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RESEARCH ARTICLE

Northern bobwhites select for native grasses on working grazing land

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Abstract

Northern bobwhite (*Colinus virginianus*; bobwhite) populations have experienced an 85% decline across most of its range since the 1960s. The most drastic decreases have been in the southeastern United States where biologists attribute the decline to widespread habitat loss, including conversion of native grasslands to tall fescue (*Lolium arundinaceum*) and other exotic cool-season grass (CSG) pasture and hayfields. Including agricultural lands in conservation programs could improve habitat conditions on a regional scale. One working-lands conservation strategy involves the use of native warm-season grasses (NWSGs) rather than cool-season exotic grasses as economically viable cattle forage. To evaluate this management practice for creating bobwhite habitat, we conducted a field study on a bobwhite population in eastern Kentucky, USA, where grazed NWSG and burned NWSG fields were adjacent to exotic grazed and exotic hayed CSG fields. Between April 2019 and October 2022, we used radio telemetry to track bobwhites to evaluate resource selection at second- and third-order scales. Bobwhites used traditionally managed CSGs less than would be expected by chance at the second-order scale in both breeding and non-breeding seasons. Bobwhite use of grazed NWSG and burned NWSG was greater than would be expected by chance at the second-order scale in both breeding and non-breeding seasons.

Similarly, at the third-order scale, bobwhites used CSGs less than would be expected by chance, whereas NWSGs and woody stems were used more than by chance alone. Our study suggests that bobwhites select NWSGs at multiple spatial scales despite broad-scale availability of managed exotic CSGs. Under a working-lands framework, the integration of NWSGs into working lands could create bobwhite habitat in the southeastern United States, especially if woody stems are present.

KEYWORDS

Colinus virginianus, fescue belt, grassland bird, native warm-season grass, resource selection, working lands conservation

The northern bobwhite (*Colinus virginianus*; hereafter bobwhite) and other North American grassland- and shrubland-associated bird species have experienced population declines across much of their range (Brennan 1991, Peterjohn and Sauer 1999, Sauer et al. 2017, Rosenberg et al. 2019). These population trends have been attributed to changes in land use leading to widespread loss of habitat (Roseberry et al. 1979, Brennan et al. 1998, Burger 2002). Bobwhite population strongholds exist in the Great Plains where native grasslands and rangelands are extant and on intensively managed properties in the southeastern United States (Lewis et al. 2025). Opportunities to create habitat for bobwhite exist on the remaining private lands, where production agriculture or forestry make up a substantial portion of the landscape. Testing and refining strategies on working lands, particularly in grazing systems, would provide a framework for landscape-scale conservation for these guilds of birds.

A working-lands approach, or land sharing rather than land sparing, has been suggested as a wildlife conservation paradigm across the globe (Phalan et al. 2011). In working-lands conservation, land is not removed from agricultural production as in other conservation programs, such as is typically the case with the Conservation Reserve Program (Monroe et al. 2017; Keyser et al. 2019, 2020). For broad-scale population restoration to occur, bobwhite conservation practices must be integrated with production systems that are profitable for the producer because producing food, fiber, fuel, and forage will drive land use decisions over bobwhite populations in most cases (Peterjohn 2003). In the southeastern United States, exotic tall fescue (*Lolium arundinaceum*) is the dominant cattle forage grown on about 14 million ha in an area known as the fescue belt (Kallenbach et al. 2012; Figure 1). A working-lands conservation approach may be effective across the fescue belt such that cattle producers can still remain productive while providing greater resources for bobwhites (Keyser et al. 2019, 2022). A possible solution is to incorporate native warm-season grasses (NWSGs) into farmlands currently dominated by exotic cool-season grasses (CSGs) like tall fescue (Giuliano and Daves 2002, Harper et al. 2015, West et al. 2016). These NWSGs have potential benefits for the livestock industry, including drought resistance, improved cattle performance (Burns and Fisher 2013, Keyser et al. 2016, Backus et al. 2017), and positive impacts on profitability (Lowe et al. 2015, 2016, Monroe et al. 2017, Brazil et al. 2020). Further, prescribed burning increases nutritive value and palatability, and thereby increases performance of stocker cattle and steers compared to unburned NWSGs (Anderson et al. 1970, Woolfolk et al. 1973, Svejcar 1989). Prescribed burning is also well-established as a beneficial management practice for bobwhites and other wildlife (Brennan et al. 1998). Yet, how grazing, fire, and NWSGs combine to affect bobwhite ecology, such as resource use, is not well understood.

Resource selection studies allow researchers to link individual animals to their environment at multiple spatial scales (Johnson 1980, Fieberg et al. 2021). Biologists can use resource selection analyses to infer the ecological needs and limitations of a species and thereby support conservation (Boyce and McDonald 1999, Cooper and Millspaugh 1999, Fieberg et al. 2021). Many of these studies are used to evaluate the impact of habitat change (Manly et al. 2002). For example, characteristics of successful nesting locations for bobwhites have been associated

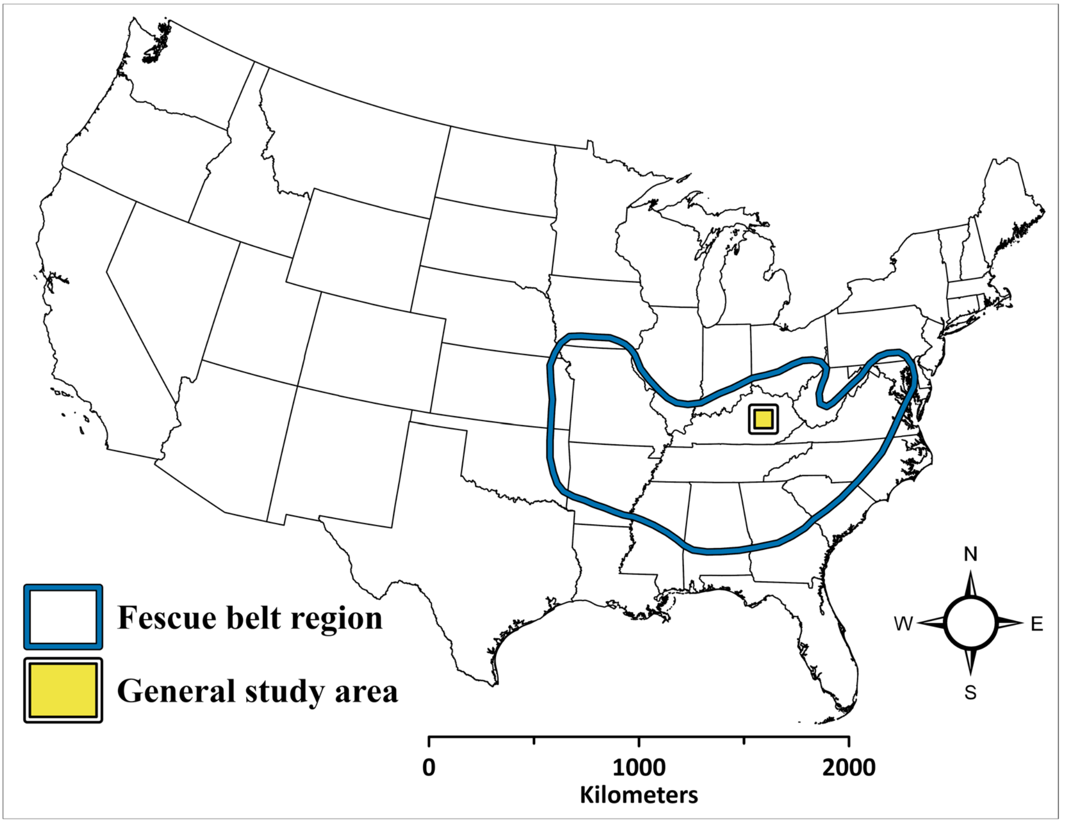

FIGURE 1 The fescue belt region of the United States (blue polygon) and the general study area (yellow square) in eastern Kentucky, USA, 2019–2022. The fescue belt map was adapted from Belesky and West (2009), and Keyser (2021). Other imagery was obtained from Esri (2022).

with greater vertical cover than what was available at random locations or failed nests (Lusk et al. 2006, Collins et al. 2009). Hill et al. (2023) illustrated differing diurnal and nocturnal resource selection in bobwhite chicks and that land management could be improved for heavily hunted areas by diversifying cover types and providing them in close proximity to each other. A recent study in Missouri, USA, suggested that brooding bobwhites selected grazed and burned NWSGs, and that brood survival was positively influenced when compared to mixed burned grasslands and idle NWSGs (Thompson et al. 2022). Other studies that focus specifically on bobwhite resource selection in relation to burned or grazed NWSGs in the fescue belt are lacking.

We evaluated whether NWSG managed with either prescribed fire or grazing within a landscape dominated by exotic CSG forage production were related to resource selection of bobwhites. Specifically, our objectives were to evaluate where bobwhites chose to place their home ranges (second-order, home range selection; Johnson 1980) and what vegetation structural and composition conditions bobwhites were using within those home ranges (third-order, local selection; Johnson 1980). Our study took place in a landscape of grazed NWSG and ungrazed-burned NWSG (hereafter burned NWSG)] and grazed and hayed CSGs during breeding season and non-breeding season. We predicted that, at the second-order scale, bobwhite home ranges would contain more NWSG (grazed or burned) cover than expected by chance and less CSG cover than expected by chance (Table S1). We also predicted that bobwhites would disproportionately use NWSGs at the third-order scale, and that proximity to woody escape cover and structural characteristics such as increased levels of visual obstruction, canopy height, and bare ground would also be associated with selection (either linear or non-linear).

STUDY AREA

We conducted our study on the Blue Grass Army Depot (BGAD) and neighboring privately owned farmland in Madison County, Kentucky, USA, between April 2019 and October 2022. The BGAD is a military facility located in the Interior Low Plateaus physiographic province on the southeast edge of the Bluegrass Region (Jones 2005) that encompasses approximately 6,070 ha (Figure 1). The southern and eastern portions of the BGAD included a mix of cattle pastures (CSG and NWSG) and fields managed in early successional cover types through periodic disturbances including grazing and prescribed fire. We designated this section of the BGAD as part of our study area and delineated 4 coarsely defined predominant cover types based on existing management: hayed CSG fields (722 ha), grazed CSG fields (622 ha), grazed NWSG fields (169 ha), and burned NWSG fields (124 ha). Grass composition of NWSG fields consisted of a mix of indiangrass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), and switchgrass (*Panicum virgatum*). These NWSGs were established in pre-existing tall fescue-dominated pastures using a no-till drill between 2012 and 2013 and were grazed as part of a previous study (Lituma et al. 2022). Grasses in CSG fields primarily consisted of tall fescue and exotic orchardgrass (*Dactylis glomerata*). Both CSG and NWSG areas also included other native and exotic species common in the fescue belt such as broomsedge (*A. virginicus*), exotic dallisgrass (*Paspalum dilatatum*), exotic Johnsongrass (*Sorghum halepense*), bluegrass (*Poa* spp.), foxtails (*Setaria* spp.), purpletop (*Tridens flavus*), and bromes (*Bromus* spp.). Forbs in both CSG and NWSG areas included ironweed (*Vernonia* spp.), goldenrod (*Solidago* spp.), and exotic sericea lespedeza (*Lespedeza cuneata*). A fifth cover type, CSG traditional, was immediately adjacent to the BGAD and included privately owned farms that were managed using a mixture of grazing and haying as is common in the fescue belt (Ball et al. 2015).

The burned NWSG areas were burned (spring burns; mid-late March) on a 3-year return interval and were otherwise undisturbed. One large area of NWSG (82 ha) was split roughly into thirds and each third was burned on a 3-year return interval. Hayed CSG fields were harvested annually (typically only once) between mid-June and early July. Cattle were stocked on grazed NWSG in mid-April to mid-May each year and removed in mid-August to mid-September, a suggested management practice to maintain stand health (Keyser and Smith 2021). Cattle were stocked continuously in grazed CSG areas on most of the BGAD. Stocking density in both grazed NWSG areas and grazed CSG areas was about 140–200 kg/ha, typically using weaned calves (250–300 kg each) or yearling heifers (350–450 kg each). Typical production scenarios for this region, although highly variable, maintained stocking densities of about 200–250 kg/ha (Ball et al. 2015, Boyer et al. 2022).

METHODS

We trapped bobwhites year-round during daylight hours ≥5 days per week (April 2019–September 2022) using anchored, wire funnel traps. We placed traps (20–30 per day) in unique locations in each cover type (1–2 week intervals) across our study area. We trapped locations for 1–2 weeks before shifting traps to another cover type. In this way, we sought to obtain a representative sample of all bobwhites across our study area. We baited traps with a mix of cracked corn, milo, millet, sunflower, and other grains and refreshed bait daily as needed (Stoddard 1931, Burger et al. 1995, West et al. 2012). We staked traps on one side and located them under overhanging cover or covered them with small branches to reduce predation and capture stress of the birds (Palmer and Wellendorf 2007). We fitted captured bobwhites with uniquely numbered aluminum leg bands (size #4), sexed and aged (juvenile or adult) birds, and estimated body mass to the nearest gram using a spring scale. We aged birds by the presence of buff-tipped wing coverts (Rosene 1969), and we fit all birds ≥129 g with a necklace-style very high frequency (VHF) transmitter with a 12-hour mortality sensor (American Wildlife Enterprises, Monticello, FL, USA). Transmitters were about 6 g and represented ≤5% of a ≥129-g bird's mass. We processed and immediately released all birds within 20 m of the trap.

We located all radio-marked birds ≥5 times per week during daylight hours (~24-hour intervals) using a handheld, 3-element folding Yagi antenna and a model R410 receiver (Advanced Telemetry Systems, Isanti, MN, USA) and homing to within 15–30 m of the bird's location (White and Garrott 1990). We varied location times throughout daylight periods during the week to capture a full range of diurnal behavior (Lohr et al. 2011). We recorded the coordinates of the observer and calculated the location of the bird using the estimated distance to the bird (m) and azimuth (degrees) using a handheld global positioning system (GPS) unit, laser rangefinder, and compass, respectively. All technicians were trained to locate hidden transmitters to within a 5-m radius. If a bird left the study area, we obtained permission from additional private landowners to track birds on their property. During the non-breeding season, we considered groups of ≥2 birds a covey if they were located within 10 m of each other for ≥7 days (Janke and Gates 2013, Mosloff et al. 2021).

We used the supervised classification method (object-based) and the Random Trees classifier in the image classification wizard in ArcGIS Pro (Esri 2022) to classify cover type imagery of the study area (Figure 2). We used high-resolution RGB aerial images from 2021 (KYfromAbove.gov; 2-m resolution) as the base maps for pixel classification. We restricted the classes (5-m pixel; an area approximating our telemetry error) to 8 land-cover types. Forest (woody stems >3.5 m tall) and shrub (woody stems <3.5 m tall) cover type definitions were associated with metrics used by the National Bobwhite and Grasslands Initiative (Morgan et al. 2016). The other 6 types were CSG-forb (cool-season grass and forb mix; primarily grazed by cattle), CSG hay, CSG traditional (tall fescue-dominated pastures typical of fescue belt conditions; located on private lands immediately adjacent to BGAD), NWSG grazed (stands grazed by cattle each summer), NWSG burned (stands burned [March] triennially), and other (roads,

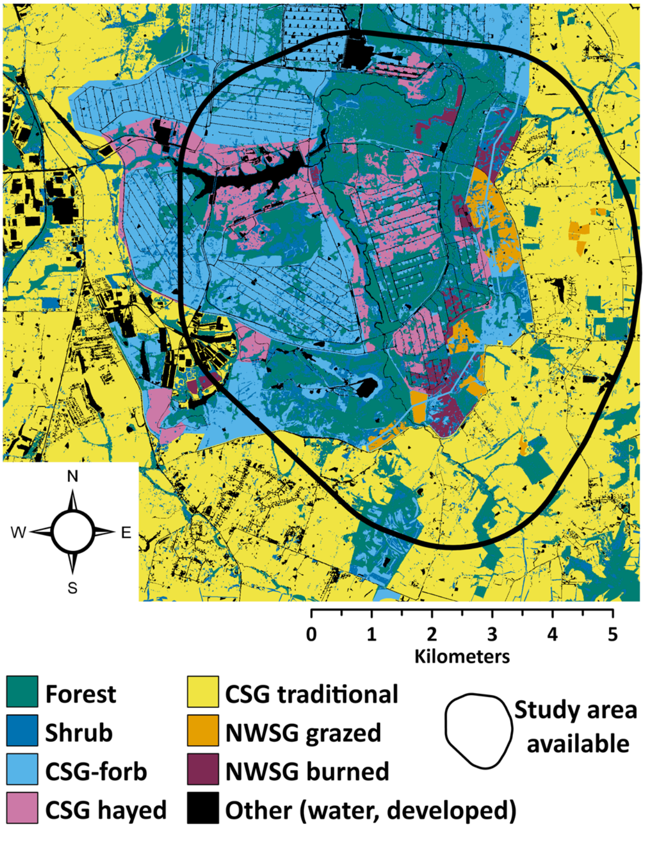

FIGURE 2 Cover types (5-m pixels) and available area for bobwhite second-order resource selection analyses (home range selection) in Madison County, Kentucky, USA, 2019–2022. Available area was determined by applying a minimum convex polygon to all trapped areas and adding a 2-km buffer. NWSG = native warm-season grass, CSG = cool-season grass. The other cover type represents water, roads, and buildings.

buildings, paved areas, and bodies of water). The majority of grass cover on BGAD was based on areas of pre-existing management and could be manually classified. We inspected representative areas of each cover type across the study area to confirm classification of training images. We completed multiple iterations of ground-truthing and manual corrections to classified imagery (Brooke et al. 2015). We assessed the accuracy using a confusion matrix with 300 points per cover type and made corrections until the predictive accuracy exceeded 85% for each cover type (Congalton 1991, Lamont et al. 2019, Ritzell et al. 2022).

We used locations of radio-tagged birds to collect data on resource selection in breeding (April–September) and non-breeding (October–March) seasons, starting in April 2019. We separately modeled breeding and non-breeding season data because differing life-history stage requirements may lead to differences in patterns of resource selection (Rosene 1969, Brooke et al. 2015). We also modeled the second- and third-order selection data separately within each season because of unequal sample sizes (Brooke et al. 2015).

Second-order selection

To assess second-order selection, we first generated 95% kernel density home ranges for each bird with ≥20 locations using the adehabitat and sp packages in the R programming language (Pebesma and Bivand 2005, Calenge 2006, R Core Team 2025). We used the reference smoothing parameter because not all home ranges converged using the least-squares cross-validation method, whereas other home range contours were broken into meaningless fragments (Gitzen et al. 2006). Then we extracted the telemetry points from inside each bird's home range polygon using the clip tool in ArcGIS Pro (Esri 2022). These served as used points for each bird. We then used the locations of all trap sites (both successful and unsuccessful locations) to generate a minimum convex polygon and added a 2-km buffer around that polygon to define the available landscape. Using this method, our inference represented the placement of home ranges compared to the available landscape. Although previous studies have chosen a variety of definitions for availability (Lohr et al. 2011, Singh et al. 2011, Janke and Gates 2013, McGrath et al. 2017), we chose a 2-km buffer distance because it is the approximate mean dispersal distance of bobwhites in our study area and the region (Cook et al. 2009) and reasoned that any bobwhite in our study could have selected resources within this polygon. We used the create random points tool in ArcGIS Pro (Esri 2022) to create a random point at a 1:1 ratio to the used points using the 2-km buffer as a restriction. These points served as the available points for each bird. We used the extract values to points tool in ArcGIS Pro to query the raster cell association for cover type of each point (Esri 2022).

Third-order selection

To assess third-order selection, we randomly chose one individual bobwhite telemetry location per week from each bird and paired it with a random location using a case-control approach to minimize temporal bias (Peters et al. 2015). We generated random points by applying a random azimuth (0-359°) and distance from the telemetered point. We chose random distances from a distribution of mean daily movements (linear distance between consecutive [~24 hr] locations) for all bobwhites on our study area (20–175 m; Terhune et al. 2006, Lohr et al. 2011, Peters et al. 2015). We generated a new random point if the initial point landed in a body of water or a building.

We used the point-intercept method (Floyd and Anderson 1987, Drezner and Drezner 2021) to measure composition (forbs, NWSG, CSG, bare ground, litter, and woody stems; all in %) and structure (plant height and litter depth; both in cm) at 1-m intervals along 2 12-m perpendicular transects centered on the telemetered and random locations and oriented to cardinal directions. We also included a point where the 2 transects crossed, for a total of 25 points. We measured visual obstruction by measuring the minimally visible height on a 2-m Robel pole (located where the transects intersected; 5-cm strata) at 1 m above the ground from 4 m away in each cardinal direction (Robel et al. 1970, Collins et al. 2009). We also measured the distance to nearest woody cover (m) from the center of the plot using a laser rangefinder. We defined litter as dead vegetation in contact with the ground at a depth of ≥0.5 cm (Rosene 1969, Peters et al. 2015). In addition to saplings and shrubs, we included semi-woody plants like brambles (*Rubus* spp.) and multiflora rose (*Rosa multiflora*) in our definition of woody stems. In the non-breeding season, we combined NWSG and CSG into a common grass category to avoid misclassification of dormant plants. We defined woody cover as a patch of predominantly woody vegetation that was sufficiently large (≥30 m^2) and dense enough to provide a bobwhite potential cover from predators (Peters et al. 2015, Morgan et al. 2016). We did not collect third-order resource selection data in summer 2022 because of logistical constraints. All third-order resource selection vegetation sampling was collected ≤7 days from the time the telemetry point was collected (Brooke et al. 2015, Peters et al. 2015).

We chose to evaluate selection during the non-breeding season at the covey level because individual birds in the same covey were in very close proximity to one another and their selection was unlikely to be independent (Brooke et al. 2015). However, the amount of bias potentially created by individuals in pairs or coveys may have been minimal because of the interchange of birds (Williams et al. 2004, Janke et al. 2013, Peters et al. 2015).

Analyses

Prior to building models, we checked for collinearity by calculating Pearson's correlation coefficients for all possible pairs of covariates using a threshold of $|r| > 0.7$ and a P-value ≤ 0.05 to define collinearity (Dormann et al. 2013). None of the covariates were correlated. We used a generalized linear mixed model (logistic) using the glmer function in the lme4 package (Bates et al. 2015) in R for second-order selection analyses. We used choice as our response variable (binomial; 1 = used, 0 = available) and included a cover type covariate as a factor with 8 levels (CSG-forb, CSG hay, CSG traditional, forest, NWSG graze, NWSG burn, shrub, and other). We chose to use a generalized linear mixed model because we included individual birds as a random effect to account for repeated sampling of individuals. We chose CSG hay as our reference category because it was the most abundant cover type and its structural and compositional properties provided the most appropriate baseline for our predictions (Unger et al. 2015, Fieberg et al. 2021).

We used the mclogit function in the mclogit package (Elff 2022) in R statistical programming language (R Core Team 2025) for third-order selection analyses. The mclogit function uses conditional logistic regression to fit a resource selection function that compares used and available resources to test for disproportionate use and provides the flexibility to incorporate random effects. We used choice as our response variable (binomial; 1 = used, 0 = available) and used 6 covariates for composition (forb, NWSG, CSG, woody stems, bare ground, litter; all in %), 3 covariates for structure (plant height, visual obstruction, litter depth; all in cm), and one covariate for distance to woody cover (m). We chose conditional logistic regression because it is appropriate for matched pair (i.e., case-control) selection data and it may provide more appropriate inference than standard logistic regression (Keating and Cherry 2004, Vittinghoff et al. 2012).

We fit models using single covariates first and then added supported (P-value and 95% CI) and biologically relevant terms in additive and interactive terms (Zhang 2016). We included terms for grass cover first and added and removed terms for relevant compositional and structural characteristics. We also added quadratic terms for all third-order covariates because we predicted that these relationships may not be linear. We also included individual (breeding season) or covey (non-breeding season) as random effects for reasons mentioned above.

Because bobwhites selected home ranges in grazed and burned NWSG more than expected in both seasons, we conducted a separate, *post hoc* analysis of third-order selection data to identify the compositional and structural factors contributing to use of these areas. To accomplish this, we plotted the coordinates of the center of each 25-point transect under a home range polygon layer in ArcGIS Pro. We then isolated bobwhite home ranges that were within grazed NWSG (for breeding season) and burned NWSG (for non-breeding season) cover types. We considered a home range was within a cover type if ≥70% of the locations were inside that cover type (Peters et al. 2015). We then extracted the local selection data inside these home ranges with the clip tool in ArcGIS Pro (Esri 2022). We used this subset of local selection data to model third-order selection by adding and subtracting logical compositional and structural covariates in linear and quadratic terms to measures of local grass cover (% NWSG and %CSG in grazed and burned NWSG during breeding season; % grass in grazed and burned NWSG during non-breeding season).

We used Akaike's Information Criterion (AIC) to rank models based on their ability to explain variation in resource selection. Models with ΔAIC < 7 were considered to have support (Burnham and Anderson 2002, Burnham et al. 2011). We considered covariates with 95% confidence intervals that did not overlap zero (for β estimates) or 1 (for odds ratios) to have a meaningful effect. We reported all covariates in top models that had statistically supported and biologically interpretable effects. We calculated odds ratios by exponentiating β estimates. For continuous covariates, we scaled odds ratios by multiplying β by 10 prior to exponentiation (i.e., $e^{\beta_k \times 10}$) to facilitate interpretation of the change in odds associated with a 10-unit increase in the covariate as a practical interpretation for land managers.

RESULTS

Between April 2019 and September 2022, we completed 18,618 trap-days and captured 211 individual bobwhites. During the breeding season, we collected data on 87 bobwhite home ranges (mean = 55.94 ± 3.61 [SE] ha) for second-order selection (3,954 pairs of observations; mean telemetry points per bird = 41.09 ± 2.46) and 68 bobwhites with third-order selection data (529 pairs of observations). During the non-breeding season, we collected data on 25 covey home ranges (mean = 52.18 ha ± 3.92) for second-order selection (1,972 pairs of observations; mean telemetry points per covey = 79.12 ± 6.72) and 22 coveys with third-order selection data (402 pairs of observations).

Second-order selection

The model containing the land cover covariate was supported more than the null model (ΔAIC > 7), and the odds ratios from this model (Table 1) indicated that bobwhites were 15 times (CI = 11.24 − 20.90) less likely to select CSG traditional over CSG hayed (the reference category) during the breeding season. Compared to CSG hayed, odds ratios indicated NWSG grazed was 8 times (CI = 6.39 – 11.49) more likely to be selected, NWSG burned was 8 times (CI = 5.94 – 11.32) more likely to be selected, and shrub cover was 3 times (CI = 2.28 – 3.42) more likely to be selected. In the non-breeding season, compared to CSG hayed, bobwhites were 8 times (CI = 5.43 – 11.86) less likely to select CSG traditional, 5 times (CI = 3.49 – 8.55) more likely to select NWSG grazed, 10 times (CI = 6.68 – 15.23) more likely to select NWSG burned, and 4 times (CI = 3.35 – 6.11) more likely to select shrub.

Third-order selection

The most parsimonious models for third-order selection included grass cover and woody stem cover (breeding season) and grass cover and plant height (non-breeding season). Models with quadratic and interactive terms marginally explained variation in the data, but estimates for these terms were not statistically supported ($P > 0.05$). Linear terms provided a better fit than quadratic terms for all the competitive models in both breeding and non-breeding seasons (Tables S2–S4). Similarly, random intercepts for individuals and coveys did not improve fit, so we removed them from our model structure. Minimal model selection uncertainty was observed as β coefficients varied little among competing models. In the top model for breeding season, a 10% increase in NWSG cover increased selection by 11% (OR = 1.11, 95% CI = 1.03 – 1.22), whereas a 10% increase in woody stem abundance was associated with increased selection by 53% (OR = 1.53, 95% CI = 1.39 – 1.70; Table 2; Figure 3). Conversely, in the *post hoc* analysis for breeding season, in grazed NWSG areas, a 10% increase in encroaching CSG cover was associated with reduced selection by 26% (OR = 1.26, 95% CI = 1.03 – 1.54; Table 3; Figure 4). In the top model for non-breeding season, relative probability of use decreased 28% with every 10%

TABLE 1 Parameter estimates explaining variation in second-order selection (home range selection) of all adult northern bobwhites (*Colinus virginianus*) in breeding season (April–September) and non-breeding season (October–March), Madison County, Kentucky, 2019–2022. Odds ratios indicate the odds of an animal's choice of a cover type compared to the cool-season grass (CSG) hayed reference cover type, where (+) indicates the odds more likely to choose and (-) indicates the odds less likely to choose.

Season and parameter	β	SE	Lower 95% CI	Upper 95% CI	Odds ratio	Relative probability of use	P
Breeding season							
CSG hayed (intercept)	−0.19	0.09	−0.36	−0.01		0.45	0.04
CSG-forb	0.22	0.10	0.02	0.43	(+) 1.25	0.56	0.03
CSG traditional	−2.73	0.16	−3.04	−2.42	(−) 15.36	0.06	<0.01
NWSG grazed	2.15	0.15	1.86	2.44	(+) 8.57	0.90	<0.01
NWSG burned	2.10	0.16	1.78	2.43	(+) 8.20	0.89	<0.01
Forest	−0.27	0.10	−0.47	−0.08	(−) 1.32	0.43	<0.01
Shrub	1.03	0.10	0.83	1.23	(+) 2.80	0.74	<0.01
Other	−1.22	0.16	−1.53	−0.91	(+) 3.39	0.23	<0.01
Random intercept SD = 0.18							
Non-breeding season							
CSG hayed (intercept)	−0.40	0.14	−0.68	−0.13		0.40	<0.01
CSG-forb	−0.18	0.16	−0.50	0.13	(−) 1.20	0.45	0.26
CSG traditional	−2.08	0.20	−2.47	−1.69	(−) 8.02	0.11	<0.01
NWSG grazed	1.70	0.23	1.25	2.15	(+) 5.46	0.85	<0.01
NWSG burned	2.31	0.21	1.90	2.72	(+) 10.09	0.91	<0.01
Forest	0.44	0.15	0.15	0.73	(+) 1.56	0.61	<0.01
Shrub	1.51	0.15	1.21	1.81	(+) 4.51	0.82	<0.01
Other	−1.25	0.25	−1.73	−0.76	(−) 3.48	0.22	<0.01
Random intercept SD = 0.22							

Abbreviations: CSG = cool-season grass; NWSG = native warm-season grass; other = bodies of water, roads and buildings.

increase in grass cover (OR = 1.28, 95% CI = 1.20 – 1.39) and increased 14% with a 10-cm increase in plant height (OR = 1.14, 95% CI = 1.02 – 1.20; Table 2; Figure 5). In the *post hoc* analysis for non-breeding season, a similar response to grass cover and plant height was predicted in areas of burned NWSG (Table 4; Figure 6).

DISCUSSION

Second-order selection

Bobwhites in eastern Kentucky used grazed NWSG and burned NWSG cover types more than expected in both breeding season and non-breeding season at the home range scale, consistent with our predictions that bobwhites

TABLE 2 Parameter estimates for the most supported models explaining variation in third-order scale selection of all adult northern bobwhites (*Colinus virginianus*) in breeding season (April–September) and non-breeding season (October–March) in Madison County, Kentucky, 2019–2022.

Season and parameter	*β*	SE	Lower 95% CI	Upper 95% CI	*P*
Breeding season					
% NWSG	0.011	0.004	0.003	0.019	0.01
% woody stems	0.043	0.005	0.033	0.053	<0.01
% CSG	−0.007	0.006	−0.016	0.002	0.12
% woody stems	0.035	0.006	0.025	0.044	<0.01
Non-breeding season					
% grass	−0.025	0.004	−0.033	−0.018	<0.01
Plant height (cm)	0.013	0.002	0.009	0.018	<0.01

Abbreviations: CSG = cool-season grass cover; NWSG = native warm-season grass cover.

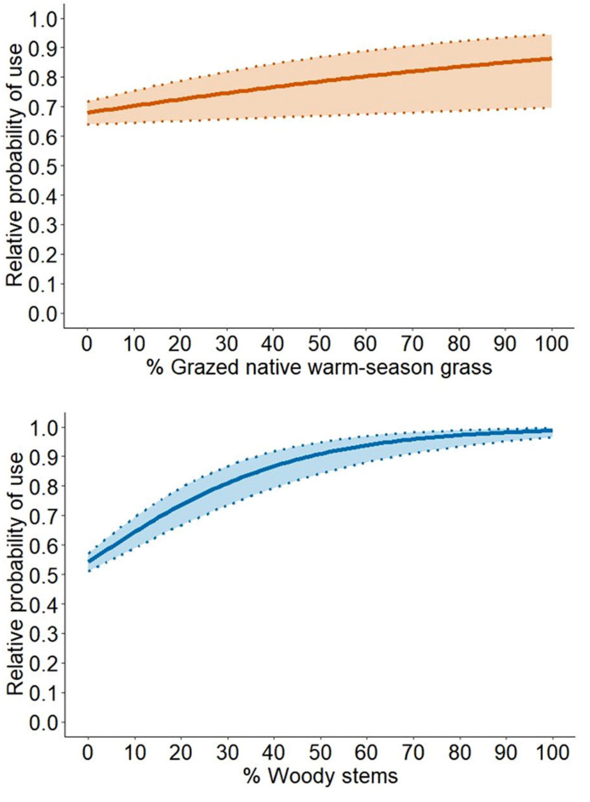

FIGURE 3 Relative probability of use at the third-order selection scale for percent grazed native warm-season grass (top) and woody stems (bottom) by all adult northern bobwhites (*Colinus virginianus*) in breeding season (April–September) in Madison County, Kentucky, USA, 2019–2022. Dotted lines indicate 95% confidence intervals.

TABLE 3 Parameter estimates from a *post hoc* analysis of most supported models explaining variation in third-order scale selection of adult northern bobwhites (*Colinus virginianus*) in grazed native warm-season grass (NWSG) and burned NWSG in breeding season (April–September) in Madison County, Kentucky, 2019–2022.

Field type and parameter	*β*	SE	Lower 95% CI	Upper 95% CI	*P*
Grazed NWSG					
% CSG[a]	−0.023	0.010	−0.043	−0.003	0.023
% woody stems	0.029	0.007	0.016	0.043	<0.001
% NWSG	0.013	0.006	0.001	0.026	0.037
% woody stems	0.041	0.008	0.025	0.058	<0.001
Burned NWSG					
% NWSG	−0.004	0.006	−0.015	0.007	0.452
Plant height (cm)	0.015	0.003	0.009	0.022	<0.001
% CSG	−0.002	0.008	−0.017	0.014	0.824
Plant height (cm)	0.015	0.003	0.009	0.022	<0.001
% NWSG	−0.020	0.016	−0.051	0.010	0.190
Plant height (cm)	0.013	0.004	0.006	0.020	<0.001
% NWSG × plant height	<0.001	<0.001	<0.001	0.001	0.260
% NWSG	0.007	0.006	−0.005	0.020	0.245
% woody stems	0.037	0.008	0.021	0.054	<0.001

[a]Cool-season grass.

would select NWSG cover types compared with fescue-based alternatives. Bobwhites also used traditional CSG less than expected in breeding and non-breeding season, which also supported our predictions.

The underlying cover type use relationships appeared to vary by season. Specifically, use of CSG traditional during breeding season was nearly two times less likely than use in non-breeding season. Grazing fescue-dominated pastures before and during the breeding season may have reduced potential nesting cover or otherwise made this cover type less attractive for bobwhite use. The lack of cover and food in CSG traditional may make the abundance of this cover type a limiting factor and influence bobwhites to avoid it even more so in breeding season (Barnes et al. 1995, Peters et al. 2015, McGarigal et al. 2016). Use of burned NWSG was also greater in the non-breeding season compared with use during the breeding season. This suggests that, at the home range scale, the structure (areas of tall grasses with forb cover) provided by triennially burned NWSGs provided valuable cover that bobwhites were attracted to during the non-breeding season (Kroeger et al. 2020).

Bobwhites also selected grazed NWSG more during the breeding season than the non-breeding season, although the magnitude of the difference was not large. This may be due to the structure this cover type provided during the breeding season, particularly the tall canopy height (mean 84 cm for used) and trails created by grazing cattle that can facilitate movement by bobwhites (Lusk et al. 2006, Palmer et al. 2021). Similarly, Brooke et al. (2015) suggested that bobwhites selected disked firebreaks for mobility and access to food. However, in early fall, after cattle were removed from NWSG pastures, grass stubble often remained at heights of 20–30 cm, below the

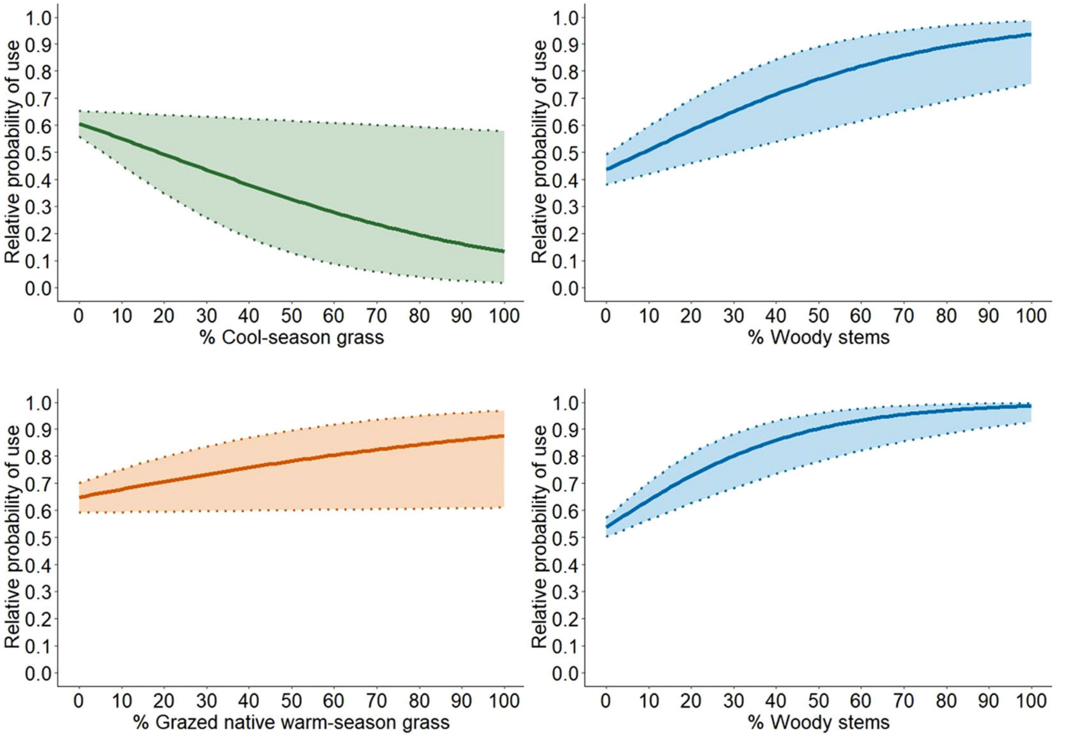

FIGURE 4 Relative probability of use at the third-order selection scale for percent cool-season grass and woody stems (top), and percent grazed native warm-season grass and woody stems (bottom) by adult northern bobwhites (*Colinus virginianus*) with home ranges in grazed native warm-season grass in breeding season (April–September) in Madison County, Kentucky, USA, 2019–2022. Dotted lines indicate 95% confidence intervals.

suggested residual height of >30 cm (Keyser and Smith 2021, Keyser et al. 2022). This stubble is considerably lower than the 1.25–1.50-m visual obstruction means that non-breeding bobwhites selected in another Kentucky study (Brooke et al. 2015). Despite the relatively low canopy height during parts of the study period, use of grazed NWSG was high for breeding and non-breeding seasons (OR = 8.57 and 5.46, respectively).

Shrub cover use was important in both non-breeding and breeding seasons. Forest was used less than expected in the breeding season but marginally more than expected (OR = 1.56) in the non-breeding season. Bobwhites are not usually associated with forest cover types (Lohr et al. 2011, Howell et al. 2021, Nolan et al. 2024). Our study site was dissected by patches of forest cover that varied from large contiguous patches >500 m wide to wooded ravines 30–100 m wide. In all grass cover types, many of these forest patches were, in turn, associated with shrub cover types around the margins and in the understory (Figure 2). Therefore, the selection of forest cover types may be attributed to the implicit availability of forest near typical cover types associated with bobwhites, a phenomenon of hierarchical spatial levels of selection (Johnson 1980, McGarigal et al. 2016). Nevertheless, shrub availability at the home range scale may be an important component to bobwhite populations, as it can affect survival rates. In southern Missouri, Mosloff et al. (2021) also found non-breeding bobwhite selected areas of shrub thickets but reported that shrubs were associated with trees and that trees created an ecological trap by attracting predators, and therefore decreased survival. Although trees and shrubs were frequently associated with each other in our study, concurrent research suggested that medium to high levels of shrub interspersion-juxtaposition indices were associated with greater bobwhite survival rates in grazed NWSG cover types (Mitchell 2025). Accordingly, Mosloff et al. (2021) suggested that maintaining adequate shrub interspersion and felling trees might prevent the ecological trap in their study.

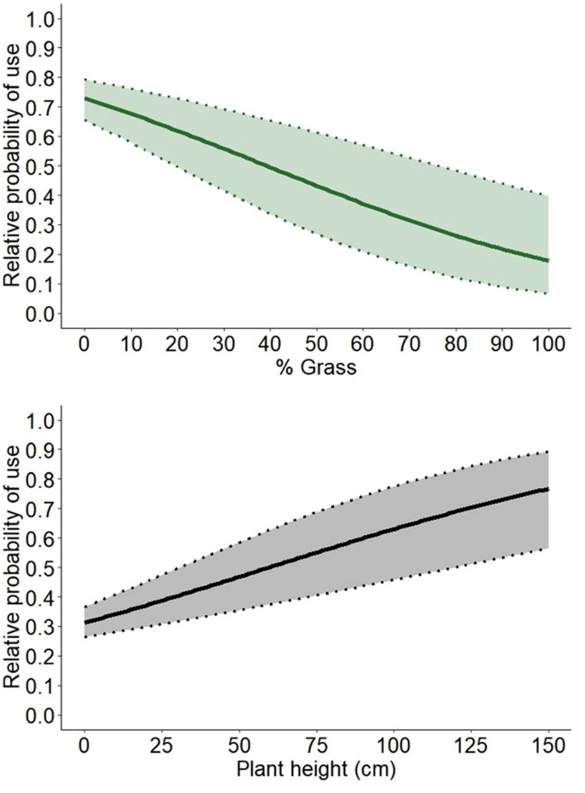

FIGURE 5 Relative probability of use at the third-order selection scale for percent grass (top) and vegetation height (bottom) by all adult northern bobwhites (*Colinus virginianus*) in non-breeding season (October–March) in Madison County, Kentucky, USA, 2019–2022. Dotted lines indicate 95% confidence intervals.

Third-order selection

Use of the grassland cover types during the breeding season was associated with availability of NWSGs and woody stems, an outcome that was consistent for models that included all birds and those restricted to only birds with home ranges within grazed NWSG. However, some bobwhites in CSG-dominated areas did not have access to NWSGs and may have instead based their selection on the amount of woody stems present. This is not unexpected because bobwhites are associated with woody cover at all times of the year in a variety of agricultural settings (Janke and Gates 2013, Gates et al. 2017).

The top model for third-order selection restricted to NWSG grazed areas suggested that during breeding season bobwhites were avoiding areas where CSGs had encroached. This may have been due to the dense structure that limits mobility of birds and the lack of available nutrition typical in CSGs like tall fescue (Washburn et al. 2000, Barnes et al. 1995, 2013). The mean cover of encroaching CSGs in the NWSG grazed areas was about 13%. Despite this relatively small amount of CSG, bobwhites used these areas less than expected (Figure 6).

During the non-breeding season, the availability of taller plants and reduced grass cover characterized selection regardless of the composition of the home range (NWSG-dominated or other). This is similar to trends in selection by bobwhites in Missouri, where birds selected areas of higher visual obstruction and lower percentage of grass cover in the non-breeding season (Thompson et al. 2022). Brooke et al. (2015) also reported that visual obstruction (0.25–0.50 and 1.75–2.00 m) was important for non-breeding season resource selection for bobwhites. In Tennessee and Kentucky, northern bobwhite detection was positively attributed to vegetation height, although

TABLE 4 Parameter estimates from a *post hoc* analysis of most supported models explaining variation in third-order scale selection of adult northern bobwhites (*Colinus virginianus*) in grazed native warm-season grass (NWSG) and burned NWSG in non-breeding season (October–March) in Madison County, Kentucky, 2019–2022.

Field type and parameter	β	SE	Lower 95% CI	Upper 95% CI	P
Grazed NWSG					
% grass	−0.003	0.015	−0.033	0.027	0.839
% woody stems^2	0.002	0.001	<0.001	0.004	0.012
% grass	0.001	0.016	−0.030	0.032	0.951
% woody stems	0.089	0.027	0.035	0.142	0.001
% grass	−0.003	0.015	−0.033	0.027	0.843
% woody stems^2	0.002	0.001	<0.001	0.005	0.068
% grass × % woody stems^2	<0.001	<0.001	<0.001	<0.001	0.918
Burned NWSG					
% grass	−0.008	0.010	−0.027	0.011	0.392
Plant height (cm)	0.020	0.005	0.011	0.029	<0.001
% grass × plant height	<−0.001	<0.001	<−0.001	<0.001	0.065
% grass	−0.024	0.006	−0.035	−0.012	<0.001
Plant height	0.014	0.003	0.008	0.020	<0.001

this was during the breeding season (West et al. 2016). In our study, bobwhites in the non-breeding season had available plant heights of 30–105 cm but selected for areas with plant heights about 50% taller than the mean height across all cover types. This result is consistent with suggestions by the previously mentioned studies that increased vertical cover provides enhanced concealment from predators and protection from extreme weather.

Patterns in second- and third-order selection

The use of burned NWSG at the home range scale, which was similar to use of grazed NWSG in the breeding season, also supported our predictions. However, the heavier use of burned NWSG over grazed NWSG during the non-breeding season (home-range scale) was unexpected. Local selection in burned NWSG was characterized by decreased grass cover and increased plant height. The mean available grass cover was 36.1%, but bobwhites used areas with a mean value of 23.1%. This pattern of use likely reflects the value of burned NWSG as cover in areas where grass is tall but relatively sparse. Similarly, non-breeding bobwhite in Missouri selected areas with low abundance of grass, possibly to facilitate movement and feeding (Mosloff et al. 2021). In addition, burned NWSGs may have provided greater vertical cover than NWSG pastures, which are typically managed to maintain canopies >30 cm (Keyser and Smith 2021). Indeed, the mean available and used plant height in burned NWSG was greater than that in grazed NWSG. This improved cover may be associated with greater survival rates in non-breeding season (Mitchell 2025). The burned NWSG stands had patches of forb and shrub that would not be tolerated in typical production scenarios (e.g., biomass). On the other hand, forbs and woody stem cover explained little variation in local selection in burned NWSG. This may have been because the availability

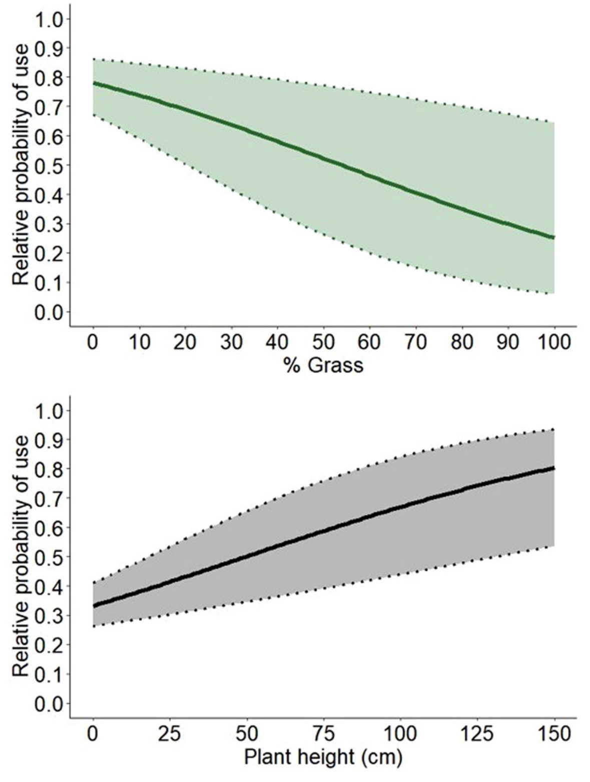

FIGURE 6 Relative probability of use at the third-order selection scale for percent grass (top) and vegetation height (bottom) by adult northern bobwhites (*Colinus virginianus*) with home ranges in burned native warm-season grass in non-breeding season (October–March) in Madison County, Kentucky, USA, 2019–2022. Dotted lines indicate 95% confidence intervals.

of forbs and woody stems in the area were within preferred ranges for this species. Similarly, bobwhites in North Carolina had forb availability similar to the burned NWSG areas in our study (~18%) and also suggested weak selection for forb cover (Rosche et al. 2019). Bobwhites in southern Missouri also did not display selection trends for forbs with an available forb abundance of about 10% (Mosloff et al. 2021).

Forb cover did not explain variation in selection in any of the cover types in either season. On our study site, the interquartile range of forb cover was about 12% to 40% in all the major cover types, with both mean and median values at about 28%. This is somewhat lower than forb cover reported elsewhere for bobwhites in the southeastern United States (30%–60%, Yeiser et al. 2015; 40–65%, Kroeger et al. 2020). Bobwhites on a reclaimed surface mine with NWSGs and 35%–65% forb cover also did not exhibit selection trends for forbs, although much of this consisted of sericea lespedeza, an invasive exotic (Brooke et al. 2015). This is likely an extension of the interchangeability of cover types required by bobwhites (Guthery 1999). Forbs are a critical component of bobwhite habitat, especially because they facilitate movement and food for juvenile bobwhites (Taylor et al. 1999). Ungrazed NWSGs in Tennessee with <10% forb cover had low invertebrate biomass (Fettinger et al. 2002). However, Harper et al. (2015) found sufficient insect forage for juvenile bobwhites in grazed NWSGs with 10% forb cover.

Our study supports the working-lands model in that grazing (CSG or NWSG) appears to be compatible with maintaining bobwhite habitat. However, the lower threshold for forb cover in grazed areas remains unclear. Further research in areas with grazed NWSG and burned NWSGs in the fescue belt may provide insight into the range of weedy encroachment in such pastures needed to support bobwhite, particularly in working lands where producers and landowners may be primarily concerned with managing forage production for cattle and may have a low tolerance for weed competition. Furthermore, the importance of woody stem cover and maintaining taller plant heights is highlighted in both breeding season and non-breeding season. Similarly, idle NWSG fields (burned in our study) may provide some critical components of bobwhite habitat, although NWSG fields that are typically undisturbed during summer (e.g., biomass or seed production) would likely have fewer woody stems than our study site.

CONSERVATION IMPLICATIONS

Incorporation of NWSGs on working lands in the fescue belt could be an effective conservation strategy for populations of northern bobwhites and associated bird species. Bobwhites in this working-lands study showed clear selection trends for NWSGs at multiple scales in an environment otherwise dominated by exotic CSG. Ultimately, the efficacy of integrating NWSGs into working lands would be contingent on other demographic parameters such as survival and recruitment. Maintaining structure through proper grazing practices supports the productivity of these pastures and provides cover for wildlife such as bobwhite. Allowing for the development of well-distributed woody stems, whether in the form of small within-pasture patches or along pasture margins, may also be critical to realizing the full potential of such a system. Conservation incentive programs could be adapted to encourage these practices across the fescue belt, thereby providing a landscape-level solution that may contribute to grassland-associated bird populations and bolster conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All trapping, handling, and marking procedures were in accordance with the University of Tennessee Institutional Animal Care and Use Committee-approved protocols (2608-0418 and 2608-0321).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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