate because habitat manipulations were progressive and cumulative. We also developed additive and interaction models among treatment covariates exclusively and subsequently as terms in our final model set to test further our hypotheses. For the third stage of analysis, we added habitat covariates at all 3 scales (home range, landscape, and microhabitat). We incorporated all covariates from the third stage of analysis as additive terms to the top biological and experimental model to evaluate effects of habitat. We also re-assessed biological and experimental covariates that had some support from previous models to explore key relationships associated with our experimental framework and that may have been masked earlier in our modeling process (Doherty et al. 2012). We used the top model based on the ΔAIC_c score to estimate seasonal survival rates. We used a ΔAIC_c value of <2 (Burnham and Anderson 2002) to determine validity of a model for explaining variance in survival. We also computed model-averaged parameter estimates for seasonal survival rates using the survival estimates from all models. We considered an effect

to be significant if the 95% confidence interval of the β value excluded 0.

RESULTS

We captured and banded 1,794 bobwhites (866 males, 652 females, and 276 birds for which we were not able to confirm sex (because of their young age) from 1 October 2009 to 30 September 2013. We captured more juveniles ($n = 1,443$) than adults ($n = 351$) during the course of our study. Of the 1,794 captured birds, we radiomarked 1,198, and were able to use 1,131 in our survival analyses (i.e., known-fate model) after censoring. Of these, 643 (57%) were assigned to treatment, 477 (42%) to control, and 11 (1%) were not associated with either (i.e., $<70\%$ of locations for these individuals were in either treatment or control) and therefore, not used in the analysis. We obtained ≥ 20 locations on each of 635 birds for which we were able to estimate home ranges and associated habitat metrics. We never documented movement of any birds between study sites. Our trap success between sites was similar during winter ($t = 0.12$, $P = 0.92$; Ken = 2.8%, $n = 13,988$; Sinclair = 2.7%, $n = 10,443$) and summer ($t = 0.69$, $P = 0.53$; Ken = 2.0%, $n = 34,372$; Sinclair = 2.4%, $n = 33,632$). Hunter harvest in our study was negligible, accounting for only 1 (0.27%) mortality.

We used the best biological model from our first stage of analysis, {season}, as the baseline model in our second (experiment models) stage of analysis (Table 2). After incorporating models that included experimental covariates with additive and interaction terms, {season \times year} became the top model and was used as the baseline for the third stage of analysis (habitat models). The model {season \times year + litter depth + core area of open + home range size} became the top model once we incorporated habitat covariates. After running additional combinations and interactions that included covariates associated with our experimental framework with this model, {season \times year + litter depth + core area of open + home range size + treatment \times season} became the final overall model based on ΔAIC_c and AIC_c weight (Table 2). Based on 95% confidence intervals of beta estimates, all variables within the top model differed from 0 except core area of open and home range size (Table 3). The model receiving the second most support did not include the {treatment \times season} interaction but was 15.47 times less likely than the top model ($\Delta AIC_c = 11.466$, AIC_c weight = 0.003; Table 2) based on deviance, indicating the effect of the treatment interaction was considerable.

Based on the top model, summer survival was 0.148 ± 0.015 and winter survival was 0.282 ± 0.022 pooled across years (Table 4). Winter survival was variable, whereas summer survival was more consistent among years (Fig. 2). Our treatment effect was included in the top model but included an interaction effect with survival being higher in summer (0.179 [SE = 0.022] vs. 0.109 [SE = 0.019]) and lower in winter (0.233 [SE = 0.025] vs. 0.355 [SE = 0.035]) on treatment than control units, respectively (Fig. 3). Among habitat covariates, litter depth was the most influential covariate, having a negative relationship with survival

Table 2. Highest ranking models (and null model) based on differences in corrected Akaike's Information Criterion (ΔAIC_c) values and AIC_c weights used to assess the influence of biological, home range, landscape, and microhabitat metrics on northern bobwhite survival on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013. Top models from stage 1 (biological) of analysis {Season} and stage 2 (experiment) of analysis {Season \times Year} are also included.

Model ^a	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K^b	Deviance ^c
season \times year + litter depth + open core area + HR size + treatment \times season	5,533.74	0.00	0.988	1	13	5,507.71
season \times year + litter depth + open core area + HR size	5,545.21	11.46	0.003	0.003	11	5,523.18
season \times year + litter depth + open core area + HR size + treatment \times year	5,546.33	12.58	0.002	0.002	15	5,516.29
season \times year + litter depth + open core area	5,546.54	12.79	0.002	0.002	10	5,526.52
season \times year + litter depth + HR size	5,547.06	13.32	0.001	0.001	10	5,527.04
season \times year + litter depth + open core area + HR size + treatment	5,547.17	13.43	0.001	0.001	12	5,523.15
season \times year + litter depth + open core area + canopy + brambles + DtoED	5,547.22	13.48	0.001	0.001	13	5,521.19
season \times year + litter depth + open core area + treatment	5,548.52	14.78	0.000	0.001	11	5,526.50
season \times year + litter depth + brambles	5,548.59	14.84	0.000	0.001	10	5,528.57
season \times year + litter depth	5,550.17	16.43	0.000	0.000	9	5,532.16
season \times year + litter depth + canopy	5,551.30	17.55	0.000	0.000	10	5,531.28
season \times year + litter depth + DtoED	5,551.51	17.76	0.000	0.000	10	5,531.49
season \times year + litter depth + treatment	5,552.18	18.43	0.000	0.000	10	5,532.16
season \times year + HR size	5,556.91	23.16	0.000	0	9	5,538.89
season \times year + open core area	5,557.44	23.69	0.000	0	9	5,539.42
season \times year	5,559.97	26.23	0.000	0	8	5,543.96
season	5,595.42	61.68	0.000	0	2	5,591.42
null ^d	5,608.63	74.89	0.000	0	1	5,606.63

^a Distance to edge covariate is represented as DtoED. Home range size covariate is represented as HR size.

^b Number of parameters in each model.

^c Deviance is the difference in $-2\ln$ (Likelihood) of the current model and $-2\ln$ (Likelihood) of the saturated model.

^d Survival rate is equal for all weeks.

(Table 3). Other habitat covariates, as well as single variable, additive, and interaction models, had no support ($\Delta AIC_c > 11$). Pooled survival rates during summer were higher on treatment (0.179) than control (0.109); however, survival was higher on control (0.355) than treatment (0.233) during winter (Table 4; Fig. 3).

Additionally, we evaluated a number of post-hoc variables to identify relationships that could explain the differences in survival associated with the treatment \times season interaction. First we assessed models for winter data using only the top model plus 5 habitat covariates that we hypothesized would influence survival during winter (shrub, core area of shrub,

forest, core area of forest, and midstory). Of these covariates, only shrub ($\beta = 0.010$, $CI = 0.001-0.018$) had a relationship (positive) with survival for both treatment and control. Similarly, we assessed a set of models for summer only using 6 covariates that may have influenced survival during this season (litter depth, canopy, brambles, forbs, ragweed, and core area of open). Among these, litter depth ($\beta = -0.514$, $CI = -0.713, -0.316$) and canopy ($\beta = -0.935$, $CI = -1.433$ to -0.436) had a negative effect on survival for both treatment and control.

DISCUSSION

In our experiment, we manipulated approximately 29% of the area (35% of non-forested portions) of our 2 treatment units and detected an interaction between treatment and season for survival rates of bobwhites. The marginal improvement in summer survival that we documented, given the starting point (0.148 pooled across 4 years and all units), could influence population growth. Indeed, compared to published estimates of survival (Burger et al. 1995, Sisson et al. 2009, Lohr et al. 2011), our treatment level remained quite low. Conversely, management negatively affected survival during winter with a 34% relative reduction in seasonal survival rates from treatment to control sites. In terms of magnitude, the decline was 0.122, a figure greater than the gain realized during summer. However, given the relatively high starting point for winter survival on our sites (0.282 pooled across 4 years and all units), it may be that the proportional impact of this decrease did not offset improvements in summer survival rates in terms of overall population impact; the treatment survival rate of 0.233 was above (Curtis et al. 1988, Burger et al. 1995) or similar (Lohr et al. 2011) to that reported in other studies.

Table 3. List of biological, home range, landscape, and microhabitat metrics with associated beta values and confidence intervals (lower: LCI, upper: UCI) contained in the top model for survival of radiomarked northern bobwhite on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013.

Metric ^a	β value	LCI	UCI
season ^b	1.4416	1.0822	1.8010
year 1	0.1862	-0.1265	0.4990
year 2	0.1249	-0.1943	0.4440
year 3	0.2173	-0.0337	0.4683
year 1 \times season	-0.9342	-1.3902	-0.4782
year 2 \times season	-1.1710	-1.6032	-0.7388
year 3 \times season	-0.9264	-1.3831	-0.4697
litter depth	-0.3870	-0.5809	-0.1930
open core area	-0.0393	-0.0823	0.0037
HR size	0.0010	-0.0001	0.0021
treatment ^c	0.2564	0.0569	0.4558
treatment \times season	-0.5984	-0.8984	-0.2985

^a Home range size covariate is represented as HR size.

^b Season was coded as 2 groups (group 1 = winter, group 2 = summer).

^c Treatment was coded as treatment = 1 and control = 0.

Table 4. Pooled winter (1 Oct–31 Mar) and summer (1 Apr–30 Sep) seasonal survival rate (SSR) estimates from Program MARK of radiomarked northern bobwhite by treatment and control on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013. We derived estimates from top model in survival analysis.

Year	Season	Pooled			Treatment			Control		
		<i>n</i>	SSR	SE	<i>n</i>	SSR	SE	<i>n</i>	SSR	SE
2010	Winter	151	0.217	0.038	72	0.172	0.038	79	0.286	0.047
	Summer	127	0.168	0.039	90	0.201	0.043	37	0.126	0.038
2011	Winter	229	0.128	0.022	151	0.094	0.021	78	0.186	0.035
	Summer	108	0.150	0.039	66	0.181	0.044	42	0.110	0.036
2012	Winter	102	0.230	0.049	53	0.184	0.048	49	0.300	0.057
	Summer	274	0.177	0.027	151	0.211	0.033	123	0.134	0.027
2013	Winter	214	0.484	0.042	152	0.434	0.044	62	0.553	0.048
	Summer	274	0.117	0.022	135	0.145	0.029	139	0.083	0.021
Pooled 4 years	Winter	696	0.282	0.022	428	0.233	0.025	268	0.355	0.035
	Summer	783	0.148	0.015	442	0.179	0.022	341	0.109	0.019

Based on our post-hoc models, litter depth and canopy cover at 1.25–1.50 m, both of which had a negative effect on summer survival, were the most influential variables explaining this finding. Our management activities focused on reducing litter, decreasing cover of densely planted, native grasses, and reducing sericea lespedeza cover, which dominated the 1.25–1.50-m vegetation strata. Litter depth also was supported in our top model and had a negative relationship with survival further reinforcing this association. The importance of bare ground for foraging, brooding, and roosting has been both qualitatively and quantitatively described (Stoddard 1931, Klimstra and Ziccardi 1963, Ellis et al. 1969, Brown and Samuel 1978).

Our post-hoc models for winter indicated that survival increased as the amount of shrub increased within bobwhite home ranges. Increasing availability of woody cover has been suggested as a means for increasing winter survival (Yoho and Dimmick 1972, Roseberry and Klimstra 1984, Flock 2006) and was explicitly linked to improved winter survival in studies in Kansas (Williams et al. 2000) and Ohio (Janke 2011). Therefore, this result was not surprising in our study. Reduced winter survival on treatment units may have been related to burning, which may have reduced the quality of treatment shrub cover, especially where it occurred in smaller, isolated patches embedded within the open matrix. Because most of the burning occurred outside of shrub or forest, it is unlikely that winter cover within these 2

vegetation types was materially affected by the burning. In open and NWSG areas, on the other hand, cover was more limited and its reduction through burning could be assumed to have been detrimental to bobwhite survival. Although the beta estimate (negative) was not different from 0, core area of open vegetation was included in 7 of the 10 most supported models in our analysis indicating larger patches of open vegetation may have depressed survival. Regardless, control units were not affected by burning and likely had more woody cover than treatment units. Disking was applied in such a manner that it did not affect existing woody cover.

Given the progression of habitat manipulations applied, we hypothesized that seasonal survival rates would increase from year 1 (0.193) to year 4 (0.301). The top model from our survival analysis included a significant interaction among seasons and years, which was mainly a result of the variation in winter survival over the 4 years of our experiment. In contrast, summer survival rates were relatively constant during this same period. Although we included a year × season interaction in our models, this interaction was not supported in the context of treatment indicating that annual variation in seasonal survival estimates were independent of the habitat manipulations that we imposed. Rather, annual and seasonal variation in survival was more likely a result of changes in weather patterns and predator abundance (Palmer and Wellendorf 2007). Similarly, Holt et al. (2009) reported

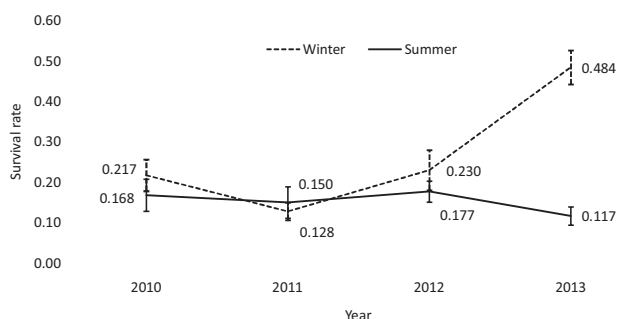


Figure 2. Seasonal survival rates and confidence intervals of radiomarked northern bobwhite as a function of year on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013.

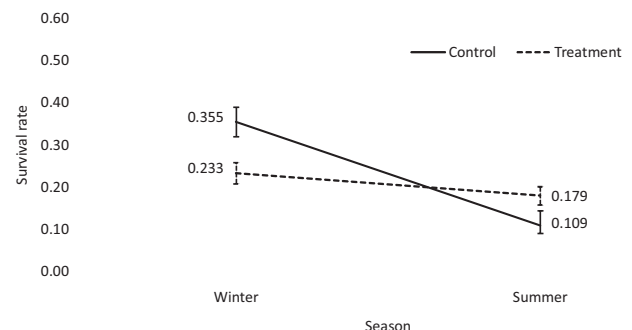


Figure 3. Treatment and control survival rates and confidence intervals of radiomarked northern bobwhite as a function of season on Peabody Wildlife Management Area, Ohio and Muhlenberg Counties, Kentucky, USA, 1 October 2009–30 September 2013.

large annual variation in winter survival rates in Mississippi, 0.060 and 0.465, during the 2 years of their study.

That estimates of survival pooled across seasons were greater during winter (0.282) than summer (0.148) is in contrast to most reported studies on bobwhite. In northern Missouri, Burger et al. (1995) estimated winter survival at 0.159 and summer survival at 0.332, whereas Lohr et al. (2011) reported winter survival rates of 0.23 and summer survival rates of 0.28 for their New Jersey study site. Sisson et al. (2009) reported summer survival estimates averaged 0.352 during a 13-year study in southern Georgia and eastern Alabama, and Curtis et al. (1988) reported winter survival rates of 0.185 in North Carolina. However, in concurrence with our estimates, Williams et al. (2012) reported greater winter survival (0.308) than summer survival (0.267) in New Jersey but did not offer any explanation for the greater winter survival.

Our relatively high winter survival rates were likely a result of the extent and quality of winter cover available on our study site. Forest vegetation on PWMA was established during reclamation and was uncharacteristic of typical forested areas within the Mid-South. Forest vegetation (22% of study area) rarely had canopy closure and as a result, was more similar to open-canopy woodlands. Furthermore, similar structure was available in shrub patches given the lack, in most cases, of canopy closure within this type. Thus, understories on a substantial portion of our study area were comprised primarily of blackberry and honeysuckle, which provided good escape cover (Yoho and Dimmick 1972, Roseberry and Klimstra 1984, Tonkovich and Stauffer 1993).

The extremely low summer survival rates observed in our study may have been because of the dominance of sericea lespedeza on our study site. Sericea lespedeza seeds were commonly found in crops of bobwhite on our study area but are virtually indigestible and provide no nutritional benefit (Davison 1958). In addition, sericea lespedeza litter accumulation has been associated with reduced forb establishment and species richness (Foster and Gross 1998) and may actively interfere with germination of other, potentially more nutritious species through allelopathic compounds generated in leaf and stem tissue (Adams et al. 1973, Wade 1989). Bugg and Dutcher (1989) reported invertebrate use of sericea lespedeza was the lowest of all plant species they studied. Thus, negative impacts of extensive stands of sericea lespedeza on nutrition combined with limited interspersions of cover within many of these open patches, may have contributed to poor survival during summer.

Although the β estimate overlapped 0, our top model also included an additive effect for the sericea-dominated core area of open vegetation (negative) and for home range size (positive), which both indicate that large blocks of open vegetation may have been problematic and led to larger areas required to meet food and cover requirements. Furthermore, the positive impact of shrub cover on survival indicates that these large open areas could be improved by greater interspersions of woody cover.

Although beta confidence intervals for all other habitat covariates contained 0 and were not included in models with a $\Delta AIC_c < 11$, we had anticipated that some of these habitat features would affect survival. For instance, we suspected that an increase in ragweed would positively affect survival. Ragweed, a valued annual plant for bobwhite providing desirable food and structure for overhead cover, was promoted by disking, an intended outcome of the practice. However, disk blocks in our study were relatively small (on average, less than 0.5 ha) and correspondence to ragweed cover was not as clear as we had anticipated initially, thus weakening the relationship between the cover of this species and disk blocks. Additionally, we hypothesized that metrics such as contagion index, forest and shrub edge densities, and distance to edge and woody cover would have an impact on survival. All of these metrics are related to the interspersions of vegetation types, which have been shown to influence bobwhite survival (Williams et al. 2000, Holt et al. 2009, Janke and Gates 2013). Because our manipulations did not directly affect these aspects of habitat, and they were quite similar between treatment and control units, they likely would only have been influential in the context of interactions with microhabitat variables, something that we did not observe in any of our models. A lack of positive impact associated with edge density metrics may have also been a function of the marginal quality of the open and NWSG patches that were associated with these edges.

A shorter return interval of disking, or additional manipulations, may have been needed to sufficiently hinder the growth of sericea lespedeza, which proved to be quite resilient to disturbance. Altered successional trajectories have been documented with other non-native species common in early-successional and/or grasslands habitats of the southeastern United States. Greenfield et al. (2002) reported that fall disking improved quality of tall fescue fields, but improvements were minimal and short-lived (i.e., confined to one growing season). Greenfield et al. (2003) also noted similar trends in tall fescue fields in Mississippi where the relative effectiveness of disking and burning diminished greatly following the first growing season. Likewise, sericea lespedeza regrew quickly after initial disking or prescribed burning on our study area. For instance, cover of sericea lespedeza on disk blocks after 3 years ($\bar{x} = 70.7$) was similar to untreated areas ($\bar{x} = 75.8$). Thus, disking needs to occur within 3 years to maintain favorable structure and composition of areas dominated by sericea lespedeza.

Assumptions of the known-fate model include independence among samples, which may have been violated in our study. We chose to include > 1 individual from a covey in the survival analysis, and survival among those individuals may not have been independent resulting in underestimates of variance. However, the number of additional radiotagged birds was relatively equitable among coveys and we documented some interchange of individuals between coveys. Unfortunately, there is no goodness-of-fit test for known-fate models because the saturated model, in the case

of known fates, fits the data perfectly. Regardless, our best models were much improved over the null models ($\Delta AIC_c = 61.68$), which implies that the data had explanatory power. Furthermore, when we ambiguously increased the variance inflation factor (\hat{c}) to 3, models with the treatment-season interaction were still well supported. Thus, our findings appear to be robust to such potential model violations. That our overall survival rates were low may reflect a negative bias in our estimates, something Sandercock et al. (2008) considered common to most published survival estimates for northern bobwhite given the seasonal survival rates required for stable populations (summer survival rates >0.79 , winter survival rates >0.52 , or an annual rate of 0.41).

Management of reclaimed surface mines may substantially contribute to bobwhite conservation because these sites are typically dominated by early successional vegetation conducive to supporting bobwhite populations. However, plant composition may not allow optimum cover and/or nutrition. Seasonal food availability may affect survival on reclaimed mines, which are dominated by perennial plant species (Jones et al. 1994). We found evidence that our treatment had an effect on improving summer survival. Our management activities reduced winter survival, which may have been attributable to impacts on the quality of shrub cover due to broadcast burning. Additionally, our estimates of summer survival were exceptionally low compared to past research (Parent et al. 2012), possibly as a result of nutritional deficiency and/or poor cover during this time period. Regardless of the mechanism, extensive stands of perennial herbaceous vegetation dominated by sericea lespedeza, led to exceptionally low summer survival.

MANAGEMENT IMPLICATIONS

Managers wishing to favor bobwhite on new reclamation sites should plant native shrubs, forbs, grasses, and woody cover well interspersed with herbaceous vegetation instead of invasive, non-native species that are potentially deleterious to bobwhite. Furthermore, we suggest that management of extensive stands of non-native vegetation on existing reclaimed surface mines that are not providing good cover or food resources be reduced by promoting bare soil (i.e., disking) and increasing plant diversity and production of seed-bearing annuals. Our data suggest that burning would be most advantageous for bobwhite if restricted primarily to forested areas where overstory and/or midstory development may restrict diverse understories and appropriate woody cover; burning of thick monocultures of perennial herbaceous vegetation did not improve species diversity or cover for bobwhite. Herbicide applications ought to be conducted in a manner that minimizes loss of desirable woody cover such as brambles. Implementation of disking at a 2–3-year interval in areas dominated by sericea lespedeza or other undesirable non-native species will enhance structure and plant composition. Establishment and interspersed of woody cover through shrub plantings, especially in association with larger blocks of open herbaceous vegetation, may help improve survival on these open landscapes.

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