



Research Article

Northern Bobwhite Non-Breeding Habitat Selection in a Longleaf Pine Woodland

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ABSTRACT Efforts to halt the decline of the northern bobwhite (*Colinus virginianus*; bobwhite) across its distribution have had limited success. Understanding bobwhite habitat requirements across the annual cycle and at varying scales is essential to aid efforts to conserve bobwhites. We monitored radio-tagged bobwhites from 2016 to 2018 on a 165-km² portion of Fort Bragg Military Installation in the Sandhills physiographic region of North Carolina, USA, to determine factors influencing non-breeding bobwhite habitat selection at multiple scales. We used generalized linear models (GLM) and generalized linear mixed models to assess bobwhite habitat selection at the microsite scale (the immediate vicinity of an animal) and the macrosite scale (across the study area), respectively, by comparing used points to available random points. At the microsite scale, bobwhites strongly selected areas with greater woody understory cover. Also, bobwhite selection increased with greater forb and switchcane (*Arundinaria tecta*) cover, but this effect plateaued at 65% forb cover and 50% switchcane cover. At the macrosite scale, bobwhites generally selected areas with greater understory cover within a 200-m radius but avoided areas with >55% understory cover; these areas primarily were located in the core areas of drainages with extensive ericaceous vegetation. Bobwhites selected areas with 3–6 m²/ha hardwood basal area in uplands, potentially because of the availability of mast, but avoided uplands when pine (*Pinus* spp.) or hardwood basal area exceeded 20 m²/ha or 12 m²/ha, respectively, likely because high basal area is associated with increased shading and subsequent loss of understory cover. In addition, bobwhites selected uplands 1 growing season (≥ 2 -month period falling entirely between 1 Apr and 1 Oct) post-fire regardless of burn season. Overall, managers seeking to improve habitat quality for bobwhites in longleaf pine (*Pinus palustris*) woodlands should employ management practices that maintain available woody understory across the landscape to provide cover during the non-breeding season. © 2020 The Wildlife Society.

KEY WORDS *Colinus virginianus*, habitat selection, hardwood, longleaf pine, non-breeding, northern bobwhite, *Pinus palustris*, prescribed fire.

Northern bobwhite (*Colinus virginianus*; bobwhite) populations have declined throughout their range (Sauer et al. 2017) because of habitat loss and fragmentation, largely through changes in land-use, including urbanization, a shift to large-scale agriculture, and forest succession (Brennan 1991, Williams et al. 2004, Hernández et al. 2013). Although the general habitat requirements of bobwhites are understood and have been for nearly 90 years (Stoddard 1931, Rosene 1969), efforts to stall or reverse their decline have had limited success (Brennan 1991, McKenzie 2009, Hernández et al. 2013). Some of this

failure may be attributable to misapplication of management efforts at scales either too fine or too coarse to be effective (Williams et al. 2004, Riddle et al. 2008, Bowling et al. 2014). Thus, efforts to increase the bobwhite population must include restoration of necessary compositional and structural components at functionally appropriate scales. Understanding habitat requirements at multiple scales and how these requirements shift throughout the year is important for effective management of most wildlife species, including bobwhites.

The non-breeding season is a particularly stressful time for bobwhites because they cope with decreased food availability and increased vulnerability to thermal stress and predation (Atuo and O'Connell 2017, Burger et al. 2017, Janke et al. 2017). Many herbaceous plants become

Received: 5 December 2019; Accepted: 14 June 2020

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senescent in winter, decreasing the availability and quality of cover and forage for bobwhites. Bobwhites respond to cold stress by seeking thermal cover and increasing caloric intake, leaving them vulnerable to shortages of cover and food during the non-breeding season (Swanson and Weinacht 1997, Tanner et al. 2017). In addition to mortality associated with thermal stress, reductions in cover may force bobwhites to travel longer distances between cover, increasing predation risk (Seckinger et al. 2008, Lohr et al. 2011). Furthermore, non-breeding survival is one of the most important factors influencing bobwhite population dynamics, and understanding the connection between habitat availability, selection, and survival is important for bobwhite restoration efforts (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012).

The availability of woody cover is one of the primary parameters affecting winter bobwhite survival (Williams et al. 2000, Janke et al. 2015, Peters et al. 2015), and is an important component of bobwhite habitat, regardless of season. Although early successional plant communities consisting of predominantly forbs and grasses may provide breeding-season (nesting and brood-rearing) cover for bobwhites, the plant community is only 1 component of bobwhite habitat and not a functional whole (Riddle et al. 2008, Harper and Gruchy 2009, Bowling et al. 2014). Woody cover provides reliable thermal and escape cover year-round, and many woody understory species produce or retain mast and seed important to bobwhites during the non-breeding season (Eubanks and Dimmick 1974, Dietz et al. 2006, Masters et al. 2016).

Although bobwhites are considered shrubland birds, open-canopy woodlands can be managed to provide adequate understory cover with the appropriate application of prescribed fire. Fires reduce understory litter and can prevent canopy closure (Peterson and Reich 2001, Vander Yacht et al. 2017). In addition, prescribed fire enhances understory species richness, retains understory structure, and promotes germination of plants beneficial to bobwhites (Brockway and Lewis 1997, Brennan et al. 1998, Sparks et al. 1998, Hiers et al. 2000). The frequency and seasonality of prescribed fire greatly affects the suitability of woodlands for bobwhites. Dormant-season fires often are used to promote and retain woody understory species (White et al. 1990, Boyer 1993, Drewa et al. 2002, Robertson and Hmielowski 2014). Growing-season fires may be used to reduce woody species and increase herbaceous understory diversity (White et al. 1990, Boyer 1993, Glitzenstein et al. 1995, Sparks et al. 1999, Haywood et al. 2001, Haywood 2009). Likely more influential than fire seasonality is fire intensity and fire frequency (Glitzenstein et al. 1995, Sparks et al. 1999, Palik et al. 2002, Knapp et al. 2009). Frequent fire, especially in the growing season, may reduce the woody understory cover necessary to support bobwhite populations (Waldrop et al. 1987). Conversely, infrequent and low-intensity fire may be insufficient to prevent midstory encroachment and shading, which has a deleterious effect on herbaceous cover. The delicate balance of fire timing and frequency is further complicated by individual site characteristics because a

fire-return interval appropriate for more fertile areas may be too frequent for relatively dry, nutrient-poor sites (Ostertag and Menges 1994, Pausas and Keeley 2014, Rosche et al. 2019).

Habitat selection for non-breeding bobwhites has been studied extensively (Dixon et al. 1996, Chamberlain et al. 2002, Singh et al. 2011, Janke et al. 2015, Unger et al. 2015), but relatively few studies (Brooke et al. 2015) have examined *in situ* measurements of non-breeding site characteristics at multiple spatial scales. Instead, much of the extant literature uses relatively coarse classifications of vegetation community types that may oversimplify and ultimately miss the specific site characteristics or thresholds required to sustain bobwhite populations. Furthermore, bobwhites are rarely the sole focus for managers in an area, and bobwhite conservation often takes place in the context of mixed priorities, including other wildlife species or silvicultural and agricultural goals. Bobwhites exist in a wide variety of landscapes and understanding the relationships between bobwhite habitat selection and stand composition, fire history, and other landscape-level features is important to the conservation and restoration of bobwhite populations, as is understanding these relationships within the context of mixed conservation or land-use goals. Lastly, bobwhites are only one of several species that rely on forbs and woody understory cover, and management for bobwhites is likely to benefit other species including wild turkey (*Meleagris gallapovo*), Bachman's sparrow (*Peucaea aestivalis*), and white-tailed deer (*Odocoileus virginianus*; Kilburg et al. 2014, Winiarski et al. 2017, Kroeger et al. 2020).

We examined the factors influencing northern bobwhite habitat selection during the non-breeding (late winter–early spring) season in a landscape dominated by fire-maintained longleaf pine (*Pinus palustris*) uplands at the microsite (immediate available vicinity of an animal) and macrosite (management unit or study area) scales. We predicted that bobwhites would select sites with greater woody understory cover at the microsite and macrosite scales and for site characteristics that would maximize understory cover, including low basal area, low tree density, and longer time since fire. We hypothesized that topographic position (i.e., uplands or bottomlands) may alter selection for ≥ 1 site characteristics.

STUDY AREA

We evaluated bobwhite winter habitat selection on a 165-km² portion of Fort Bragg Military Installation (i.e., Fort Bragg) in the Sandhills physiographic region of North Carolina, USA, 2016–2018. Fort Bragg is an active joint Army and Air Force installation owned and managed by the United States Department of Defense. The Sandhills region was characterized by rolling hills with open canopy longleaf pine uplands interspersed with bottomlands or lowland drainage areas (Sorrie et al. 2006, Franklin 2008). The region averaged 99 m above sea level, and precipitation averaged 115 cm/year. Average yearly temperature ranged from 10°C to 23°C. Over the course of the study, the monthly low temperature was –3.8–19°C, and the monthly high temperature was 10.4–29.7°C. Monthly precipitation

ranged from 2.2 cm to 12.1 cm over the same time period. The region experienced 4 distinct climatic seasons consisting of winter (Jan–Mar), spring (Apr–Jun), summer (Jul–Sep), and fall (Oct–Dec), and botanical growing and dormant seasons (Apr–Oct and Nov–Mar, respectively). Coarse sandy, well-drained soils predominated, resulting in relatively low site productivity throughout the region. The most abundant upland plant community consisted primarily of an open longleaf pine canopy, sparse hardwood subcanopy (oak [*Quercus* spp.], especially turkey oak [*Q. laevis*], sand post oak [*Q. margaretta*], and blackjack oak [*Q. marilandica*]), and mockernut hickory [*Carya tomentosa*]), with a variable groundcover dominated by wiregrass (*Aristida stricta*; Sorrie et al. 2006). In mesic lowlands, canopy species included loblolly pine (*Pinus taeda*), pond pine (*Pinus serotina*), blackgum (*Nyssa biflora*), red maple (*Acer rubrum*), and assorted oaks. Likewise, as soil moisture and nutrient levels increased, the groundcover was less dominated by wiregrass, and transitioned to more diverse grass and forb communities (Sorrie et al. 2006). Dominant fauna at Fort Bragg included longleaf pine community associates such as fox squirrels (*Sciurus niger*), Bachman's sparrows, and red-cockaded woodpeckers (*Leuconotopicus borealis*), with bobwhites, wild turkeys, and white-tailed deer present in relatively low densities.

Land management at Fort Bragg primarily attempted to maintain sparse midstory for ease of military training and creating habitat for the federally endangered red-cockaded woodpecker. Red-cockaded woodpeckers require mature, open pine communities promoted by frequent fire (U.S. Fish and Wildlife Service 2003), and managers at Fort Bragg applied prescribed fire in a 3-year return interval to forested areas to prevent hardwood encroachment into the midstory. Firebreaks and streams divided the study area into management units averaging 33.5 ha (range = 0.4–136 ha), with forested bottomlands resulting in mixed hardwood-pine plant communities from natural fire suppression. Prescribed burns on Fort Bragg primarily were conducted April–June, with occasional fires occurring later in the growing season. Uplands were intensively managed with fire and occasional thinning, but bottomlands were not thinned. Although bottomlands were not managed differently with fire (bottomlands within a burn unit were assumed to burn along with uplands), many bottomland areas were surrounded by remnant firebreaks, which, combined with greater moisture in bottomlands, reduced fire intensity and fire coverage in bottomlands. Logistical constraints often resulted in management units missing a scheduled burn rotation, and in these cases, units were burned during the following dormant season (Jan–Mar). Non-forested, undeveloped areas, such as military drop zones, artillery firing points, and landing strips, were burned or mowed annually or biennially to remove woody growth. More than 480 wildlife openings were scattered throughout the study area with some actively maintained in planted species, including shrub lespedeza (*Lespedeza bicolor*), millet, rye, sorghum, and showy partridge pea (*Chamaecrista fasciculata*), and others left fallow (Sorrie et al. 2006). We defined the end of the non-breeding season

as the date of median covey break-up (the date at which half of the coveys with radio-tagged birds had broken up), which we considered to be the start of the breeding season.

METHODS

Capture and Radio-Telemetry

We captured bobwhites from February–April 2016, January–April 2017, and January–April 2018. We used modified walk-in funnel cage traps (Stoddard 1931), baited with scratch feed, whole corn, millet, or wheat. We checked traps every evening starting ≤ 30 minutes before sunset. We limited our trapping efforts to the mid-late dormant season because we specifically wanted to evaluate northern bobwhite nonbreeding habitat selection during that period, rather than during the relatively mild fall–early winter.

We weighed, aged, sexed, and marked all captured birds. We used a 300-g Pesola spring scale (Pesola, Schindellegi, Switzerland) to weigh individual birds and attached necklace-style 6.2-g very high frequency (VHF) transmitters with 12-hour mortality sensors (model AWE-Q, American Wildlife Enterprises, Monticello, FL, USA) to individuals weighing ≥ 130 g. We used the presence or absence of buffy tips on the upper primary coverts to classify birds as juveniles or adults, respectively, and determined sex based on plumage color and pattern (Brennan et al. 2014). All individuals received number 7 aluminum butt-end leg bands (National Band and Tag Company, Newport, KY, USA). All capture and handling methods followed protocols approved by the North Carolina State University Institutional Animal Care and Use Committee (number 15-126-O).

We located individuals 3–5 times/week from 10 February–22 April of 2016, 15 February–28 April of 2017, and 27 January–15 May of 2018. Telemetry equipment consisted of VHF receivers and 3-element Yagi directional antennas (receiver model R4000; Advanced Telemetry Systems, Isanti, MN, USA). We used vehicle-mounted omnidirectional antennas (Laird Technologies, Chesterfield, MO, USA and Telonics Mesa, AZ, USA) to establish coarse locations as needed for further refinement using 3-element Yagi antennas. We homed to individuals to within 50 m (White and Garrott 1990), and used handheld global positioning system (GPS) units (eTrex 20, Dakota 20, and Oregon 450; Garmin International, Olathe, KS, USA) to record locations for each radio-tagged bird, or for each covey in cases where a covey contained >1 radio-tagged bird. Our recorded used locations ultimately were estimates of the actual bird location, and some location error was unavoidable. Prior to beginning data collection, we placed practice transmitters in a variety of vegetation, cover, and topographic conditions to establish a baseline estimate of the relationship between signal strength and distance and thus minimize location error, typically within 5–10 m. If we observed a mortality signal, we recovered the transmitter that day. If we could not locate an individual, we continued searching in expanding areas for ≥ 2 weeks.

Variable Measurement and Synthesis

We surveyed vegetation at all bobwhite or covey locations, and at 1 microsite random point per location. We generated

random points using a random bearing (1–360°) and distance (10–250 m) from each bobwhite or covey location. We used 250 m as the limit for random distance based on the radial conversion of average home range size for northern bobwhites in similar vegetation types (Terhune et al. 2006). Where random points fell outside of vegetated areas (e.g., roads, bodies of water, military buildings, restricted access areas), we decreased the distance along the original azimuth until the entire plot fell within a vegetated area. Each vegetation plot was formed by 2 perpendicular 10-m transects, with the midpoint at the bird location or paired random point. At the midpoint and each 1-m interval (21 points), we used a modified 2-m Wiens pole to determine percent horizontal cover of woody understory, switchcane (*Arundinaria tecta*), forbs, and grasses (excluding switchcane) by dividing the number of points where a given plant classification touched anywhere on the pole by the number of points (Rotenberry and Wiens 1980, Moorman and Guynn 2001). In addition, we recorded the predominant groundcover at the base of the pole (bare ground, grass, forb, litter). At the midpoint of vegetation plots, we visually estimated canopy cover as 0–20%, 21–40%, 41–60%, 61–80%, or 81–100% and used a 10-factor prism to determine hardwood and pine basal area. We conducted all vegetation sampling within 1 week of the bobwhite location being recorded.

We used geographic information system (GIS) and Lidar layers provided by the Fort Bragg Directorate of Public Works to derive broader landscape characteristics, including days since fire, immediate fire history, topographic position, stand basal area, tree density and height, vegetation community type, understory cover, and proximity to key landscape features. The Lidar data was collected in November 2015 and had an average point density of 5.59 pulses/m², with a maximum of 7 returns/point. We calculated days since fire as the number of days elapsed between the date of collection for the bobwhite location and random points, and the most recent fire for that point location. We created a 7-level categorical variable corresponding to immediate fire history by combining the number of growing seasons since fire with the season of that most recent fire (e.g., dormant or growing season). We defined growing seasons since fire as a minimum 2-month period falling entirely between 1 April and 1 October. We combined areas with zero growing seasons since fire into a single category regardless of whether the most recent fire occurred in the dormant or growing season.

At the macrosite scale, we derived the immediate fire history for random locations by assigning each random location a collection date corresponding to that of a randomly sampled used location, without replacement. Thus, for each used location collected on a given date, there were 5 random locations assigned that same collection date. We used 5 random locations per used location for macrosite analysis because that was an appropriate representation of the landscape available to bobwhites at the scale we wished to examine without becoming computationally prohibitive (Northrup et al. 2013). We derived vegetation community

type, stand basal area, and proximity to landscape features from GIS layers provided by the Fort Bragg Directorate of Public Works using ArcMap (10.6.1; Esri, Redlands, CA, USA). We calculated topographic position using Lidar-derived slope and elevation with Land Facet Corridor Designer: Extension for ArcGIS (Jenness Enterprises, Flagstaff, AZ, 2018). We used R statistical software (R version 3.6.0, www.r-project.org, accessed 10 Jun 2019) to calculate tree density from 1-m resolution Lidar imagery. We first identified individual trees using the variable window filter function in the ForestTools package (Plowright and Roussel 2018). Then, we used the focal statistics tool in ArcMap to calculate a 200-m-radius circular neighborhood average of density for trees ≥ 5 m in height. In addition, we calculated a 200-m-radius circular neighborhood average of understory cover using the presence or absence of Lidar returns classified as vegetation with height < 2 m. The relatively coarse Lidar resolution strongly favored the detection of woody or particularly dense vegetation over sparse herbaceous vegetation (e.g., wiregrass). We used a 200-m-radius circular window because this distance is similar to many estimates of the average daily movement for bobwhites in winter and greater than estimates of average flushing distances after disturbance or during predator avoidance (Madison et al. 2000, Williams et al. 2000, Perez et al. 2002, Janke et al. 2013, Perkins et al. 2014).

Statistical Analysis

At the microsite scale, we evaluated 9 continuous variables describing vegetation, 2 continuous variables that described proximity to important landscape features, and 3 categorical variables that described broader site characteristics (Table 1). Bottomlands and uplands at Fort Bragg have different moisture and light regimes, soil texture, and realized fire regimes (i.e., bottomlands may experience lower fire intensity or burn incompletely because of increased soil and vegetation moisture content). To account for this variation, we considered interactions between topographic position and other variables, including vegetation type, basal area, and fire history. Finally, we included quadratic terms for all continuous variables to allow for non-linearity and threshold effects. We removed all interaction and quadratic terms if they did not improve model performance by > 2 Akaike's Information Criterion (AIC) values per parameter (Arnold 2010).

At the macrosite scale, we generated 5 random points distributed across the study area in ArcMap for each bobwhite location ($n = 911$), for 4,555 random points. We evaluated 8 continuous and 3 categorical variables describing site characteristics at the macrosite scale (Table 2). We hypothesized that topographic position may interact with other influences of habitat selection (e.g., basal area, fire history), and included interaction terms between those variables. In addition, we included quadratic terms with all continuous variables, and removed all higher order terms if they did not improve model performance (Arnold 2010).

At both scales, we began with a generalized linear model (GLM) consisting of all potential covariates. We tested for

Table 1. Variables used to evaluate northern bobwhite non-breeding habitat selection at the microsite scale, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. Variables removed from consideration because of correlation or collinearity are noted with an asterisk (*).

Parameter description	Parameter range	\bar{x}	Median	SD
Canopy cover (20% increments)	1, 2, 3, 4, 5			
Season (D = dormant, G = growing) and growing seasons (0S, 1, 2, ≥ 3) since last fire	0S, D1, D2, D ≥ 3 , G1, G2, G ≥ 3			
Topographic position	Bottomlands, uplands			
Bare ground (%)	0–100	10.13	0.00	20.01
Grass-groundcover (%)*	0–100	6.64	0.00	13.65
Grass understory (%)	0–100	31.64	23.81	30.02
Woody understory (%)	0–100	34.19	23.81	31.27
Forb understory (%)	0–100	12.01	4.76	18.05
Switchcane understory (%)	0–95.24	8.18	0.00	19.02
Distance to wildlife opening (m)	0–1,417.89	337.68	299.40	260.72
Distance to riparian area (m)*	0–521.04	124.67	79.58	130.71
Days since fire*	2–2,198	732.17	438.50	571.58
Fire frequency*	0.08–0.59	0.30	0.30	0.08
Pine basal area (m ² /ha)	0–50.50	8.66	6.89	7.80
Hardwood basal area (m ² /ha)	0–45.91	3.57	0.00	6.07

collinearity of continuous variables using Pearson's correlation coefficients with a $|r| < 0.7$ limit and examined variance inflation factors (VIF) and removed variables from consideration if $VIF > 3$. We examined residuals using the car package (Fox 2011) in R and built a set of *a priori* models containing variables of known interest for both scales.

For the microsite analysis, we constructed logistic regressions in the form of generalized linear mixed models in the glmmTMB package (Brooks et al. 2017) in R to compare vegetation characteristics of telemetry (used) and random (available) points. We began with a maximally specified model, including all terms of the *a priori* model, all potentially informative variables and suspected interactions and both random intercepts and random slopes for these terms with bird or covey identification (ID) as the random term. Where the ratio of used to available points is constant and under the control of the researcher, random intercepts can be uninformative and return a random effect variance of nearly zero (Fieberg et al. 2010). Random slopes ensure that variable coefficients and standard errors can vary between levels of the random term (in this case, bird or covey ID),

and failure to include random slopes in use-availability study designs may result in biased (overly confident) estimates of fixed effects (Schielzeth and Forstmeier 2008, Fieberg et al. 2010).

We determined the optimal random-effects structure by comparing models with iteratively removed random effects (intercepts and slopes) using restricted maximum likelihood estimation and a likelihood-ratio test, with *P*-values corrected for testing on the boundary (Zuur et al. 2009). We determined the optimal fixed-effects structure beginning with the *a priori* fixed-effects model and optimal random-effects structure. We examined 85% confidence intervals for estimates of other potentially influential variables, with and without interactions with topographic position, when added individually to the *a priori* models and discounted these variables if the intervals overlapped zero (Arnold 2010). We built model selection tables using the reduced set of potentially informative variables when fitted with maximum likelihood (ML; Zuur et al. 2009). We ranked the ML-fitted models by the lowest Akaike's Information Criterion corrected for sample size (AIC_c) score and chose the most parsimonious model within 2 AIC_c per parameter

Table 2. Variables used to evaluate northern bobwhite non-breeding habitat selection at the macrosite scale, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. Variables removed from consideration because of correlation or collinearity are noted with an asterisk (*).

Parameter description	Parameter range	\bar{x}	Median	SD
Season (D = dormant, G = growing) and growing seasons (0S, 1, 2, ≥ 3) since last fire	0S, D1, D2, D ≥ 3 , G1, G2, G ≥ 3			
Topographic position	Bottomlands, uplands			
Vegetation community*	Bottomlands, ecotone, large openings, upland pine, other			
Distance to wildlife opening (m)	0–2,493.36	482.04	385.29	391.02
Distance to riparian area (m)*	0–1,339.81	152.19	107.94	164.35
Mean crown height (m)	0–24.50	15.89	16.62	4.27
Trees/ha	0–603.7	271.10	271.10	101.74
Days since fire*	0–2,659	741.70	613.00	637.84
Fire frequency*	0–0.67	0.31	0.30	0.10
Upland pine basal area (m ² /ha)	0–33.29	10.35	10.79	5.98
Upland hardwood basal area (m ² /ha)	0–23.19	2.28	1.15	2.87
Bottomland basal area (m ² /ha)	0–43.16	15.46	16.76	5.20
Understory cover (%)	0–71.72	17.25	13.37	13.46

difference of the top-ranked model (Zuur et al. 2007). Finally, we re-fit the chosen model using restricted maximum likelihood estimation to ensure accurate estimates (Zuur et al. 2009).

For the macrosite analysis, we used the `glm` function in R to fit logistic generalized linear models because we were only interested in population-level selection across the study site, and available points were not specific to individual birds or coveys. We calculated cluster-robust standard errors using the `sandwich` package to account for the spatial and temporal autocorrelation of successive used locations and ensure that standard errors and associated confidence intervals were not underestimated because of pseudoreplication (Andrews 1991, Zeileis 2006). We used the median bias-reduced adjustment method from the `brglm2` package outlined in Kosmidis et al. (2020) because one of our categorical variables had levels for which events (used locations) were rare, often resulting in complete separation. We examined 85% confidence intervals for estimates of other potentially influential variables with and without interactions with topographic position when added individually to the *a priori* models and discounted these variables if the intervals overlapped zero (Arnold 2010). We built model selection tables using this reduced set of potentially influential variables and identified the top models by the lowest AIC_c (Zuur et al. 2007). If a model within 2 AIC_c of the top model was the most parsimonious, we chose it as the new top model. We tested for overly influential observations by examining Cook's distances and comparing the final model coefficients with potentially influential observations removed.

RESULTS

In 2016, we captured 59 individuals over 3,420 trap nights, comprising 52 juveniles and 7 adults. In 2017, we captured 71 individuals over 9,646 trap nights, comprising 50 juveniles and 21 adults. In 2018, we captured 86 individuals over 8,356 trap nights, comprising 59 juveniles and 27 adults. We collected 202 locations for 38 individuals or coveys during the 2016 non-breeding season (10 Feb–22 Apr), 216 locations for 34 individuals or coveys during the 2017 non-breeding season (15 Feb–28 Apr), and 493 locations for 16 individuals or coveys during the 2018 non-breeding season (27 Jan–1 May). We documented 17 mortalities during the 2016 non-breeding season, and 7 individuals either left the study area or were lost because of transmitter malfunction. During the 2017 non-breeding season, we documented 19 mortalities, and 3 individuals either left the study area or were lost because of transmitter malfunction. We documented 27 mortalities during the 2018 non-breeding season, and 14 individuals either left the study area or were lost because of transmitter malfunction. Throughout this section we use the terms selection and avoidance to reflect bobwhite use of an area where the 95% confidence interval of the variable did not overlap with the calculated probability of selection with all variables held at median values.

At the microsite scale, the best model included pine and hardwood basal area, quadratic effects for forb and

switchcane cover, an interaction between topographic position and grass cover, an interaction between topographic position and woody understory cover, and random slopes for woody understory cover (Table 3). Bobwhites selected areas with >30% woody understory cover and avoided areas with <13% woody understory cover, and the effect was 55% stronger in uplands than in bottomlands (Fig. 1A). The probability of selection increased as forb and switchcane cover increased, but these relationships were limited by quadratic effects to maxima of 65% and 50% cover for forbs and switchcane, respectively, after which the probability of selection plateaued or decreased slightly (Figs. 1B, C, respectively). Bobwhites selected areas with >13% or >7% forb and switchcane cover, respectively, but did not avoid areas lacking forb or switchcane cover altogether. In addition, the probability of selection increased as grass cover exceeded 28% in uplands (Fig. 1D). The relative probability of selection decreased with increasing pine and hardwood basal area, and bobwhites avoided areas with >15 m²/ha pines and >6 m²/ha hardwoods (Figs. 1E and F, respectively).

At the macrosite scale, the top model included proximity to wildlife opening, topographic class, growing seasons since fire, and season of most recent fire, and quadratic effects for understory cover, tree density, and pine and hardwood stand basal area (Table 4). We documented interactions between topographic class and the number of growing seasons since fire, topographic class and the season of most recent fire, and between topographic class and basal area. Bobwhites selected uplands with 3–6 m²/ha hardwood basal area but avoided uplands when hardwood or pine basal area exceeded 12 m²/ha or 20 m²/ha, respectively (Figs. 2A, B). Conversely, the probability of selection increased as basal area in bottomlands approached 14 m²/ha and decreased with further increases in basal area, although significant uncertainty limits our ability to make specific inferences regarding this relationship (Fig. 2C). The relative probability of selection decreased as distance to wildlife opening increased, and bobwhites avoided areas >600 m from a wildlife opening (Fig. 2D). Understory cover, defined as

Table 3. Model parameters, coefficients, standard errors, and random effects for the top model predicting northern bobwhite non-breeding season habitat selection at the microsite scale, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. The reference level for topographic position was bottomlands. Bird or covey identification was the random effect term.

Parameter	β	SE
Uplands	-0.187	0.125
Pine basal area (m ² /ha)	-0.168	0.057
Hardwood basal area (m ² /ha)	-0.194	0.058
Woody understory ^a (%)	0.620	0.103
Uplands × woody understory (%)	0.352	0.149
Forb understory (%)	0.533	0.091
Forb understory ² (%)	-0.097	0.036
Switchcane understory (%)	0.604	0.146
Switchcane understory ² (%)	-0.124	0.048
Grass understory (%)	-0.181	0.103
Uplands × grass understory (%)	0.588	0.131

^a Random slope SD = 0.329.

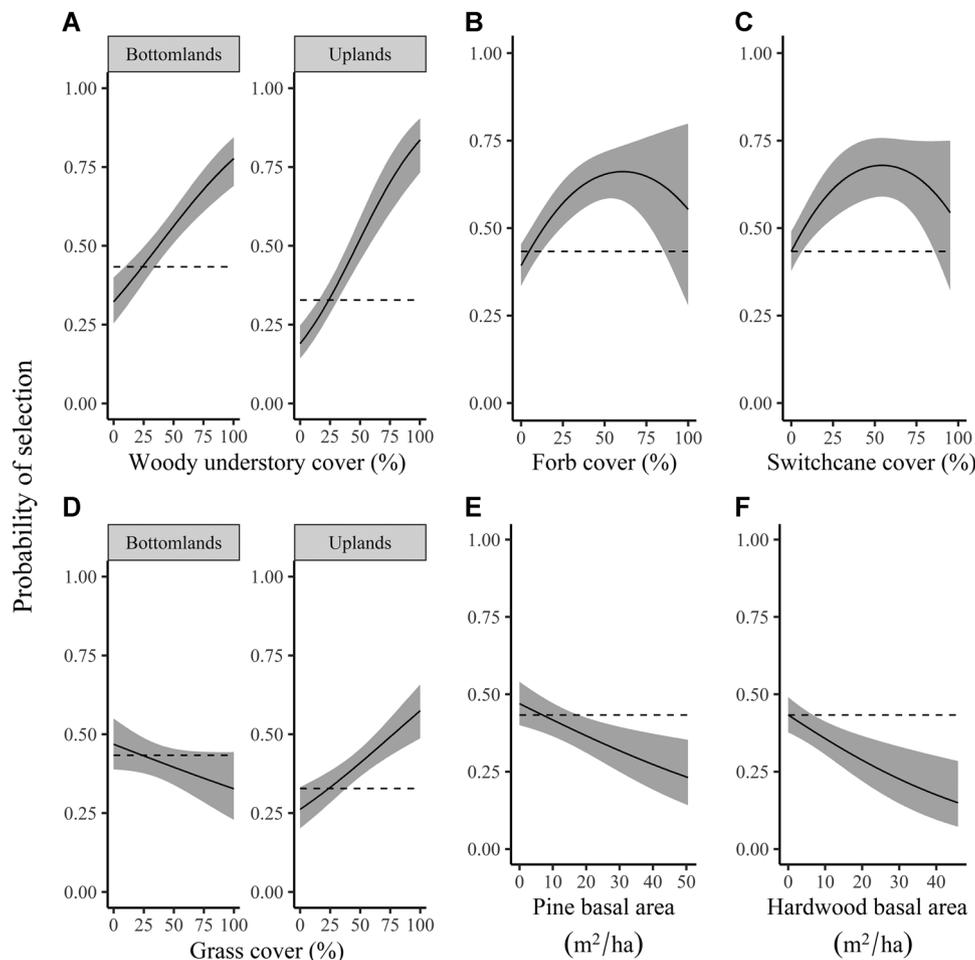


Figure 1. Probabilities and 95% confidence intervals for predictors of microsite selection for non-breeding northern bobwhites, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. We generated all plots with all other variables held at their respective median values. The horizontal dashed line represents the probability of selection with all variables held at median values, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.

Lidar-classified vegetation with height <2 m, was positively associated with selection, but this relationship was quadratically limited to a maximum of 28% understory cover (Fig. 2E). Consequently, bobwhites avoided areas with <8% or >55% understory cover. Also, increased tree density was negatively associated with selection, and bobwhites selected areas with 75–150 trees/ha and avoided areas with >320 trees/ha (Fig. 2F). Finally, bobwhites selected upland areas 1 growing season since fire regardless of burn season and upland areas ≥ 3 growing seasons since fire if the recent fire occurred in the dormant season (Fig. 3).

DISCUSSION

We detected strong support for our hypothesis that woody cover was important for bobwhites at both the microsite and macrosite scales. Our hypothesis that bobwhites would select for site characteristics that would maximize understory cover was similarly supported. Lastly, we detected strong support for our hypothesis that topographic position would alter selection for some site characteristics (e.g., number of growing seasons since fire, season of the most recent fire, and basal area).

Woody understory cover had the largest standardized effect size at the microsite scale, and understory cover was likewise a strong predictor of macrosite selection, further reinforcing the importance of woody understory cover for northern bobwhites across its range (Yoho and Dimmick 1972, Kopp et al. 1998, Palmer et al. 2012, Janke and Gates 2013, Rosche et al. 2019). Although bobwhites avoided areas with >55% understory cover at the macrosite scale, this was likely because areas at our study site with >55% understory cover across a 200-m radius are predominantly the core areas of large bottomland drainages with extensive ericaceous vegetation in the understory. Although these areas provide cover, they have little food compared to the margins of bottomlands where gallberry (*Ilex coriacea*), inkberry (*Ilex glabra*), and swamp bay (*Persea palustris*) are more common and productive. In addition, the effect of woody understory cover on microsite selection was noticeably stronger in uplands than in bottomlands, reflecting the important nature of woody cover for bobwhite in frequently burned pine woodlands. Although proximity to wildlife opening was not a predictor of selection at the microsite scale, bobwhites did show strong selection for closer

Table 4. Model parameters, coefficients, and standard errors for the top model predicting northern bobwhite non-breeding season habitat selection at the macrosite scale, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. 0S = zero growing seasons since fire. G1 = 1 growing season since fire, most recent fire in the growing season. G2 = 2 growing seasons since fire, most recent fire in the growing season. G ≥ 3 = 3 or more growing seasons since fire, most recent fire in growing season. D1 = 1 growing season since fire, most recent fire in dormant season. D2 = 2 growing seasons since fire, most recent fire in dormant season. D ≥ 3 = 3 growing seasons since fire, most recent fire in dormant season. Reference level for topographic class was bottomlands. Reference level for recent fire was G ≥ 3.

Parameter	β	SE
Uplands	-0.862	0.971
Bottomland basal area (m ² /ha)	1.085	0.605
Bottomland basal area ² (m ² /ha)	-0.311	0.167
Upland pine basal area (m ² /ha)	-0.453	0.123
Upland hardwood basal area (m ² /ha)	0.664	0.225
Upland hardwood basal area ² (m ² /ha)	-0.298	0.078
Understory cover (%)	0.757	0.178
Understory cover ² (%)	-0.423	0.098
Distance to wildlife opening (m)	-0.691	0.186
Trees/ha	-1.096	0.185
Trees/ha ²	-0.266	0.118
0S	-1.092	0.770
Uplands × 0S	0.894	0.618
D1	-0.315	0.279
Uplands × D1	1.463	0.416
D2	-5.587	0.352
Uplands × D2	6.016	0.635
D ≥ 3	-3.186	0.987
Uplands × D ≥ 3	4.412	1.060
G1	-0.527	0.461
Uplands × G1	1.472	0.481
G2	-0.884	0.619
Uplands × G2	0.902	0.698

proximity to wildlife openings at the macrosite scale, indicating tree density in the woodlands limited habitat quality for bobwhites. Wildlife openings contained less tree cover and likely greater herbaceous and woody understory cover and available food. In addition, the majority of areas >600 m from a wildlife opening at our study site were centrally located in drop zones (non-forested, undeveloped open areas used for paratrooper training) or large bottomlands, both areas bobwhites may be expected to avoid. Drop zones in particular were burned or mowed annually or biennially, and often lacked cover and food during the winter. Understory shrubs and hardwood sprouts maintain structure during winter, providing important thermal and escape cover, and many of the most common woody understory species produced or retained mast in fall or winter (e.g., American beautyberry [*Callicarpa americana*], dwarf huckleberry [*Gaylussacia dumosa*], gallberry, inkberry, swamp bay, greenbrier [*Smilax* spp.], and smooth witherod [*Viburnum nudum*]), providing food for bobwhites.

Forb and switchcane cover were positively associated with selection, but these positive associations plateaued at approximately 50% switchcane and 65% forb cover. Although switchcane maintains its structure during winter and provides cover, it provides no food and usually existed as a monoculture when coverage exceeded 50%. Average forb coverage at our study site was only 10%, and the detection of forbs during the non-breeding season was largely limited to

those species that remain erect while senesced, potentially biasing the observed effects and thresholds. For example, one of the most common forb species detected during the non-breeding season was dogfennel (*Eupatorium capillifolium*), which provided limited cover but no food. Furthermore, areas in our study site exhibiting >65% forb cover were predominantly large patches of non-native sericea lespedeza (*Lespedeza cuneata*). Although sericea lespedeza provides some cover during the nonbreeding season for bobwhites, the seeds are virtually indigestible and should not be considered bobwhite food (Davison 1958, Newlon et al. 1964). Furthermore, large patches of sericea lespedeza reduce invertebrate abundance (Bugg and Dutcher 1989) and limit establishment of other forbs, including important bobwhite foods such as spurge (*Euphorbia* spp.) and tick-trefoil (*Desmodium* spp.; Brandon et al. 2004). Also, prior researchers have linked extensive coverage of sericea lespedeza to low fecundity and survival of bobwhites, and bobwhites in these studies consistently selected areas managed to control sericea lespedeza (Brooke et al. 2015, 2017; Peters et al. 2015). Therefore, the plateau effect of forb coverage at 65% that we documented may have been biased low because of dense sericea lespedeza that negatively influenced usability of those areas by bobwhites.

Fire history was a significant predictor at the macrosite scale, but we did not detect selection for season or time since fire at the microsite scale, likely because available points for microsite selection were constrained to within 250 m of the bird locations, and most available points would have fire histories similar to used points. Cram et al. (2002) reported bobwhites selected areas 3 years after fire where woody cover was most prevalent in the Ouachita National Forest in Arkansas, USA, but grasses at that study area were primarily bluestems (*Andropogon* spp.), some of which remain upright after senescence and provide cover for multiple dormant seasons (Harper et al. 2007). In contrast, bobwhites at our site selected areas 1 growing season since fire at the macrosite scale, likely because wiregrass, the dominant upland groundcover, flowers the growing season it is burned, and the resulting grass structure provides the highest quality cover for bobwhites during the following non-breeding season. With increased time since last burn, wiregrass becomes matted, reducing cover and restricting movement for wildlife (Burke et al. 2008, Taillie et al. 2015). Thus, although greater grass cover was positively associated with microsite selection in uplands, the association was likely a result of the sparsity of available woody understory cover rather than any reliance of bobwhites on grass cover specifically. In addition, bobwhites selected uplands ≥ 3 years since fire but only if that fire occurred during the dormant season. Dormant-season burns can favor sprouting of woody stems and shrubs, which provide important cover for bobwhites in uplands (Boyer 1993, Brockway and Lewis, 1997, Drewa et al. 2006, Robertson and Hmielowski 2014, Harper et al. 2016). Although bobwhites avoided bottomlands most recently burned during the dormant season, it is impractical and unrealistic to manage bottomlands differently from their

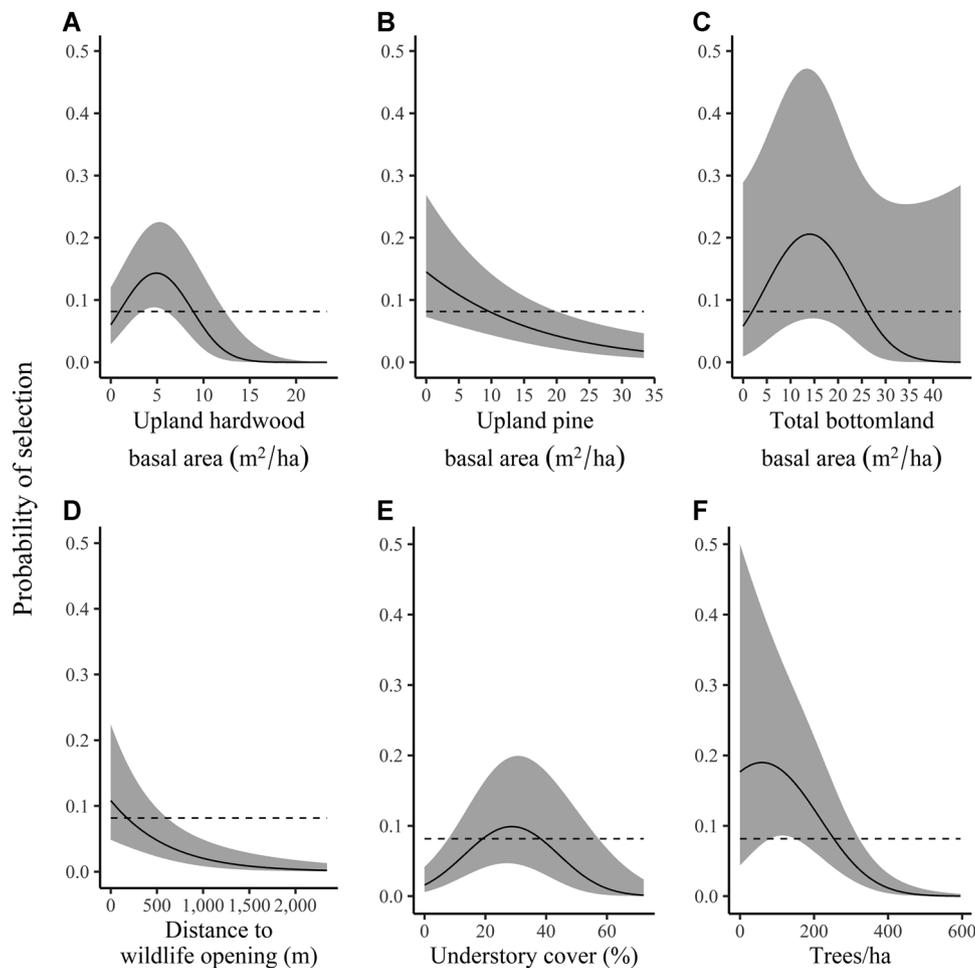


Figure 2. Probabilities and 95% confidence intervals for continuous predictors of macrosite selection for non-breeding northern bobwhites, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. We generated all plots with all other variables held at their respective median values. The horizontal dashed line represents the probability of selection with all variables held at median values, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.

surrounding uplands using prescribed fire. Rather, managers should simply incorporate variability into fire prescriptions, creating a heterogeneous mosaic of fire frequency and intensity (Lashley et al. 2015).

Bobwhite response to pine and hardwood basal area differed between the microsite and macrosite scales. At the microsite scale, bobwhites consistently selected areas with lower basal area regardless of tree type, where local woody and herbaceous understory cover would be less shaded by canopy cover. At the macrosite scale, selection for basal area was strongly influenced by topographic position (i.e., bottomlands or uplands). Although the probability of selection reached a maximum at 14 m²/ha in bottomlands, bobwhites used bottomlands with a wide range of basal area in proportion to their availability. Fertile bottomlands may support sufficient understory cover for bobwhites during the nonbreeding season, even at relatively high basal area, and bobwhites did not avoid bottomlands even where total basal area exceeded 38 m²/ha. Additionally, some bottomland hardwoods provide mast (swamp bay and oak species, especially water oak [*Quercus nigra*]), which may partially compensate for any loss of understory density from

overstory shading. Crop surveys from bobwhites hunted at Fort Bragg from 1970–1990 indicated the importance of swamp bay and oak mast, and to a lesser extent that of longleaf and loblolly pine (Wildlife Branch, Fort Bragg Directorate of Public Works, unpublished report). In uplands, bobwhite selection weakly declined with increasing pine basal area, and although the confidence intervals indicate that bobwhites may use areas with a range of pine basal area, the predicted response suggests that bobwhites will select areas with <10 m²/ha pines (Fig. 2B). Conversely, bobwhite selection increased with upland hardwood basal area up to 4 m²/ha before declining, likely because of mast provided by mature hardwoods. Similarly, bobwhites avoided areas with particularly high tree density; these areas may have been unable to support sufficient understory cover for bobwhites.

The presence or absence of woody understory cover has been demonstrated repeatedly to be a stronger influence on bobwhite habitat selection than herbaceous cover during the nonbreeding season, and managers should strive to provide high-quality woody understory cover on the landscape (Cram et al. 2002, Lusk et al. 2006, Janke and Gates 2013,

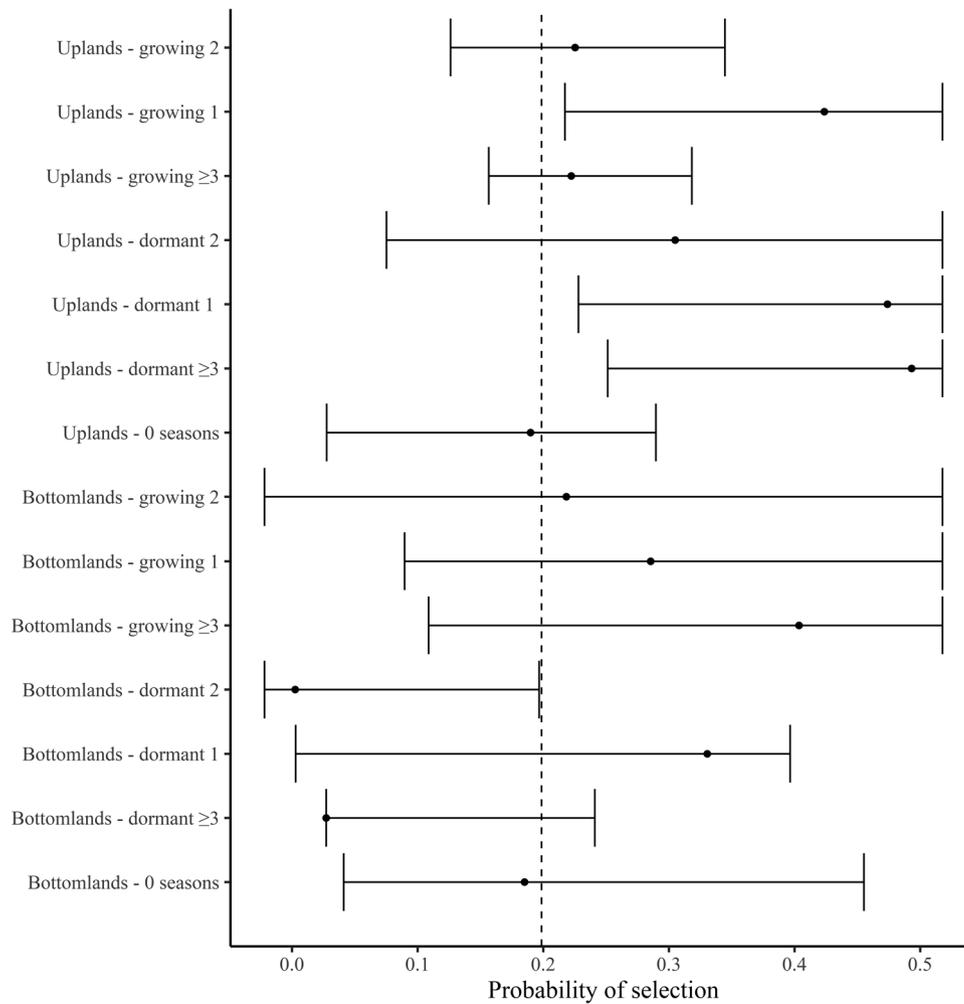


Figure 3. Estimated marginal mean probabilities and pairwise comparisons for categorical predictors of macrosite selection for non-breeding northern bobwhites, Fort Bragg Military Installation, North Carolina, USA, 2016–2018. Overlapping error bars indicate non-significant pairwise comparisons. The vertical dashed line represents the probability of selection with all variables held at median values, with probabilities to the right and left of this line indicating positive and negative selection (avoidance) for the factor of interest, respectively. Predictors include topographic class (upland or bottomland), season of most recent fire (growing or dormant), and growing seasons since last fire (0 to ≥ 3).

Brooke et al. 2015, Rosche et al. 2019). Woody understory cover, however, is likely to be sparse in open-canopy, pine-dominated woodlands burned during the growing season every 2 to 3 years, especially in areas with less productive soils. Understory composition is dictated by a combination of environmental conditions and management activities, including fire regime, soil texture, and overstory coverage, and bobwhite response to time since fire and fire seasonality suggests managers may be able to improve understory quality for bobwhites by altering fire regimes. Although a 2 to 3-year return interval may be ideal for maintaining wiregrass groundcover, it is too frequent and invariant to allow sufficient woody cover to develop for bobwhites on sites with low soil productivity similar to Fort Bragg. The range of acceptable basal area for Bachman's sparrow, red-cockaded woodpecker, and northern bobwhites all share significant overlap (Engstrom and Palmer 2005, Allen and Burt 2014), which may present an opportunity for managers under regulatory constraints precluding significant basal area reduction, provided managers are willing to alter fire

prescriptions to include longer time since fire, particularly on sites with low-quality soils. Furthermore, ensuring woody understory cover for bobwhite will also benefit other wildlife species, providing nesting and fledgling cover for Bachman's sparrow, nesting cover for wild turkey, and browse for white-tailed deer (Johnson et al. 1995, Hewitt 2011, Kilburg et al. 2014, Winiarski et al. 2017, Fish et al. 2020)

Our results further illustrate the importance of evaluating habitat selection and management activities at multiple scales for wildlife, as the influence of habitat characteristics on selection was not evident or equally important at all scales. Had we limited our research to the microsite scale, for example, we would have been unable to detect the influence of fire or wildlife openings on bobwhite habitat selection. Conversely, although microsite selection was overwhelmingly influenced by woody understory cover, the effect sizes of basal area and tree density were comparatively greater at the macrosite scale. Thus, although effective management of bobwhite habitat requires ensuring

adequate understory cover, management activities such as thinning or burning often target scales larger than single birds or coveys, and measurements of basal area and tree density provide a useful metric for managers seeking to improve habitat quality for bobwhites. Further research and evaluation of management for northern bobwhites should continue to examine multiple spatial scales.

MANAGEMENT IMPLICATIONS

Conservation efforts aimed at increasing northern bobwhite populations in open pine woodlands with understories dominated by grasses should focus on increasing forb and woody understory cover, and woody understory cover should be patchily distributed across the landscape. High basal area and associated shade preclude understory development, and we recommend maintaining total basal area of open pine woodlands below 10 m²/ha. Within this limit, we suggest upland hardwood basal area up to 4 m²/ha be retained to promote hard mast during the non-breeding season. We recommend prescribed fire on an average return interval of 3 years but allowing some areas to go 4 or 5 years between burning, particularly in sandy, low-productivity soils similar to those at our study area. Bobwhites selected areas 1–2 growing season since fire in uplands during the non-breeding season. Hence, a variable return interval averaging 3 years should maximize the food and cover resources for bobwhites during the non-breeding and breeding seasons, provided managers incorporate variation in frequency sufficient to allow regeneration of woody species, particularly when bobwhites are a priority. Variation in prescribed fire seasonality and frequency will improve habitat quality for northern bobwhites by promoting a diverse mix of woody and herbaceous understory species, which in turn provide year-round food and cover (Knapp et al. 2009, Lashley et al. 2015).

ACKNOWLEDGMENTS

We thank the Fort Bragg Wildlife Branch, particularly J. G. Jones and A. D. Schultz, for technical and logistical support. We are grateful for the assistance and hard work from field technicians M. Richard, A. Bledsoe, F. Gigliotti, W. White, R. Cruz, S. Hermann, and E. Foden. D. Hannon provided invaluable assistance in data processing and variable synthesis. The United States Department of Defense and Fort Bragg Military Installation provided financial support for the research.

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Associate Editor: Adam Janke.