ABSTRACT

KROEGER, ANTHONY JAMES. Multi-scale Assessment of Northern Bobwhite and White-tailed Deer Habitat Selection in Longleaf Pine Woodlands. (Under the direction of Christopher E. Moorman and Christopher S. DePerno).

Restoration of the longleaf pine ecosystem is a conservation priority throughout the southeastern United States, as is the conservation of game species such as northern bobwhite (*Colinus virginianus*) and white-tailed deer (*Odocoileus virginianus*). However, the effect of management practices commonly used in longleaf pine ecosystems on habitat for bobwhite and white-tailed deer are not fully understood. Our objectives were to determine the primary drivers of non-breeding bobwhite habitat selection and to assess the importance of hardwoods for white-tailed deer in the longleaf pine-wiregrass community on Fort Bragg Military Installation, located in the Sandhills physiographic region of North Carolina. We used radio-telemetry to locate and monitor non-breeding bobwhite from 10 Feb–22 Apr of 2016, 15 Feb–28 Apr of 2017, and 27 Jan–15 May of 2018. We used GPS collars to locate and monitor white-tailed deer continuously from 9 March 2011–31 July 2013. We used generalized linear and generalized linear mixed models to assess bobwhite habitat selection at the macrosite scale (across the study area) and at the microsite scale (the immediate vicinity of an animal), respectively, by comparing used points to available random points. We used generalized linear mixed models and step-selection functions to determine the influence of hardwood overstory, pine overstory, and understory cover on seasonal white-tailed deer habitat selection. At the microsite scale, bobwhite selected areas with greater woody understory cover. Also, bobwhite selection increased with greater forb and switchcane cover, but this effect plateaued at 65% and 50% forb and switchcane cover, respectively. At the macrosite scale, bobwhite selected areas with greater understory cover within a 200-m radius but avoided areas with >55% understory cover, as these areas were located primarily in the centers of large drainages. Bobwhite selected areas with basal area from 2–7

m^2/ha hardwoods in uplands, potentially because of the availability of mast, but avoided uplands when either pine or hardwood basal area exceeded 12 m^2/ha, likely because too high basal area is associated with increased shading and subsequent loss of understory cover. In addition, bobwhite selected uplands one growing season (defined as a minimum 2-month period falling entirely between 1 April and 1 October) post-fire regardless of burn season. Deer selected areas with greater upland hardwood overstory in fall and winter, but we detected upper thresholds for this response of 12% and 8% in fall and winter, respectively. In addition, deer selected areas with <22% upland hardwood overstory in the spring. Also, deer selected areas with greater bottomland hardwood overstory in fall and winter, but we detected an upper threshold for this response of 33% bottomland hardwood overstory in fall, suggesting that deer were not using the core areas of large bottomlands. The effect size of understory cover was considerably larger than any other variable, regardless of season, and deer generally selected areas with 20–75% understory cover. Overall, managers seeking to improve habitat quality for bobwhite in longleaf pine woodlands should focus on maintaining scattered dense woody understory cover across the landscape to provide cover during the non-breeding season. Similarly, where white-tailed deer are a priority, we suggest managers maintain 20–75% woody understory cover and 20-50% canopy closure, of which 4–7% should comprise mature oaks for mast production.

Multi-scale Assessment of Northern Bobwhite and White-tailed Deer Habitat Selection in
Longleaf Pine Woodlands

by
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DEDICATION

To my wonderful wife, Laura, for putting up with me, and to my parents for instilling in me a deep love and respect for the outdoors.

BIOGRAPHY

Tony was born and raised in Saint Louis, MO, but spent much of his childhood roaming the backwoods of the Ozarks, and hiking, camping, and fishing with his family, fostering a deep love of wildlife and the outdoors. He attended Truman State University, where he completed his Bachelor of Science and Master of Arts, Education degrees before deciding that being a teacher was a bad idea and spending the next 7 years working around the world as a wildlife research technician. In August 2017, he began working toward a Master of Science in Fisheries, Wildlife, and Conservation Biology at North Carolina State University.

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Chapter 1. Northern Bobwhite Non-breeding Habitat Selection in a Longleaf Pine Woodland

ABSTRACT

Efforts to halt the decline of northern bobwhite (*Colinus virginianus;* hereafter 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 bobwhite. We monitored radio-tagged bobwhite from 2016 to 2018 on a 165-km^2 portion of Fort Bragg Military Installation in the Sandhills physiographic region of North Carolina to determine the strongest drivers of non-breeding bobwhite habitat selection at multiple scales. We used generalized linear models 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, bobwhite strongly selected areas with greater woody understory cover. Also, bobwhite selection increased with greater forb and switchcane cover, but this effect plateaued at 65% and 50% forb and switchcane cover, respectively. At the macrosite scale, bobwhite generally selected areas with greater understory cover within a 200-m radius but avoided areas with >55% understory cover, as these areas primarily were located in the core area of large bottomlands. Bobwhite selected areas with 2–7 m^2/ha hardwoods in uplands, potentially because of the availability of mast, but avoided uplands when either pine or hardwood basal area exceeded 12 m^2/ha, likely because too high basal area is associated with increased shading and subsequent loss of understory cover. In addition, bobwhite selected uplands one growing season (defined as a minimum 2-month period falling entirely between 1 April and 1 October) post-fire regardless of burn season. Overall, managers seeking to improve habitat quality for bobwhite in longleaf pine

woodlands should employ management practices that maintain woody understory over 12 to

43% of the landscape to provide cover during the non-breeding season.

INTRODUCTION

Northern bobwhite (*Colinus virginianus*, hereafter bobwhite) populations have declined

dramatically throughout their distribution (Sauer *et al.* 2017). The reasons for this decline are

associated with habitat loss and fragmentation, largely through changes in land-use, including

urbanization, a shift to large-scale agriculture, and forest succession. Although the general

habitat requirements of bobwhite are well 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, and see Hernández *et al.* 2013 for an overview). 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). Thus, efforts to increase the bobwhite

population must include restoration of necessary compositional and structural components at

functionally appropriate scales. Understanding bobwhite habitat requirements at multiple scales

and how these requirements shift throughout the year is essential for effective management.

       The non-breeding season is a particularly stressful time for bobwhite as 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

senescent in winter, decreasing the availability and quality of cover and forage for bobwhite.

Bobwhite 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 bobwhite to travel longer distances between patches of high-

quality 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 imperative 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 a critical 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 bobwhite, these areas are only one 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 and/or retain mast and seed important to bobwhite during the non-breeding season (Eubanks and Dimmick 1974, Dietz *et al.* 2006, Masters *et al.* 2016).

Although bobwhite are considered shrubland birds, open-canopy woodlands can be managed to provide adequate woody 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 bobwhite (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 bobwhite. 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 2013). 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 1987). Conversely, infrequent and low-intensity fire may be insufficient to prevent midstory encroachment and shading that has a deleterious effect on herbaceous cover. The delicate balance of fire timing and frequency is further complicated by individual site characteristics, as 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).

Non-breeding bobwhite habitat selection 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 have examined *in situ* measurements of non-breeding site characteristics at multiple spatial scales (although see Brooke *et al.* 2015). 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. For example, management priorities at our study site revolve primarily around military training needs and meeting recovery thresholds for the federally endangered red-cockaded woodpecker (*Leuoconotopicus borealis*). Bobwhite 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 critical to

conserving and restoring bobwhite populations, as is understanding these relationships within the context of mixed conservation or land-use goals.

We examined the drivers of 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 hypothesized that bobwhite would select sites with greater woody understory cover at the microsite and macrosite scales, as well as for site characteristics that would maximize understory cover, including low basal area, low tree density, and longer time since fire. Lastly, we hypothesized that topographic position (i.e., uplands vs bottomlands) may alter selection for one or more site characteristics. Uplands and bottomlands on the study site had vastly different soils textures and moisture regimes. In addition, 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.

STUDY AREA

We evaluated bobwhite winter habitat selection on a 165-km^2 portion of Fort Bragg Military Installation (hereafter Fort Bragg) in the Sandhills physiographic region of North Carolina, USA. Fort Bragg was an active joint army and air force installation owned and managed by the U.S. Department of Defense. The Sandhills region was characterized by rolling hills with open canopy longleaf pine uplands interspersed with bottomlands or lowland drainage areas (Franklin 2008, Sorrie *et al.* 2006). Coarse sandy, well-drained soils predominated, resulting in generally

low site productivity throughout the region. The most abundant upland plant community consisted primarily of an open longleaf pine canopy, sparse hardwood subcanopy (*Quercus* spp., especially *laevis*, *margaretta*, and *marilandica*, and *Carya alba*), 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 (*Quercus* spp.). 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).

Land management at Fort Bragg primarily was aimed at maintaining sparse understories 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 (ranging from 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. Logistical constraints often resulted in management units missing a scheduled burn rotation, and in these cases, units were burned during the following dormant season (January–March). 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 *Lespedeza bicolor*, millet (*Pennisetum glaucum*), rye (*Secale cereal*),

sorghum (*Sorghum bicolor*), and showy partridge pea (*Chamaecrista fasciculata*), and others left fallow (Sorrie *et al.* 2006).

METHODS

Capture and Radio-telemetry

We captured bobwhite from Feb–Apr 2016, Jan–Apr 2017, and Jan–Apr 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 no more than 30 minutes before sunset.

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

We located individuals 3-5 times per week from 10 Feb–22 Apr of 2016, 15 Feb–28 Apr of 2017, and 27 Jan–15 May of 2018. We defined the end of the non-breeding season as the date of mean covey break-up, which we considered to be the start of the breeding season. Telemetry equipment consisted of VHF receivers and 3-element yagi directional antennas from Advanced Telemetry Systems, Isanti, MN (receiver model #R4000). We used vehicle mounted omnidirectional antennas (Laird Technologies, Chesterfield, MO and Telonics Inc., Mesa, AZ) to establish coarse locations as needed for further refinement using 3-element yagis. 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, Inc., Olathe, KS) to record locations for each individual bird, or for each covey in cases where a covey contained >1 marked bird. If we observed a mortality signal, we recovered the transmitters immediately, and used the site characteristics, bobwhite remains, and transmitter condition to determine the cause of mortality (Dumke and Pils 1973). If an individual could not be located, we continued searching in expanding areas for at least 2 more weeks.

Variable Measurement and Synthesis

We surveyed vegetation at all bobwhite or covey locations, and at random points. Random points were generated using a random bearing (1–360°) and distance (10–250 m) from each bobwhite or covey location. We used 250 meters as the limit for random distance based on the average home range size for northern bobwhite in similar vegetation types (Terhune *et al.* 2006). Where random points fell outside of vegetated areas (e.g., roads, bodies of water, military buildings, or 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 total), 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 total number of points (Rotenberry and Weins 1980, Moorman and Guynn 2001). In addition, we recorded the predominant groundcover at the base of the pole (bare ground, grass, forb, or 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 one 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. 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 derived immediate fire history by combining the number of growing seasons since fire (defined as a minimum 2-month period falling entirely between 1 April and 1 October) with the season of that most recent fire (e.g., dormant or growing season). Vegetation community type, stand basal area, and proximity to landscape features were derived from GIS layers provided by the Fort Bragg Directorate of Public Works using ArcMap (ArcGIS Desktop: Release 10.6.1, Redlands, CA: Environmental Systems Research Institute, 2018). Topographic position was calculated 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 June 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 (Andrew Plowright, ForestTools: Analyzing Remotely Sensed Forest Data, version 0.2.0, 2018). Then, we used the focal statistics tool in ArcMap to calculate 200-m radius circular moving window averages of density for trees ≥5 m in height. In addition, we calculated a 200-m radius circular moving window average of understory cover using the presence/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 we believed it to be a reasonable approximation of vegetation characteristics at the macrosite scale.

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 drastically 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. All interaction and quadratic terms were subject to removal if they proved uninformative (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 a total of 4555 random points. We evaluated 8 continuous and 3 categorical variables describing site characteristics at the macrosite scale (Table 2). We included an interaction between tree density and mean crown height, as we believed that selection would decrease with greater tree density, depending on mean crown height. We hypothesized that topographic position may interact with other drivers of habitat selection (e.g., basal area and fire history), and included interaction terms between those

variables. In addition, we included quadratic terms with all continuous variables, and all higher order terms were subject to removal 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 collinearity of continuous variables using Pearson's correlation coefficients with a $+/-0.7$ limit and examined variance inflation factors for variables with 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 (GLMMs) in the "glmmTMB" package (Brooks *et al.* 2017) in R to compare vegetation characteristics of telemetry, or "used", and random, or "available" points. We began with a maximally specified model, including all terms of the *a priori* model, all potentially informative variables and suspected interactions, as well as both random intercepts and random slopes for these terms with bird or covey 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/covey ID), and failure to include random slopes in use-availability study designs may results 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 (REML) 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 lowest AICc

score and chose the most parsimonious model within 2 ΔAICc of the top ranked model (Zuur *et

al.* 2008). Finally, we re-fit the chosen model using REML to ensure accurate estimates (Zuur *et

al.* 2009).

For the macrosite analysis, we used the 'lme4' (Bates *et al.* 2015) and 'brglm2'

(Kosmidis *et al.* 2019) packages in R and remained in the binomial GLM framework, 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 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 lowest Akaike's Information

Criterion, corrected for small sample size (AICc) (Zuur *et al.* 2008). If a model within 2 ΔAICc

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. Finally, we re-fit the chosen

model using the median bias-reduced adjustment method outlined in Kosmidis *et al.* (2019)

because one of our categorical variables had levels for which events were rare, resulting in complete separation.

RESULTS

Captures, Radio-telemetry, and Mortality

In 2016, we captured 59 individuals over 3420 trap nights, comprising 52 juveniles and 7 adults. In 2017, we captured 71 individuals over 9646 trap nights, comprising 50 juveniles and 21 adults. In 2018, we captured 86 individuals over 8356 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 April), 216 locations for 34 individuals or coveys during the 2017 non-breeding season (15 Feb–28 April), and 493 locations for 16 individuals or coveys during the 2018 non-breeding season (27 Jan–1 May). For all 3 seasons, we estimated cause-specific mortality from field evidence as either avian, mammalian, or unknown predation (evidenced by blood or feathers present at transmitter site, but inconclusive as to cause). We documented 17 mortalities during the 2016 non-breeding season, including mammalian predation (11, 65%), avian predation (2, 12%) and predation from unknown causes (4, 24%). Seven individuals either left the study area or were lost because of transmitter malfunction. During the 2017 non-breeding season, we documented 19 mortalities, including 10 from unknown predation (58%), 5 from avian predation (26%), and 3 from mammalian predation (16%). Three individuals either left the study area in 2017 or were lost due to transmitter malfunction. We documented 27 mortalities during the 2018 non-breeding season, including avian predation (13, 52%), mammalian predation (9, 36%), and unknown predation (3, 12%). Fourteen individuals either left the study area or were lost due to transmitter malfunction during the 2018 non-breeding season.

Habitat Selection–Microsite

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). We present all results for variables of interest with other variables held at their respective median (for continuous variables) or reference values (for categorical variables). Bobwhite 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 (Figure 1). 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 (Figure 1). Bobwhite 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 (Figure 1). The relative probability of selection decreased with increasing pine and hardwood basal area, and bobwhite avoided areas with >15 m^2/ha pines and >6 m^2/ha hardwoods (Figure 1).

Habitat selection – Macrosite

At the macrosite scale, the top model included proximity to wildlife opening, topographic class, growing seasons since fire, season of most recent fire, tree density, and quadratic effects for understory cover and pine and hardwood stand basal area (Table 4). We documented interactions between topographic class and growing seasons/season of most recent fire, and basal area. We present all results for variables of interest with other variables held at their respective median (for continuous variables) or reference values (for categorical variables). The relative probability

of selection decreased as distance to wildlife opening increased, and bobwhite selected areas <225 m and avoided areas >500 m from a wildlife opening (Figure 2). Bobwhite selected uplands with 2–7 m^2/ha hardwood basal area but avoided uplands when either pine or hardwood basal area exceeded 12m^2/ha (Figure 2). Conversely, bobwhite selected bottomlands with total basal area 3–25 m^2/ha and avoided areas with >35 m^2/ha. Understory cover, defined as 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. Consequently, bobwhite avoided areas with <8% or >50% understory cover and selected areas with 12–43% understory cover. Also, increased tree density was negatively associated with selection, and bobwhite selected areas with <300 trees/ha and avoided areas with >350 trees/ha (Figure 2). Finally, bobwhite selected areas one growing season since fire regardless of burn season or topographic position, as well as upland areas 3+ growing seasons since fire if the recent fire occurred in the dormant season (Figure 3).

DISCUSSION

Woody understory cover had the largest standardized effect size at the microsite scale, and understory cover was one of the strongest predictors of macrosite selection, further reinforcing the importance of woody understory cover for northern bobwhite across its range (Yoho and Dimmick 1972, Kopp *et al.* 1998, Palmer *et al.* 2012, Janke and Gates 2013, Brooke *et al.* 2015, Rosche *et al.* 2019). Although bobwhite 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 bottomlands. Although these areas provide cover, they have little food compared to the edges 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 critical 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, bobwhite did show strong selection for closer proximity to wildlife openings at the macrosite scale, indicating tree density in the woodlands limited habitat quality for bobwhite. Wildlife openings contained less tree cover and correspondingly greater herbaceous and woody cover, and likely had greater available food. In addition, the majority of areas >500 m from a wildlife opening at our study site were centrally located in drop zones or large bottomlands, both areas bobwhite may be expected to avoid. Drop zones in particular were burned and/or mowed annually or biennially, and often lacked cover and food. Understory shrubs and hardwood sprouts maintain structure during the winter, providing critical 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 bobwhite during the fall and winter months.

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 bobwhite, 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 research has linked extensive coverage of sericea lespedeza to low fecundity and survival of bobwhite, and bobwhite 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 likely was biased because of dense sericea lespedeza that may have negatively influenced usability of those areas by bobwhite.

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 likely have similar fire histories as used points. Cram *et al.* (2002) reported bobwhite selected areas 3 years post fire where woody cover was most prevalent in the Ouachita National Forest, 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, bobwhite at our site selected areas one 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

bobwhite during the following growing season. With increased time since last burn, wiregrass becomes matted, reducing cover and restricting movement for wildlife (Burke 2008, Taillie *et al*. 2015). However, even in areas >1 growing season since fire, wiregrass was the most abundant, albeit relatively poor, groundcover available to bobwhite. Thus, although greater grass cover was positively associated with microsite selection in uplands, that association was likely because of the sparsity of available woody understory cover rather than any reliance of bobwhite on grass cover specifically. Although bobwhite selected areas one growing season post fire in uplands regardless of season of burning, they avoided uplands burned in the same dormant season that locations were collected, likely because of the reduction in herbaceous and woody understory cover in recently burned areas and lack of regrowth during the dormant season. In addition, bobwhite 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 critical cover for bobwhite in uplands (White *et al.* 1990, Boyer 1993, Brockway and Lewis, 1997, Drewa *et al.* 2006, Robertson and Hmielowski 2013). Conversely, bobwhite selected bottomlands most recently burned during the growing season. Regardless, it is impractical and unrealistic to manage bottomlands differently from their 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, bobwhite 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. However, at the macrosite scale, selection for basal area was significantly influenced by topographic position (i.e., bottomlands or uplands). Although the

probability of selection reached a maximum at 14 m^2/ha in bottomlands, bobwhite selected

bottomlands with a wide range of basal area. Fertile bottomlands may support sufficient

understory cover for bobwhite during the nonbreeding season, even at relatively high basal area,

and bobwhite did not begin to avoid bottomlands until total basal area exceeded 35 m^2/ha, when

overstory cover was likely 100%. Additionally, some bottomland hardwoods provide mast

(swamp bay and oak species, especially *Quercus nigra*) that may partially compensate for any

loss of understory density from overstory shading. Crop surveys from bobwhite 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 (Unpublished report: Wildlife Branch, Fort Bragg

Directorate of Public Works). In uplands, bobwhite selection weakly declined with increasing

pine basal area, but increased with upland hardwood basal area up to 4 m^2/ha before declining,

likely because of mast provided by mature hardwoods. Similarly, bobwhite avoided areas with

particularly high tree density, as these areas may have been unable to support sufficient

understory cover for bobwhite.

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, Brooke *et al.* 2015,

Rosche *et al.* 2019). However, greater woody understory cover is not likely in open-canopy,

pine-dominated woodlands under a 3-year fire return interval. Understory composition is dictated

by a combination of factors, 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 bobwhite by altering fire regimes. Although a 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 bobwhite on many sites at Fort Bragg. The range of acceptable basal area for Bachman's sparrow, red-cockaded woodpecker, and northern bobwhite 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.

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 m^2/ha. Within this limit, we suggest upland hardwood basal area up to 4 m^2/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. Bobwhite selected areas one growing season since fire in uplands during the non-breeding season, and prior research has indicated selection for 2 growing seasons since fire for nesting (Rosche 2018). Hence, a variable return interval averaging 3 years should maximize the food and cover resources for bobwhite during the non-breeding and breeding seasons, provided managers incorporate variation in frequency sufficient to allow regeneration of woody species, particularly when bobwhite are a priority. Variation in prescribed fire seasonality and frequency will improve habitat quality for northern bobwhite 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).

LITERATURE CITED

Allen, R., and D. B. Burt. 2014. Vegetative characteristics of Bachman's sparrow habitat in the west gulf coastal plain. Southeastern Naturalist 13:41–51.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Atuo, F. A., and T. J. O'Connell. 2017. The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. Ecology and Evolution 7:4782–4793.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 1.

Bowling, S. A., C. E. Moorman, C. S. DePerno, and B. Gardner. 2014. Influence of landscape composition on northern bobwhite population response to field border establishment. Journal of Wildlife Management 78:93–100.

Boyer, W. D. 1993. Season of burn and hardwood development in young longleaf pine stands. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, General Technical Report SO-93, New Orleans, Louisiana, USA.

Brandon, A. L., D. J. Gibson, and B. A. Middleton. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. Biological Invasions 6:483–493.

Brennan, L. A. 1991. How can we reverse the northern bobwhite population decline? Wildlife Society Bulletin 19:544–555.

Brennan, L. A., R. T. Engstrom, W. E. Palmer, S. M. Hermann, G. A. Hurst, L. W. Burger, and C. L. Hardy. 1998. Whither wildlife without fire? Pages 402–414 *in* Transactions of the 63rd North American Wildlife and Natural Resources conference. Wildlife Management Institute, Orlando, FL.

Brennan, L. A., F. Hernández, and D. Williford. 2014. Northern Bobwhite (Colinus virginianus), version 2.0. A. F. Poole, editor. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bna.397>. Accessed 31 May 2019.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167–183.

Brooke, J. M., E. P. Tanner, D. C. Peters, A. M. Tanner, C. A. Harper, P. D. Keyser, J. D. Clark, and J. J. Morgan. 2017. Northern bobwhite breeding season ecology on a reclaimed surface mine. The Journal of Wildlife Management 81:73–85.

Brooke, J. M., D. C. Peters, A. M. Unger, E. P. Tanner, C. A. Harper, P. D. Keyser, J. D. Clark, and J. J. Morgan. 2015. Habitat manipulation influences northern bobwhite resource selection on a reclaimed surface mine. Journal of Wildlife Management 79:1264–1276.

Brooks, M., E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378.

Bugg, R. L., and J. D. Dutcher. 1989. Warm-season cover crops for pecan orchards: Horticultural and entomological implications. Biological Agriculture & Horticulture 6:123–148.

Burger Jr, L. W., T. V. Dailey, M. R. Ryan, and E. Kurzejeski. 2017. Effect of temperature and wind on metabolism of northern bobwhite in winter. National Quail Symposium Proceedings 8:300–307.

Burke, J. D., M. J. Chamberlain, and J. P. Geaghan. 2008. Effects of understory vegetation management on brood habitat for northern bobwhites. Journal of Wildlife Management 72:1361–1368.

Chamberlain, E., R. D. Drobney, and T. V. Dailey. 2002. Winter macro-and microhabitat use of winter roost sites in Central Missouri. National Quail Symposium Proceedings 5:140–145.

Cram, D. S., R. E. Masters, F. S. Guthery, D. M. Engle, and W. G. Montague. 2002. Northern bobwhite population and habitat response to pine-grassland restoration. Journal of Wildlife Management 66:1031–1039.

Davison, V. E. 1958. A summary and reclassification of bobwhite foods. Journal of Wildlife Management 22:437–439.

Dietz, D. R., R. M. Whiting, N. E. Koerth, and J. P. Carroll. 2006. Winter food habits and preferences of northern bobwhites in east Texas. Pages 160–171 *in* Gamebird 2006: Quail VI and Perdix XII. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA.

Dixon, K. R., M. A. Horner, S. R. Anderson, W. D. Henriques, D. Durham, and R. J. Kendall. 1996. Northern bobwhite habitat use and survival on a South Carolina plantation during winter. Wildlife Society Bulletin 24:627–635.

Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83:755–767.

Drewa, P. B., J. M. Thaxton, and W. J. Platt. 2006. Responses of root-crown bearing shrubs to differences in fire regimes in *Pinus palustris* (longleaf pine) savannas: Exploring old-growth questions in second-growth systems. Applied Vegetation Science 9:27–36.

Dumke, R. T., and C. M. Pils. 1973. Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. Dept. of Natural Resources, Madison, Wisconsin, USA.

Engstrom, R. T., and W. E. Palmer. 2005. Two species in one ecosystem: Management of northern bobwhite and red-cockaded woodpecker in the Red Hills. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-191, Albany, CA.

Eubanks, T. R., and R. W. Dimmick. 1974. Dietary patterns of bobwhite quail on Ames plantation. University of Tennessee Agricultural Experiment Station, Bulletin 534, Knoxville, Tennessee, USA.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: Problem, red herring or opportunity? Philosophical transactions of the Royal Society of London. Series B, Biological Sciences 365:2233–2244.

Folk, T. H., R. R. Holmes, and J. B. Grand. 2007. Variation in northern bobwhite demography along two temporal scales. Population Ecology 49:211–219.

Fox, J. 2011. An R companion to applied regression. SAGE Publications, Thousand Oaks, California, USA.

Franklin, R. M. 2008. Stewardship of longleaf pine forests: A guide for landowners. Longleaf Alliance, Solon Dixon Forestry Education Center, Andalusia, Alabama, USA.

Gates, R. J., A. K. Janke, and M. R. Liberati. 2012. Demographic analysis of a declining northern bobwhite population in southwestern Ohio. National Quail Symposium Proceedings 7:11.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441–476.

Guthery, F. S. 2000. On bobwhites. Texas A&M University Press, College Station, Texas, USA.

Harper, C. A., G. E. Bates, M. P. Hansbrough, M. J. Gudlin, J. P. Gruchy, and P. D. Keyser. 2007. Native warm-season grasses: Identification, establishment and management for wildlife and forage production in the mid-South. University of Tennessee Extension, Institute of Agriculture, Knoxville, Tennessee, USA.

Harper, C. A., and J. P. Gruchy. 2009. Eradicating tall fescue and other non-native perennial cool-season grasses for improved early successional wildlife habitat. Pages 87–116 *in* L. W. Burger Jr and K. O. Evans, editors. Managing working lands for northern bobwhite: the USDA NRCS Bobwhite Restoration Project. U.S. Department of Agriculture, Washington, D.C., USA.

Haywood, J. D. 2009. Eight years of seasonal burning and herbicidal brush control influence sapling longleaf pine growth, understory vegetation, and the outcome of an ensuing wildfire. Forest Ecology and Management 258:295–305.

Haywood, J. D., F. L. Harris, H. E. Grelen, and H. A. Pearson. 2001. Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. Southern Journal of Applied Forestry 25:122–130.

Hernández, F., L. A. Brennan, S. J. DeMaso, J. P. Sands, and D. B. Wester. 2013. On reversing the northern bobwhite population decline: 20 years later. Wildlife Society Bulletin 37:177–188.

Hiers, J. K., R. Wyatt, and R. J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? Oecologia 125:521–530.

Janke, A. K., and R. J. Gates. 2013. Home range and habitat selection of northern bobwhite coveys in an agricultural landscape. Journal of Wildlife Management 77:405–413.

Janke, A. K., R. J. Gates, and T. M. Terhune. 2015. Habitat influences northern bobwhite survival at fine spatiotemporal scales. The Condor: Ornithological Applications 117:41–52.

Janke, A. K., T. M. Terhune, R. J. Gates, and C. R. Long. 2017. Northern bobwhite population responses to winter weather along their northern range periphery. Wildlife Society Bulletin 41:479–488.

Knapp, E. E., B. L. Estes, and C. N. Skinner. 2009. Ecological effects of prescribed fire season: A literature review and synthesis for managers. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-224, Albany, CA.

Kopp, S. D., F. S. Guthery, N. D. Forrester, and W. E. Cohen. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. Journal of Wildlife Management 62:884–895.

Kosmidis, I., E. C. Kenne Pagui, and N. Sartori. 2019. Mean and median bias reduction in generalized linear models. Statistics and Computing.

Lashley, M. A., M. C. Chitwood, C. A. Harper, C. S. DePerno, and C. E. Moorman. 2015. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology 11:62–79.

Lohr, M., B. M. Collins, P. M. Castelli, and C. K. Williams. 2011. Life on the edge: Northern bobwhite ecology at the northern periphery of their range. Journal of Wildlife Management 75:52–60.

Masters, R. E., W. G. Montague, and D. S. Cram. 2016. Northern bobwhite autumn and winter food habits in restored pine–bluestem habitats. Wildlife Society Bulletin 40:300–309.

McKenzie, D. F. 2009. Taking the northern bobwhite conservation initiative to the next level. National Quail Symposium Proceedings 16–23:3.

Moorman, C. E., and D. C. Guynn Jr. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. Ecological Applications 11:1680–1691.

Newlon, C. F., T. S. Baskett, R. P. Breitenbach, and J. A. Stanford. 1964. Sustaining values of emergency foods for bobwhites. Journal of Wildlife Management 28:532–542.

Ostertag, R., and E. S. Menges. 1994. Patterns of reproductive effort with time since last fire in Florida scrub plants. Journal of Vegetation Science 5:303–310.

Pagui, E. C. K., A. Salvan, and N. Sartori. 2017. Median bias reduction of maximum likelihood estimates. Biometrika 104:923–938.

Palik, B. J., R. J. Mitchell, and J. K. Hiers. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: Balancing complexity and implementation. Forest Ecology in the next Millennium : Putting the long view into Practice 155:347–356.

Palmer, W. E., D. C. Sisson, S. D. Wellendorf, A. M. Bostick III, T. M. Terhune, and T. L. Crouch. 2012. Habitat selection by northern bobwhite broods in pine savanna ecosystems. National Quail Symposium Proceedings 7:108–112.

Pausas, J. G., and J. E. Keeley. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. The New Phytologist 204:55–65.

Peters, D. C., J. M. Brooke, E. P. Tanner, A. M. Unger, P. D. Keyser, C. A. Harper, J. D. Clark, and J. J. Morgan. 2015. Impact of experimental habitat manipulation on northern bobwhite survival. Journal of Wildlife Management 79:605–617.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecological Applications 11:914–927.

Robel, R. J., A. R. Bisset, T. M. Clement, A. D. Dayton, and K. L. Morgan. 1979. Metabolizable energy of important foods of bobwhites in Kansas. Journal of Wildlife Management 43:982–987.

Robertson, K. M., and T. L. Hmielowski. 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174:765–776.

Rosche, S.B. 2018. Nesting ecology of northern bobwhite in the presence of early growing-season prescribed fire. Thesis, North Carolina State University, Raleigh, North Carolina, USA.

Rosche, S. B., C. E. Moorman, K. Pacifici, J. G. Jones, and C. S. DePerno. 2019. Northern bobwhite breeding season habitat selection in fire-maintained pine woodland. Journal of Wildlife Management 83:1226-1236.

Rosene, W. 1969. The bobwhite quail: Its life and management. Rutgers University Press, New Brunswick, N.J.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate analysis. Ecology 61:1228–1250.

Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. Journal of Wildlife Management 72:970–982.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. The North American breeding bird survey, results and analysis 1966 - 2017. U.S. Geological Survey, Patuxent Wildlife Research Center, Version 2.07.2017 Laurel, MD, USA.

Schielzeth, H., and W. Forstmeier. 2009. Conclusions beyond support: overconfident estimates in mixed models. Behavioral ecology : official journal of the International Society for Behavioral Ecology 20:416–420.

Seckinger, E. M., L. W. Burger, R. Whittington, A. Houston, and R. Carlisle. 2008. Effects of landscape composition on winter survival of northern bobwhites. Journal of Wildlife Management 72:959–969.

Singh, A., T. C. Hines, J. A. Hostetler, H. F. Percival, and M. K. Oli. 2011. Patterns of space and habitat use by northern bobwhites in south Florida, USA. European Journal of Wildlife Research 57:15–26.

Sorrie, B. A., J. B. Gray, and P. J. Crutchfield. 2006. The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71:129–161.

Sparks, J. C., R. E. Masters, D. M. Engle, M. W. Palmer, and G. A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science 9:133–142.

Sparks, J. C., R. E. Masters, D. M. Engle, M. E. Payton, and G. A. Bukenhofer. 1999. Influence of fire season and fire behavior on woody plants in red-cockaded woodpecker clusters. Wildlife Society Bulletin (1973-2006) 27:124–133.

Stoddard, H. L. 1931. The bobwhite quail: Its habits, preservation and increase. Charles Scribner's Sons, New York, New York, USA.

Swanson, D. L., and D. P. Weinacht. 1997. Seasonal effects on metabolism and thermoregulation in northern bobwhite. The Condor: Ornithological Applications 99:478–489.

Taillie, P., C. E. Moorman, and M. N. Peterson. 2015. The relative importance of multiscale factors in the distribution of Bachman's sparrow and the implications for ecosystem conservation. The Condor 117:137-146.

Tanner, E. P., R. D. Elmore, S. D. Fuhlendorf, C. A. Davis, D. K. Dahlgren, and J. P. Orange. 2017. Extreme climatic events constrain space use and survival of a ground-nesting bird. Global Change Biology 23:1832–1846.

Terhune, T. M., D. C. Sisson, H. L. Stribling, and J. P. Carroll. 2006. Home range, movement, and site fidelity of translocated northern bobwhite (*Colinus virginianus*) in southwest Georgia, USA. European Journal of Wildlife Research 52:119–124.

Unger, A. M., E. P. Tanner, C. A. Harper, P. D. Keyser, F. T. Van Manen, J. J. Morgan, and D. L. Baxley. 2015. Northern bobwhite seasonal habitat selection on a reclaimed surface coal mine in Kentucky. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:235–246.

U.S. Fish and Wildlife Service. 2003. Recovery plan for the red-cockaded woodpecker (*Picoides borealis*): Second revision. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate. 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. Forest Ecology and Management 390:187–202.

Waldrop, T. A., D. H. van Lear, F. T. Lloyd, and W. R. Harms. 1987. Long-term studies of prescribed burning in loblolly pine forests of the southeastern coastal plain. U.S. Department of Agriculture, Forest Service, Southern Research Station, General Technical Report SE-45, Asheville, North Carolina, USA.

White, D. L., T. A. Waldrop, and S. M. Jones. 1990. Forty years of prescribed burning on the Santee fire plots: Effects on understory vegetation. U.S. Department of Agriculture, Forest Service, Southern Research Station, General Technical Report SE-69, Asheville, North Carolina, USA.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Williams, C. K., F. S. Guthery, R. D. Applegate, and M. J. Peterson. 2004. The northern bobwhite decline: Scaling our management for the twenty-first century. Wildlife Society Bulletin 32:861–869.

Williams, C. K., R. S. Lutz, R. D. Applegate, and D. H. Rusch. 2000. Habitat use and survival of northern bobwhite (Colinus virginianus) in cropland and rangeland ecosystems during the hunting season. Canadian Journal of Zoology 78:1562–1566.

Williams, C., B. Sandercock, B. Collins, M. Lohr, and P. Castelli. 2012. A Mid-Atlantic and a national population model of northern bobwhite demographic sensitivity. National Quail Symposium Proceedings 7:163–172.

Yoho, N. S., and R. W. Dimmick. 1972. Habitat utilization by bobwhite quail during winter. National Quail Symposium Proceedings 1:90–99.

Zuur, A. F., editor. 2009. Mixed effects models and extensions in ecology with R. Statistics for biology and health, Springer, New York, NY.

Zuur, A. F., G. M. Smith., and E. N. Ieno. 2008. Analyzing ecological data. Springer, New York, New York, USA.

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 due to correlation or collinearity are noted with *.

Parameter Description	Range/Levels	Mean	Median	SD
Canopy cover (20% increments)	1, 2, 3, 4, 5	n/a	n/a	n/a
Season (Dormant: D, Growing: G) and growing seasons (0, 1, 2, 3+) since last fire	D0, D1, D2, D3+, G0, G1, G2, G3+	n/a	n/a	n/a
Topographic position	Bottomlands, Uplands	n/a	n/a	n/a
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	34.189	23.81	31.27
Forb understory (%)	0–100	12.01	4.76	18.05
Switchcane understory (%)	0–95.24	8.18	0	19.02
Distance to wildlife opening (m)	0–1417.89	337.68	299.40	260.72
Distance to riparian area (m)*	0–521.04	124.67	79.58	130.71
Days since fire*	2–2198	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	6.887	7.80
Hardwood basal area (m^2/ha)	0–45.91	3.57	0.00	6.07

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 due to correlation or collinearity are noted with *.

Parameter Description	Range/Levels	Mean	Median	SD
Season (Dormant: D, Growing: G) and growing seasons (0, 1, 2, 3+) since last fire	D0, D1, D2, D3+, G0, G1, G2, G3+	n/a	n/a	n/a
Topographic position	Bottomlands, Uplands	n/a	n/a	n/a
Vegetation community*	Bottomlands, Ecotone, Large Openings, Upland Pine, Other	n/a	n/a	n/a
Distance to wildlife opening (m)	0–2493.36	482.04	385.3	391.02
Distance to riparian area (m)*	0–1339.81	152.19	107.94	164.35
Mean crown height (m)	0–24.50	15.89	16.62	4.27
Trees per hectare	0–603.7	271.10	271.1	101.74
Days since fire*	0–2659	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

Table 3. Model parameters, coefficients, standard errors, and random effects for 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. Random effects were conditioned on Bird/Covey ID.

Parameter	β	SE
Uplands	–0.187	0.125
Pine basal area	–0.168	0.057
Hardwood basal area	–0.194	0.058
Woody understory	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
Random effects	**Var**	**SD**
Random slope - Woody understory |Bird/Covey ID	0.108	0.329

Table 4. Model parameters, coefficients, and standard errors for top model predicting northern bobwhite non–breeding season habitat selection at the macrosite scale. Fort Bragg Military Installation, North Carolina, USA, 2016–2018. G1, D2, etc. refer to recent fire, coded as season of (G=Growing, D=Dormant) and growing seasons since (1=1 growing season, etc.) most recent fire. Reference level for topographic class was Bottomlands. Reference level for recent fire was G3+.

Parameter	β	SE
Uplands	–0.830	0.427
Bottomland basal area	1.099	0.279
Bottomland basal area^2	–0.313	0.077
Upland pine basal area	–0.455	0.079
Upland hardwood basal area	0.663	0.110
Upland hardwood basal area^2	–0.297	0.057
Understory cover	0.755	0.081
Understory cover ^{2}	–0.421	0.050
Distance to wildlife opening	–0.691	0.063
Trees per hectare	–1.094	0.081
Trees per hectare^2	–0.265	0.041
D0	–1.008	0.316
Uplands : D0	0.793	0.385
D1	–0.311	0.234
Uplands : D1	1.458	0.288
D2	–5.586	2.476
Uplands : D2	6.015	2.490
D3+	–3.185	0.715
Uplands : D3+	4.411	0.738
G0	–3.188	2.593
Uplands : G0	3.341	2.699
G1	–0.526	0.198
Uplands : G1	1.472	0.253
G2	–0.885	0.213
Uplands : G2	0.903	0.286
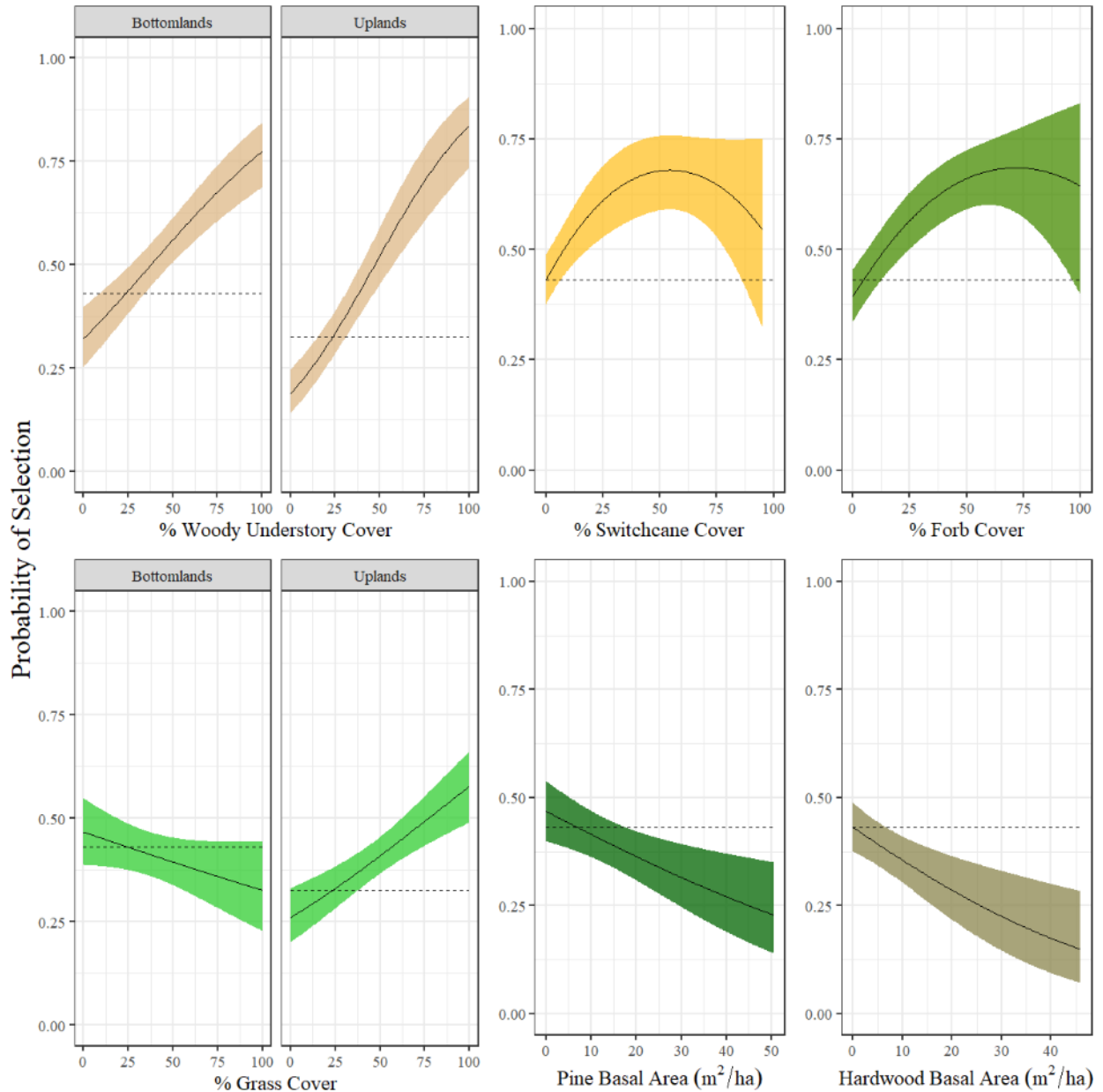
Figure 1. Probabilities and 95% CI for predictors of microsite selection for non-breeding northern bobwhite. Fort Bragg Military Installation, North Carolina, USA, 2016–2018. All plots were generated with all other variables held at their respective median values. The horizontal dashed line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.
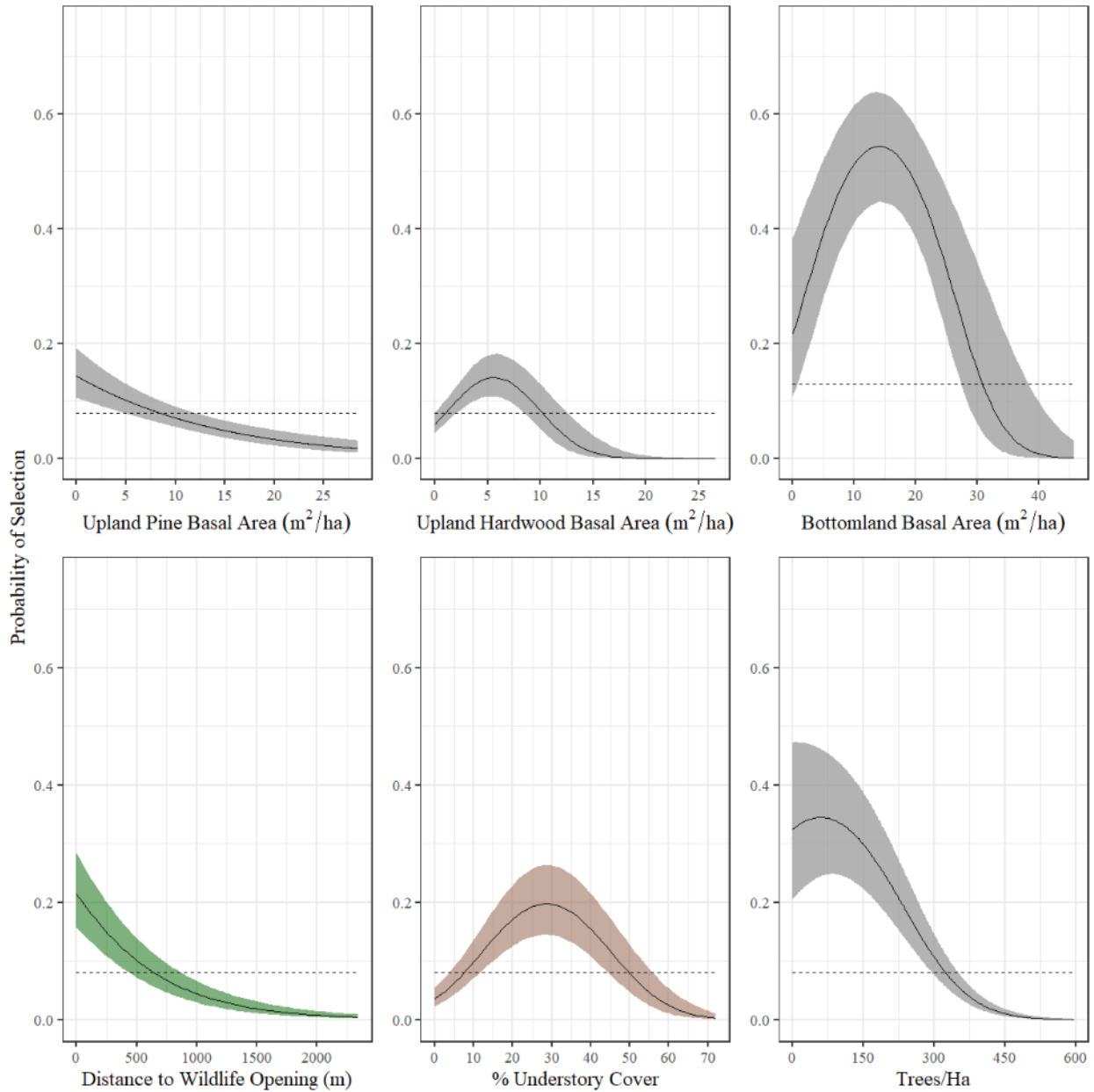
Figure 2. Probabilities and 95% CI for continuous predictors of macrosite selection for non-breeding northern bobwhite. Fort Bragg Military Installation, North Carolina, USA, 2016–2018. All plots were generated with all other variables held at their respective median values. The horizontal dashed line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.
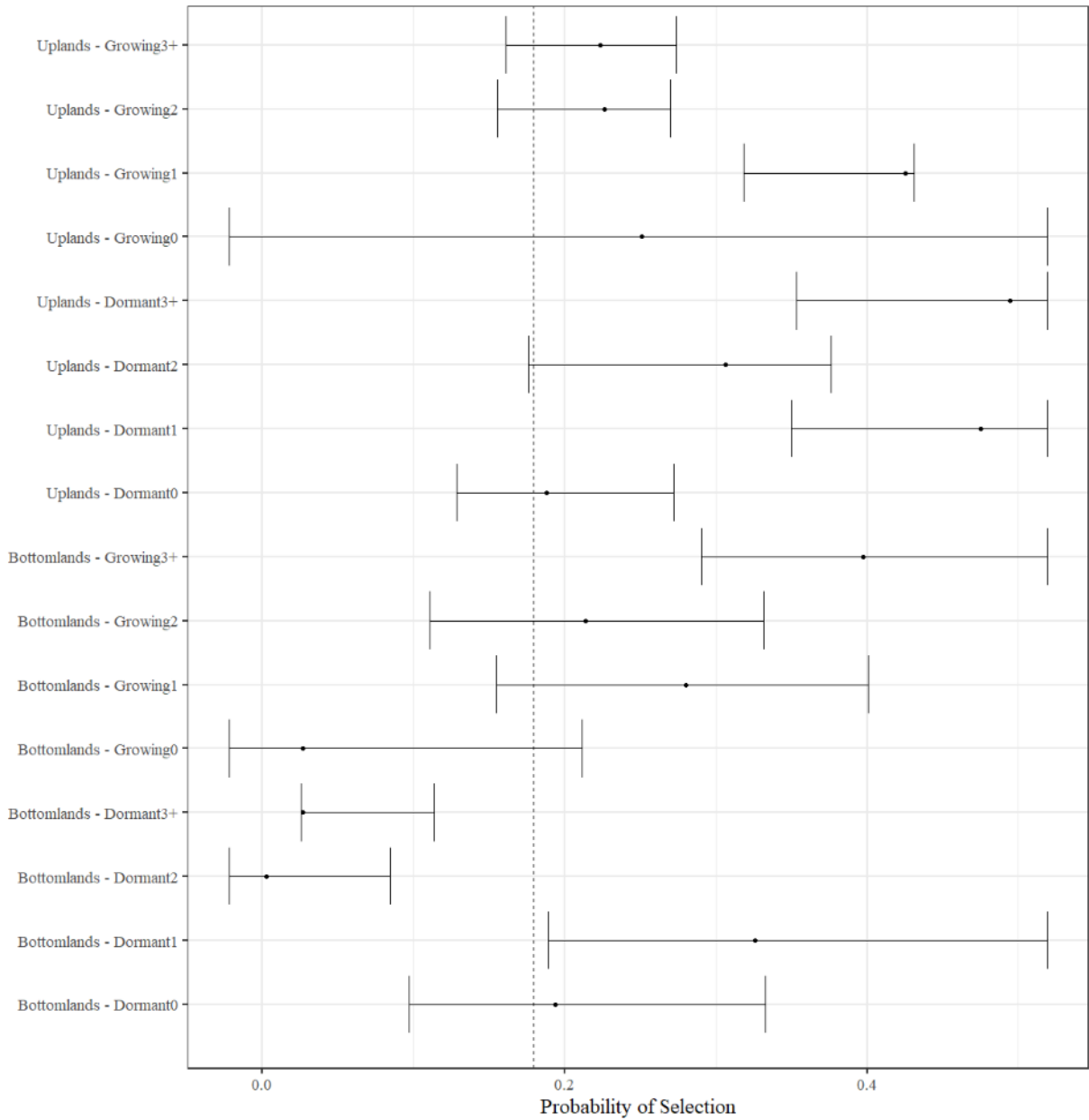
Figure 3. Estimated marginal mean probabilities and pairwise comparisons for categorical predictors of macrosite selection for non-breeding northern bobwhite. Fort Bragg Military Installation, North Carolina, USA, 2016–2018. Overlapping error bars indicate non-significant pairwise comparisons. The vertical dashed line represents the overall probability of selection, with probabilities to the right and left of this line indicating positive and negative selection (avoidance) for the factor of interest, respectively.

Chapter 2. Are Overstory Hardwoods Important for White-tailed Deer in Longleaf Pine Woodlands?

ABSTRACT

Restoration of the longleaf pine ecosystem is a conservation priority throughout the southeastern United States, but the role of hardwoods in providing food and cover for wildlife within this system is poorly understood. We investigated white-tailed deer (*Odocoileus virginianus*) movement and habitat selection in relation to overstory hardwood distribution in a longleaf pine ecosystem at Fort Bragg Military Installation in the Sandhills physiographic region of North Carolina from March 2011–July 2013. We monitored GPS-collared female white-tailed deer and used generalized linear mixed models and step-selection functions to determine the influence of overstory composition and understory cover on seasonal white-tailed deer habitat selection. Deer selected areas with greater upland hardwood overstory in fall and winter, but we detected upper thresholds of 12% and 7% for this response, respectively. In addition, deer selected areas with <22% upland hardwood overstory in the spring. Deer also selected areas with greater bottomland hardwood overstory in fall and winter, but we detected an upper threshold for this response of 33% bottomland hardwood overstory in fall. The effect size of understory cover, defined as lidar-classified vegetation with eight <2 m, was considerably larger than any other variable, regardless of season, and deer consistently selected areas with 20–75% understory cover. Thus, we suggest that deer managers in longleaf pine woodlands focus primarily on maintaining woody understory cover from 20–75%, which could include the dense understory along drainages and other moist soil areas. In addition, we suggest managers maintain 20-50% total canopy closure, of which 4–7% should comprise mature upland hardwood overstory for mast production.

INTRODUCTION

The longleaf pine (*Pinus palustris*) ecosystem harbors some of the highest biodiversity on the continent and covered nearly 37 million ha at its peak (Frost *et al.* 2006). Widespread logging, forest conversion to agriculture, and mesophication and canopy closure from fire suppression reduced the longleaf pine ecosystem to ~600,000 ha of its former extent (Frost 1993, Gilliam and Platt 1999, Brockway *et al.* 2005). Hence, restoration of the longleaf pine ecosystem is a priority for managers across the southeastern United States. Restoration efforts commonly attempt to return sites to their "historical" state (Jose *et al.* 2006), but without a clear understanding of what "historical" means in a dynamic, fire-climax system, restoration efforts are likely to be ineffective (Chapman 1932, Hobbs and Harris 2001, Van Lear 2005). Restoring the longleaf pine ecosystem requires more than a static picture of homogenous "park-like" savannah gleaned from historical accounts, and managers should incorporate spatial and temporal variability in structure, composition, and fire regime into their efforts (Van Lear *et al.* 2005, Hiers *et al.* 2014, Mitchell and Duncan 2009, Lashley *et al.* 2015a).

Although longleaf pine restoration typically includes hardwood reduction, hardwoods historically were an ecologically important component of the longleaf pine ecosystem and served a variety of ecosystem functions (Frost 1993, Greenberg and Simons 1999, Jacqmain *et al.* 1999, Brockway *et al.* 2005, Hanberry *et al.* 2018). Upland midstory hardwoods serve as nursery species for longleaf pine, mitigating the effects of low precipitation and facilitating longleaf pine seedling survival (Loudermilk *et al.* 2016). In addition, upland hardwoods alter the realized fire regimes of their surroundings, alternatively increasing or decreasing fire longevity and intensity depending on conditions. For example, burning turkey oak (*Quercus laevis*) leaves reach lower maximum temperatures than longleaf pine needles, and broadleaf litter collects dew to a greater

degree than pine needles, potentially resulting in less intense fires or incomplete ignition where fuel moisture remains high (Williamson and Black 1981, Matthews 2014, Kreye *et al.* 2018). Conversely, turkey oak leaves have nearly the energy content of pine needles, and burn with high intensity relative to other, more mesic oak species (Kane *et al.* 2008). In addition, oak leaves curl as they dry, holding other litter above the ground and facilitating a dry, elevated litter bed, greater fuel loads, and more intense fires than pine needles alone (Rebertus *et al.* 1989a, Rebertus *et al.* 1989b, Wenk *et al.* 2011). The influence of upland hardwoods on fire behavior thus variably favors fire-tolerant or fire-sensitive species, contributing to overall species diversity.

In addition to contributing to plant community diversity and heterogeneity, hardwoods provide essential food and cover to a variety of wildlife species in the longleaf pine ecosystem. Sherman's fox squirrel (*Sciurus niger shermani*) require a mix of mature hardwoods and pines for nesting and daytime refugia, and hardwoods provide seasonal hard and soft mast (Perkins *et al.* 2008). Hardwood mast is an important food source for rodent populations, including white-footed mice (*Peromyscus leucopus*) and deer mice (*Peromyscus maniculatus*), prey for raptors, snakes, and other mesopredators (Clotfelter *et al.* 2006). Cavity-nesting birds represent a significant portion of the avian biodiversity present in the longleaf pine ecosystem, many of which are known to excavate or use hardwoods for nesting or foraging (Blanc and Walters 2008). Likewise, hardwood mast is important for game species such as wild turkey (*Meleagris gallopavo silvestris*) and northern bobwhite (*Colinus virginianus*) in fall and winter, and hardwoods may provide roosting, escape, and thermal cover for turkey in spring and summer (Streich *et al.* 2015, Little *et al.* 2016, Kroeger 2019).

White-tailed deer (*Odocoileus virginianus*) are the only native large herbivore currently present in the longleaf pine woodlands (Means 2006), and deer herbivory may help maintain open midstories characteristic of longleaf pine woodlands by delaying succession (Bressette *et al.* 2012, DiTommaso *et al.* 2014). Although white-tailed deer overabundance can have detrimental effects on plant communities (McShea and Rappole 1992, Waller and Alverson 1997, Rooney 2001, Rooney and Waller 2003, Côté *et al.* 2004), much of the longleaf pine range is unable to support herd densities as high as other regions because poor soil productivity limits the availability of high-quality forage (Shea *et al.* 1992, Shea and Osborne *et al.* 1995, Keyser *et al.* 2005, Diefenbach and Shea 2011, Lashley *et al.* 2015b). Despite the overall low quality of longleaf pine woodlands for deer, the species is an economically and culturally important game animal, and a critical source of funding for state wildlife agencies (Heffelfinger *et al.* 2013). Consequently, management for deer is often a priority on properties with longleaf pine woodlands.

Although the importance of hard mast to white-tailed deer is well-documented across the species' distribution (Korschgen 1962, Lay 1965, Nixon 1970, Johnson *et al.* 1995, Hewitt 2011), little research has investigated the relationship between hardwoods and deer in longleaf pine woodlands. We examined the relationship between white-tailed deer habitat selection and hardwood overstory distribution in a landscape dominated by fire-maintained longleaf pine woodland. We hypothesized that deer would consistently select areas with a greater proportion of hardwood overstory and that deer selection for hardwood overstory would vary according to seasonal shift in food and cover availability.

STUDY AREA

We evaluated white-tailed deer habitat selection in the context of hardwood-pine overstory composition at Fort Bragg Military Installation (hereafter Fort Bragg) in the sandhills physiographic region of North Carolina, USA. Fort Bragg is a 650-km^2 active joint army and air force installation owned and managed by the U.S. Department of Defense. The sandhills region is characterized by open-canopy longleaf pine or loblolly xeric uplands interspersed with mesic bottomlands or lowland drainage areas (Franklin 2008, Sorrie *et al.* 2006). Coarse sandy, well-drained soils predominate, resulting in generally low site productivity throughout the region. The most abundant upland plant community consisted primarily of an open longleaf pine canopy, a sparse hardwood subcanopy consisting primarily of oaks (*Quercus* spp., especially *laevis*, *margarettiae*, and *marilandica*) and mockernut hickory (*Carya tomentosa*), and wiregrass (*Aristida stricta*) groundcover with variable amounts of forb cover. In mesic lowlands, canopy species include loblolly (*Pinus taeda*) and pond pine (*Pinus serotina*), blackgum (*Nyssa biflora*), red maple (*Acer rubrum*), and various *Quercus* species. Likewise, as soil moisture and nutrient levels increase, understory communities become less dominated by *A. stricta*, and transition to more diverse herbaceous and woody communities, including switchcane (*Arundinaria* spp.), *Eupatorium* spp., sweet pepperbush (*Clethra alnifolia*), gallberry (*Ilex coriacea*), inkberry (*Ilex glabra*), and greenbrier (*Smilax* spp.) (Sorrie *et al.* 2006).

Land management at Fort Bragg focuses on maintaining sparse midstory for ease of military training and creating habitat for the federally endangered red-cockaded woodpecker (*Leuoconotopicus borealis*). Red-cockaded woodpeckers occur in mature longleaf pine communities promoted by frequent fire, and managers at Fort Bragg apply prescribed fire in a 3-year return interval to forested areas to limit woody stem encroachment into the midstory and

prevent mesic hardwood encroachment. Firebreaks and streams divide the base into fire

management units averaging 18.03 ha (range 0.4–1598 ha), with forested bottomlands resulting

in mixed hardwood-pine plant communities from natural fire suppression. Prescribed burns on

Fort Bragg primarily are conducted during the growing season (primarily April–June), but

logistical constraints occasionally result in a management unit missing the scheduled burn

rotation. In these cases, stands are burned during the following dormant season (primarily

January–March). Large, non-wooded, undeveloped areas such as military drop zones, artillery

firing points, and landing strips are burned or mowed annually to remove woody growth. Over

1280 wildlife openings are scattered throughout the study area with some actively maintained in

planted species, including *Lespedeza bicolor*, millet (*Pennisetum glaucum*), rye (*Secale cereal*),

sorghum (*Sorghum bicolor*), and showy partridge pea (*Chamaecrista fasciculata*) (Sorrie, *et al.*

2006).

METHODS

Capture and Field Locations

We captured female white-tailed deer ≥1.5 years old using tranquilizer guns containing Telazol

(5 mg/kg; Midwest Veterinary Supply, Burnsville, MN), xylazine hydrochloride (2.5 mg/kg;

Congaree Veterinary Pharmacy, Cayce, SC), and ketamine hydrochloride (5 mg/kg; Midwest

Veterinary Supply, Burnsville, MN) in 2-cc transmitter darts. At 80 minutes post-injection, we

administered a reversal agent for xylazine hydrochloride, tolazoline hydrochloride (10 mg/kg,

Midwest Veterinary Supply, Burnsville, MN), and visually monitored deer until fully recovered.

We fitted individuals with Global Positioning System (GPS) collars (Wildcell, Lotek Wireless

Inc., Newmarket, ON, Canada) and ear tags. All capture and handling methods were approved by

the Institutional Animal Care and Use Committee (#10-143-O) at North Carolina State

University and followed the guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon *et al.*, 2007). The GPS collars calculated and transmitted location data every 2.5 hours to a remote site via the short messaging service network, and all data were uploaded to the Movebank online database (www.movebank.org) (Kranstauber *et al.* 2011).

White-tailed Deer Step Selection

We analyzed white-tailed deer habitat selection by using a step-selection function, which compared observed steps (a pair of consecutive GPS fixes) with a set of available steps, created using an observed GPS fix as the starting point, and a random GPS coordinate as the end point (Fortin *et al.* 2005). We used functions within the 'amt' package in R statistical software to generate the sets of available steps (Signer *et al.* 2019, R version 3.6.0, www.r-project.org, accessed 10 June 2019). We cleaned the data in a two-step process. Before generating random steps, we censored data from the first 2 weeks of deployment, as well as all locations for which positional dilution of precision (PDOP) was greater than 10 (D'Eon and Delparte 2005, Cargnelutti *et al.* 2006). We further cleaned the pre-step data by removing locations for which the time between consecutive points was either negative, or greater than 2.5 hours (missing fixes or invalid timestamps collected by the GPS unit). We then generated 20 random steps for each used step by fitting the gamma distribution to the observed step lengths and the von Mises distribution to the turn angles for each deer (Avgar *et al.* 2016 Appendix 2, Duchesne *et al.* 2015). After generating random steps, we censored valid used-random sets where either the used location or ≥5 random locations occurred in areas for which covariate data was unavailable (i.e., outside the study area). Lastly, we censored 2 individuals because persistent collar malfunctions,

combined with the cleaning process resulted in few usable steps. The resulting dataset comprised 100175 steps from 31 individuals, collected from 9 March 2011–31 July 2013.

Variable Synthesis

We used Geographical Information System (GIS) and lidar layers provided by the Fort Bragg Wildlife Branch to derive one categorical and 4 continuous variables describing site characteristics pertinent to our questions about white-tailed deer habitat selection (Table 1). Three continuous variables described overstory composition, including bottomland hardwood overstory, upland hardwood overstory, and pine overstory. Also, we included a categorical variable describing the general topographic position of points and a continuous variable representing understory cover. Topographic position was calculated using lidar-derived slope and elevation with Land Facet Corridor Designer: Extension for ArcGIS (Jenness Enterprises, Flagstaff, AZ, 2018) in ArcGIS Desktop (ArcGIS Desktop: Release 10.5, Redlands, CA: Environmental Systems Research Institute, 2018). First, we derived overstory types from high-resolution (0.3m) aerial imagery using the Image Analyst toolbox in ArcGIS Pro (ArcGIS Pro: Release 2.3.0, Redlands, CA: Environmental Systems Research Institute, 2019). Second, we calculated 36-m radius circular moving window averages of the proportion of each overstory type using the focal statistics tool in ArcMap. Lastly, we calculated a 36-m radius circular moving window average of understory cover using the presence/absence of lidar returns classified as vegetation with height <2m. The relatively coarse lidar resolution (<1 return/m) strongly favors the detection of woody or particularly dense vegetation over sparse herbaceous vegetation such as wiregrass. We used a 36-m radius window because we judged 36 m to be a reasonable range to account for differences between recorded and actual deer locations due to GPS error.

Statistical Analysis

We began by splitting the data into 8 subsets by season and activity, as we believed deer step-selection would vary based on season and whether the deer was actively moving. We first designated deer steps as active (step length >36m) or inactive (step length <36m). We used 36m as reasonable range to avoid classifying steps as active because of GPS drift (Moen *et al.* 1996, Frair *et al.* 2010). We split the data into fall (Oct–Dec), winter (Jan–Mar), spring (Apr–Jun), and summer (Jul–Sep) seasons for analysis, as we believed that deer selection for hardwood overstory would vary according to seasonal shifts in hardwood mast availability, as well as to seasonal changes in deer nutritional requirements. Accordingly, these seasons correspond to the rut, overwinter, fawning, and lactation periods for white-tailed deer in North Carolina, as well as matching the seasonal stages of plant development, such as acorn drop and fall senescence, as well as spring emergence. We constructed generalized linear mixed models (GLMMs) for each season and activity class using the "glmmTMB" package (Brooks *et al.* 2017). We began with fully specified models and included quadratic terms for all variables to allow for non-linearity and threshold effects. In addition, we included interactions between pine overstory and topographic position, and between understory cover and topographic position. Also, we included step length and turning angle in all models to avoid introducing bias (Forester *et al.* 2009). We included random intercepts and random slopes for all main effects. We fixed the random intercept variance to 10^6, following procedures outlined in Muff *et al*. (2019) to avoid shrinkage and subsequent bias. Random slopes further ensure that model coefficients and standard errors are unbiased and allowed to vary between levels of the random term (in this case, individual deer ID). We determined the optimal random-effects structure by iteratively removing the random slope term with the lowest variance when fit by restricted maximum likelihood estimation and

comparing the resulting model to the original with a likelihood-ratio test, with p-values corrected

for testing on the boundary (Zuur *et al.* 2009). We determined the optimal fixed-effects structure

by re-fitting the optimal random-effects model using maximum likelihood (ML). We constrained

our optimization of fixed effects to the removal of quadratic and interaction terms because all

main effect terms were, *a priori*, of interest. After removing uninformative interactions and

quadratic terms, we re-fit the overall optimized model using REML to ensure accurate estimates

of coefficients and standard errors (Zuur *et al.* 2009, Arnold *et al.* 2010).

RESULTS

Throughout this section we use the terms "selection" and "avoidance" to reflect deer use of an

area where the lower and upper confidence intervals (respectively) of the variable did not overlap

with the overall probability of selection with all other variables held at median values.

Active Deer Step Selection

The model for active deer during fall included quadratic terms for understory cover (vegetation

of height <2 m), pine overstory, upland hardwood overstory, and bottomland hardwood

overstory. In addition, we detected an interaction between understory cover and topographic

position (Table 2). Increased upland hardwood overstory was positively associated with

selection, but the probability of selection decreased as upland hardwood overstory exceeded

10%. Consequently, deer selected areas with 3–12% upland hardwood overstory and avoided

areas with >41% upland hardwood overstory (Figure 1A). The probability of selection during fall

increased as bottomland hardwood overstory approached 25% but plateaued or declined with

further increases, and deer selected areas with 5–33% bottomland hardwood overstory (Figure

2A). Pine overstory was positively associated with selection, and deer avoided areas with <22%

pine overstory (Figure 3A). Greater understory cover was positively associated with selection in

bottomlands and uplands, and the effect was over twice as strong in uplands. The effect size of

understory cover was considerably larger than any other variable. Consequently, deer selected

areas with 14–40% understory cover in bottomlands, and selected areas with 10–85% understory

density in uplands (Figure 4A).

The model for active deer in winter included quadratic terms for understory cover, pine

overstory, and upland hardwood overstory, and interactions between understory cover and

topographic position and between pine overstory and topographic position (Table 3). Upland

hardwood overstory was positively associated with selection and deer selected areas with 4–8%

upland hardwood overstory (Figure 1B). Bottomland hardwood overstory was positively

associated with selection, and deer selected areas with >12% bottomland hardwood overstory

(Figure 2B). Deer selected areas with >80% pine overstory in bottomlands and avoided areas

with <22% pine overstory in uplands (Figure 3B). Understory vegetation was positively

associated with selection as understory cover approached 75% in bottomlands and 62% in

uplands, but the probability of selection declined or plateaued with additional increases in

understory cover. Consequently, deer selected areas with >10% understory cover in bottomlands,

and 9–88% understory cover in uplands, and avoided areas with <3% and <5% understory cover

in bottomlands and upland, respectively (Figure 4B). In addition, the effect size of understory

cover was considerably larger than any other variable.

The model for active deer during the spring included quadratic terms for understory

cover, and pine and upland hardwood overstory. In addition, the model included interactions

between understory cover and topographic position and between pine overstory and topographic

position. (Table 4). The probability of selection increased as upland hardwood overstory

approached 8% but decreased with additional increases in upland hardwood overstory such that

deer avoided areas with >22% upland hardwood overstory (Figure 1C). Bottomland hardwood overstory did not affect selection in spring (Figure 2C). Deer avoided uplands with <14% or >58% pine overstory, but pine overstory did not affect selection in bottomlands (Figure 3C). The probability of selection increased as understory cover approached 65%, and the effect was stronger in uplands. However, the probability of selection plateaued or decreased slightly as understory cover exceeded >65%. Consequently, deer selected areas with 12–88% understory cover in bottomlands and 10–95% understory cover in uplands but avoided areas with <6% understory cover in uplands and bottomlands (Figure 4C). In addition, the effect size of understory cover was considerably larger than any other variable.

The model for active deer during the summer included quadratic terms for understory cover and pine, bottomland, and upland hardwood overstory, as well as interactions between understory cover and topographic position and pine overstory and topographic position (Table 5). Selection increased as upland hardwood overstory approached 9%, but significant uncertainty around the estimate limited our ability to make specific inferences regarding this relationship (Figure 1D). Finally, increased bottomland hardwood overstory was negatively associated with selection, and deer avoided areas with >37% bottomland hardwood overstory (Figure 2D). In addition, deer avoided uplands with <20% pine overstory, but pine overstory did not affect selection in bottomlands (Figure 3D). The probability of selection generally increased as understory cover approached 50%, and either declined or plateaued after that point. Specifically, deer avoided areas with <5% understory cover and selected areas with 8–64% in uplands and bottomlands (Figure 4D). Lastly, the effect size of understory cover was considerably larger than any other variable.

Inactive Deer Step Selection

The model for inactive deer during the fall included a quadratic term for understory vegetation (Table 6). Deer avoided areas with <4% understory vegetation and selected areas with >10% understory vegetation. However, the probability of selection plateaued or declined with >80% understory cover (Figure 5A). The effect size of understory cover was considerably larger than any other variable. Upland hardwood and bottomland hardwood overstory were positively associated with selection, and deer selected areas with >12% and >10% upland and bottomland hardwood overstory, respectively (Figures 6A and 6B).

The model for inactive deer during the winter included a quadratic term for understory cover (Table 7). The probability of selection was positively associated with understory cover of up to 50% but began to plateau with further increases in understory cover, and deer selected areas with >14% understory cover and avoided areas with <2% understory cover (Figure 5B). The effect size of understory cover was considerably larger than any other variable. In addition, deer selected areas with >45% bottomland hardwood overstory (Figure 6C).

The model for inactive deer during the spring included quadratic terms for understory cover and pine overstory, and an interaction between understory cover and topographic position (Table 8). Increased understory vegetation was positively associated with selection in uplands and bottomlands, but the probability of selection plateaued as understory cover reached 65% in bottomlands. Consequently, deer selected areas with >22% understory cover in uplands and >20% understory cover in bottomlands and avoided areas with <6% understory cover in bottomlands (Figure 5C). The effect size of understory cover was considerably larger than any other variable. In addition, deer selected areas with >75% pine overstory in uplands and bottomlands (Figure 6D).

The model for inactive deer during the summer contained a quadratic term for understory cover as well as an interaction between understory cover and topographic positions (Table 9). Increased understory vegetation was positively associated with selection in uplands and bottomlands, but the probability of selection plateaued as understory cover reached 65% in bottomlands. Consequently, deer selected areas with >23% understory cover in uplands and >12% understory cover in bottomlands but avoided areas with <2% understory cover in bottomlands (Figure 5D). The effect size of understory cover was considerably larger than any other variable.

DISCUSSION

Upland hardwood overstory had the strongest influence on active deer habitat selection in fall, winter, and spring, but did not strongly affect deer habitat selection in summer. In spring, deer avoided areas with >22% upland hardwood overstory, likely because the combined pine and hardwood overstory shading at those areas was sufficient to suppress the understory forb community. Deer selected areas with 3–12% upland hardwood overstory in fall, and 4–8% upland hardwood overstory in winter, likely because of the increasing importance of mast produced by upland hardwoods, especially oaks and common persimmon (Korschgen 1962, Lay 1969, Nixon *et al.* 1970, Sotala and Kirkpatrick 1973, Smith 1990, Johnson *et al.* 1995). In particular, turkey oak (*Quercus laevis*) and other red oak acorns do not germinate until after the dormant season, persisting on the landscape longer than white oak acorns and forming an important component of white-tailed deer diets in winter (Korschgen 1962, Core 1971). Inactive white-tailed deer selected areas with >12% upland hardwoods in fall, perhaps because deer were consuming high concentrations of mast in small localized areas, and either bedded in the

immediate vicinity, or remained in the immediate area long enough to result in misclassification of these deer as inactive.

The detection of upper thresholds for active deer selection of upland hardwood overstory in fall and winter was surprising given that hardwood mast, especially acorns, forms a seasonally important component of white-tailed deer diets when available (Lay 1965, Korschgen 1962, Weckerly and Nelson 1990, Johnson *et al.* 1995, Hewitt 2011). However, we noted considerable uncertainty in the estimates at >10% upland hardwood overstory in fall and winter (see Figure 3), and the actual thresholds may be considerably higher. Very few areas in our study area contained upland hardwood overstory >10%, and the sparsity of data for those areas makes estimating these thresholds difficult. In addition, areas of high upland hardwood overstory were highly concentrated around the centers of artillery impact areas, which deer may avoid because of frequent shelling or other disturbance. Regardless, any upper thresholds for upland hardwood overstory are unlikely to impact managers of longleaf pine woodlands, as current restoration targets for longleaf pine overstory composition as well as estimates of historical conditions typically include upland hardwood overstory lower than the thresholds we detected (Frost 1993, Hanberry *et al.* 2018).

Although the standardized effect size of understory cover varied seasonally and topographically, understory cover was consistently the strongest driver of habitat selection for deer throughout the year, particularly in frequently burned uplands where woody understory cover is limited. In addition, we consistently detected nonlinearity in deer response to understory cover, suggesting that an upper threshold existed beyond which additional increases in understory cover resulted in diminishing returns. Consequently, management for white-tailed deer must ensure adequate understory cover and forage, regardless of overstory composition. In

addition, our metric of understory cover does not include wiregrass, the predominant groundcover species in uplands, which provides poor food and cover for white-tailed deer (Ramírez *et al.* 1997). Understory cover was most important in the spring, when active deer forage extensively on the tender buds of woody species and freshly sprouted forbs (Lay 1965, Lay 1969, Johnson *et al.* 1995, Hewitt 2011), and in winter when cover and forage are more limited than other seasons. Conversely, understory cover was least important in fall, when active deer rely less on forbs and browse than in other seasons (Johnson *et al.* 1995, Hewitt 2011, but see Lay 1965). Furthermore, deer movement in fall may be strongly influenced by rut activity, and female deer have been found to make excursions beyond their normal home range during the breeding season (Kolodzinksi *et al*. 2010). Habitat selection of inactive deer was overwhelmingly driven by understory cover, as inactive deer primarily select areas with adequate cover that provides protection from predation and thermal extremes. Regardless of variation from season, deer activity, or topographic position, deer consistently selected 20–75% understory cover.

Pine overstory was the weakest driver of active deer habitat selection throughout the year, but the specific effects were highly variable depending on season and topographic position. Pine overstory had little effect on selection in bottomlands, but deer consistently avoided uplands areas with <13% pine overstory. However, the largest proportion of areas lacking pine overstory on our study site were large, open areas such as drop zones, landing strips, artillery firing points, or the central areas of artillery impact zones that have been denuded of vegetation by repeated shelling. Overstory pines provide limited food and cover for deer, and pine overstory likely influences deer habitat selection primarily through overstory shading and litter accumulation and resulting changes in understory structure and composition. Prior research in frequently burned

xeric sites found that understory diversity was not reduced by increased canopy cover until 60–70% closure was reached, although that threshold may be lower in sites with low-quality soils (Kirkman *et al.* 2001, Pecot *et al.* 2007). Accordingly, we detected upper thresholds of pine overstory, beyond which selection plateaued in summer (50%) and declined in spring (60%). In spring and summer, increasing pine overstory above a critical threshold likely results in shading sufficient to limit understory cover (Kato and Komiyama 2002, Brouwer *et al.* 2012). Likewise, deer in summer increasingly rely on soft mast-producing species that benefit from decreased competition for light, nutrients, and water, such as blackberry (*Rubus* spp.), blueberry (*Vaccinium* spp.), grape (*Vitis* spp.), and *Prunus* spp. (Hall and Ludwig 1961, Austin and Bondari 1988, Sorrie *et al.* 2006, Gallagher *et al.* 2015).

White-tailed deer had a seasonally variable response to bottomland hardwood overstory, primarily reflecting changing food and cover available to deer in bottomlands, relative to that available in uplands. In spring and summer, deer consume forbs and succulent new browse found in uplands, such as ragweed (*Ambrosia* spp.), showy partridge pea, butterfly pea (*Clitoria mariana*), milkpea (*Galactia* spp.), tick-trefoil (*Desmodium* spp.), pokeweed (*Phtolacca* spp.) or *Eupatorium* spp. rather than the evergreen browse of swamp bay, dwarf huckleberry (*Gaylussacia dumosa*), inkberry, or gallberry common in bottomlands (Lashley 2015b). Consequently, bottomland hardwood overstory did not affect selection in spring. Similarly, bottomland hardwood overstory did not affect active deer selection in summer until the bottomland hardwood overstory reached 40%, suggesting that deer were avoiding the core areas of bottomlands but using the ecotone between uplands and bottomlands, which would still have some amount of bottomland hardwood overstory. We detected a similar threshold in fall, suggesting deer selected the ecotone between uplands and bottomlands in fall where there would

be a mix of hard mast from overstory upland hardwoods and available browse from evergreen understory species common in bottomlands. Similarly, deer increasingly selected areas with greater bottomland hardwood overstory in winter because those areas were associated with greater coverage of evergreen browse. As senescence proceeds, cover and browse is reduced, and deer may be expected to increase use of bottomlands with understory species that are evergreen or produce or retain mast in the fall and winter, such as redbay (*Persea* spp.), dwarf huckleberry, inkberry, and gallberry. Likewise, mesic oaks in bottomlands provide an additional source of hard mast. Lastly, inactive deer selected areas with greater bottomland hardwood overstory during the fall and winter, because these areas contained dense woody understory that provides critical cover, even at high levels of overstory cover.

CONCLUSIONS

Although the carrying capacity of longleaf pine woodlands may be lower than many other community types (Shea *et al.* 1992, Shea and Osborne *et al.* 1995, Keyser *et al.* 2005, Diefenbach and Shea 2011, Lashley *et al.* 2015b), we suggest that managers can improve habitat quality for white-tailed deer in longleaf pine woodlands by maintaining 20-50% total canopy closure, of which 4–7% should comprise mature upland hardwood overstory for mast production. However, managers should remain cognizant that high total overstory may suppress understory cover and composition, especially at sites with low-quality soils. In addition, we suggest that managers maintain woody understory cover of 20–75%, some of which includes the dense understory cover of bottomlands, ecotones, and other higher-productivity areas. To that end, we suggest that managers interested in white-tailed deer conservation consider altering fire regimes and allowing longer intervals between fire in some burn units to allow for greater woody understory development and overall heterogeneity across the landscape (Lashley *et al*. 2015a).

LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Austin, M. E., and K. Bondari. 1988. A study of cultural and environmental factors on the yield of *Vitis rotundifolia*. Scientia Horticulturae 34:219–227.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Blanc, L. A., and J. R. Walters. 2008. Cavity-nest webs in a longleaf pine ecosystem. The Condor 110:80–92.

Bressette, J. W., H. Beck, and V. B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos 121:1749–1760.

Brockway, D., K. Outcalt, D. Tomczak, and E. Johnson. 2005. Restoration of longleaf pine ecosystems. U.S. Department of Agriculture, Forest Service, Southern Research Station, General Technical Report SRS-83, Asheville, North Carolina, USA.

Brouwer, B., A. Ziolkowska, M. Bagard, O. Keech, and P. Gardeström. 2012. The impact of light intensity on shade-induced leaf senescence. Plant, Cell & Environment 35:1084–1098.

Büchi, L., and S. Vuilleumier. 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. The American Naturalist 183:612–624.

Cargnelutti, B., A. Coulon, A. J. M. Hewison, M. Goulard, J.-M. Angibault, and N. Morellet. 2007. Testing global positioning system performance for wildlife monitoring using mobile collars and known reference points. The Journal of Wildlife Management 71:1380–1387.

Chapman, H. H. 1932. Is the longleaf type a climax? Ecology 13:328–334.

Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154:493–503.

Core, E. L. 1971. Silvical characteristics of the five upland oaks. Pages 16–20 in. Oak Symposium Proceedings. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA, USA.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430–439.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

Diefenbach, D. R., and S. M. Shea. 2011. Managing white-tailed deer: Eastern North America. Pages 481–500 in D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, FL, USA.

DiTommaso, A., S. H. Morris, J. D. Parker, C. L. Cone, and A. A. Agrawal. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. PLOS ONE 9:e91155.

Duchesne, T., D. Fortin, and L.-P. Rivest. 2015. Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. PLOS ONE 10:e0122947.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fox, J. 2011. An R companion to applied regression. SAGE Publications, Thousand Oaks, California, USA.

Frost, C. 2006. History and future of the longleaf pine ecosystem. Pages 9–48 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer New York, New York, NY.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 in. Proceedings of the Tall Timbers fire ecology conference. Volume 18. Tallahassee, FL, USA.

Gallagher, E. J., K. W. Mudge, M. P. Pritts, and S. D. DeGloria. 2015. Growth and development of 'Illini Hardy' blackberry (*Rubus* subgenus *Eubatus* focke) under shaded systems. Agroforestry Systems 89:1–17.

Gilliam, F. S., and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. Plant Ecology 140:15–26.

Greenberg, C. H., and R. W. Simons. 1999. Age, composition, and stand structure of old-growth oak sites in the Florida high pine landscape: Implications for ecosystem management and restoration. Natural Areas Journal 19:30–40.

Hall, I. V., and R. A. Ludwig. 1961. The effects of photoperiod, temperature, and light intensity on the growth of the lowbush blueberry (*Vaccinium angustifolium* ait.). Canadian Journal of Botany 39:1733–1739.

Hanberry, B. B., K. Coursey, and J. S. Kush. 2018. Structure and composition of historical longleaf pine ecosystems in Mississippi, USA. Human Ecology 46:241–248.

Heffelfinger, J. R., V. Geist, and W. Wishart. 2013. The role of hunting in North American wildlife conservation. International Journal of Environmental Studies 70:399–413.

Hewitt, D. G. 2011. Nutrition. Pages 75–105 in D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, Boca Raton, FL, USA.

Hiers, J. K., J. R. Walters, R. J. Mitchell, J. M. Varner, L. M. Conner, L. A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. The Journal of Wildlife Management 78:383–393.

Hobbs, R. J., and J. A. Harris. 2001. Restoration ecology: Repairing the earth's ecosystems in the new millennium. Restoration Ecology 9:239–246.

Jacqmain, E. I., R. H. Jones, and R. J. Mitchell. 1999. Influences of frequent cool-season burning across a soil moisture gradient on oak community structure in longleaf pine ecosystems. The American Midland Naturalist 141:85–100.

Johnson, A. S., P. E. Hale, W. M. Ford, J. M. Wentworth, J. R. French, O. F. Anderson, and G. B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. The American Midland Naturalist 133:18–35.

Jose, S., E. J. Jokela, and D. L. Miller. 2006. The longleaf pine ecosystem: An overview. Pages 3–8 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem. Springer New York, New York, NY.

Kane, J. M., J. M. Varner, and J. K. Hiers. 2008. The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeders. Forest Ecology and Management 256:2039–2045.

Kato, S., and A. Komiyama. 2002. Spatial and seasonal heterogeneity in understory light conditions caused by differential leaf flushing of deciduous overstory trees. Ecological Research 17:687–693.

Keyser, P. D., D. C. Guynn Jr., and H. S. Hill Jr. 2005. Density-dependent recruitment patterns in white-tailed deer. Wildlife Society Bulletin 33:222–232.

Kirkman, L. K., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. American Journal of Botany 88:2119–2128.

Kolodzinski, J. J., L. V. Tannenbaum, L. I. Muller, D. A. Osborn, K. A. Adams, M. C. Conner, W. M. Ford, and K. V. Miller. 2010. Excursive behaviors by female white-tailed deer during estrus at two mid-Atlantic sites. The American Midland Naturalist 163:366–373.

Korschgen, L. J. 1962. Foods of Missouri deer, with some management implications. The Journal of Wildlife Management 26:164–172.

Kranstauber, B., A. Cameron, R. Weinzerl, T. Fountain, S. Tilak, M. Wikelski, and R. Kays. 2011. The Movebank data model for animal tracking. Environmental Modelling & Software 26:834–835.

Kreye, J. K., J. K. Hiers, J. M. Varner, B. Hornsby, S. Drukker, and J. J. O'Brien. 2018. Effects of solar heating on the moisture dynamics of forest floor litter in humid environments: composition, structure, and position matter. Canadian Journal of Forest Research 48:1331–1342.

Kroeger, A.J. 2019. Northern bobwhite non-breeding habitat selection in a longleaf pine woodland. Thesis, North Carolina State University, Raleigh, USA.

Lashley, M. A., M. C. Chitwood, C. A. Harper, C. S. DePerno, and C. E. Moorman. 2015a. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology 11:62–79.

Lashley, M. A., M. C. Chitwood, C. A. Harper, C. E. Moorman, and C. S. DePerno. 2015b. Poor soils and density-mediated body weight in deer: Forage quality or quantity? Wildlife Biology 21:213–219.

Lay, D. W. 1965. Fruit utilization by deer in southern forests. The Journal of Wildlife Management 29:370–375.

Lay, D. W. 1969. Foods and feeding habits of white-tailed deer. Pages 8–13 in. U.S. Department of Agriculture, Forest Service, Southern Forest Experimental Station, Nacogdoches, TX, USA.

Little, A. R., M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2016. Habitat selection of wild turkeys in burned longleaf pine savannas. The Journal of Wildlife Management 80:1280–1289.

Loudermilk, E. L., J. K. Hiers, S. Pokswinski, J. J. O'Brien, A. Barnett, and R. J. Mitchell. 2016. The path back: Oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7:e01361.

Matthews, S. 2014. Dead fuel moisture research: 1991–2012. International Journal of Wildland Fire 23:78–92.

McShea, W. J., and J. H. Rappole. 1992. White-tailed deer as keystone species within forest habitats of Virginia. Virginia Journal of Science 43:177–186.

Means, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157–213 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem. Springer New York, New York, NY.

Mitchell, R. J., and S. L. Duncan. 2009. Range of variability in southern coastal plain forests: Its historical, contemporary, and future role in sustaining biodiversity. Ecology and Society 14.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. The Journal of Wildlife Management 60:659–668.

Muff, S., J. Signer, and J. Fieberg. 2019. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology: in press. doi:10.1111/1365-2656.13087.

Nixon, C. M., M. W. McClain, and K. R. Russell. 1970. Deer food habits and range characteristics in Ohio. The Journal of Wildlife Management 34:870–886.

Palacio, R. D., C. Valderrama-Ardila, and G. H. Kattan. 2016. Generalist species have a central role in a highly diverse plant–frugivore network. Biotropica 48:349–355.

Pecot, S. D., R. J. Mitchell, B. J. Palik, E. B. Moser, and J. K. Hiers. 2007. Competitive responses of seedlings and understory plants in longleaf pine woodlands: Separating canopy influences above and below ground. Canadian Journal of Forest Research 37:634–648.

Perkins, M. W., L. M. Conner, and M. Brent Howze. 2008. The importance of hardwood trees in the longleaf pine forest ecosystem for Sherman's fox squirrels. Forest Ecology and Management 255:1618–1625.

Platt, W., D. Streng, and J. Glitzenstein. 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. Pages 143–162 in. Proceedings of the Tall Timbers Fire Ecology Conference. Volume 17.

Ramírez, R. G., J. B. Quintanilla, and J. Aranda. 1997. White-tailed deer food habits in northeastern Mexico. Small Ruminant Research 25:141–146.

Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989*a*. Fire-induced changes in *Quercus laevis* spatial pattern in Florida sandhills. Journal of Ecology 77:638–650.

Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989*b*. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology 70:60–70.

Richmond, C. E., D. L. Breitburg, and K. A. Rose. 2005. The role of environmental generalist species in ecosystem function. Ecological Modelling 188:279–295.

Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. Forestry: An International Journal of Forest Research 74:201–208.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

Schmitz, O. J. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. Ecography 14:104–111.

Shea, S. M., T. A. Breault, and M. L. Richardson. 1992. Herd density and physical condition of white-tailed deer in Florida flatwoods. The Journal of Wildlife Management 56:262–267.

Shea, S. M., and J. S. Osborne. 1995. Poor-quality habitats. Pages 193–209 in. Quality whitetails: The why and how of quality deer management. Stackpole Books, Mechanicsburg, PA, USA.

Short, H. L., E. A. Epps, and R. M. Blair. 1975. Composition and digestibility of deer browse in southern forests. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, Research Paper SO-111, New Orleans, LA, USA.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880–890.

Smith, H. C. 1990. Mockernut hickory. Pages 226–233 *in*. Silvics of North America. Volume 2, Hardwoods. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Sorrie, B. A., J. B. Gray, and P. J. Crutchfield. 2006. The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71:129–161.

Sotala, D. J., and C. M. Kirkpatrick. 1973. Foods of white-tailed deer, *Odocoileus virginianus*, in Martin county, Indiana. The American Midland Naturalist 89:281–286.

Streich, M. M., A. R. Little, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2015. Habitat characteristics of eastern wild turkey nest and ground-roost sites in 2 longleaf pine forests. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:164–170.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. Forest Ecology and Management 211:150–165.

Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: A keystone herbivore. Wildlife Society Bulletin (1973–2006) 25:217–226.

Weckerly, F. W., and J. P. Nelson. 1990. Age and sex differences of white-tailed deer diet composition, quality, and calcium. The Journal of Wildlife Management 54:532–538.

Wenk, E. S., G. G. Wang, and J. L. Walker. 2011. Within-stand variation in understory vegetation affects fire behaviour in longleaf pine xeric sandhills. International Journal of Wildland Fire 20:866–875.

Whelan, W. A., W. S. Bigelow, F. M. Nieminen, and B. S. Jack. 2018. Fire season, overstory density and groundcover composition affect understory hardwood sprout demography in longleaf pine woodlands. Forests 9.

Williamson, G. B., and E. M. Black. 1981. High temperature of forest fires under pines as a selective advantage over oaks. Nature 293:643–644.

Zuur, A. F., editor. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Table 1. Variables used to evaluate white-tailed deer step selection. Fort Bragg Military Installation, North Carolina, USA, 2011–2013.

Parameter	Range/Levels	Median	Mean	SD
Topographic Class	Bottomlands, Uplands	n/a	n/a	n/a
Understory Cover (%)	0–99.70	8.02	18.67	21.42
Pine Overstory (%)	0–96.82	32.95	33.60	18.93
Upland Hardwood Overstory (%)	0–46.14	1.21	2.24	3.18
Bottomland Hardwood Overstory (%)	0–70.92	0	2.75	6.78

Table 2. Model parameters, coefficients and standard errors for active white-tailed deer step selection in fall. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

Parameter	β	SE
Uplands	0.082	0.031
Understory Cover	0.146	0.085
Understory Cover^2	–0.02	0.023
Pine Overstory	0.049	0.03
Bottomland Hardwood Overstory	0.136	0.031
Upland Hardwood Overstory	0.17	0.035
Bottomland Hardwood Overstory^2	–0.019	0.007
Upland Hardwood Overstory^2	–0.032	0.01
Uplands:Understory Cover	0.307	0.043
Uplands:Understory Cover^2	–0.067	0.026
Random Effect		**SD**
Random Slope|Understory Cover		0.419
Random Slope|Pine Overstory		0.14
Random Slope|Bottomland Hardwood Overstory		0.077
Random Slope|Upland Hardwood Overstory		0.161
Random Slope|Bottomland Hardwood Overstory^2		0.015
Random Slope|Upland Hardwood Overstory^2		0.039
Random Slope|Understory Cover^2		0.099

Table 3. Model parameters, coefficients and standard errors for active white-tailed deer step selection in winter. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

Parameter	β	SE
Uplands	0.059	0.042
Understory Cover	0.402	0.065
Understory Cover^2	–0.064	0.021
Pine Overstory	0.035	0.03
Bottomland Hardwood Overstory	0.071	0.033
Upland Hardwood Overstory	0.109	0.038
Upland Hardwood Overstory^2	–0.021	0.008
Pine Overstory^2	0.041	0.02
Uplands:Understory Cover	0.24	0.049
Uplands:Understory Cover^2	–0.093	0.037
Uplands:Pine Overstory	0.06	0.025
Uplands:Pine Overstory^2	–0.052	0.02
Random Effect		**SD**
Random Slope|Understory Cover		0.282
Random Slope|Pine Overstory		0.104
Random Slope|Bottomland Hardwood Overstory		0.129
Random Slope|Upland Hardwood Overstory		0.159
Random Slope|Pine Overstory^2		0.065
Random Slope|Upland Hardwood Overstory^2		0.027
Random Slope|Understory Cover^2		0.072

Table 4. Model parameters, coefficients and standard errors for active white-tailed deer step selection in spring. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

Parameter	β	SE
Uplands	0.014	0.034
Understory Cover	0.614	0.066
Understory Cover^2	–0.172	0.028
Pine Overstory	–0.06	0.039
Bottomland Hardwood Overstory	–0.032	0.035
Upland Hardwood Overstory	0.065	0.031
Upland Hardwood Overstory^2	–0.021	0.004
Pine Overstory^2	0.009	0.017
Uplands:Understory Cover	0.133	0.038
Uplands:Understory Cover^2	–0.012	0.028
Uplands:Pine Overstory	0.08	0.021
Uplands:Pine Overstory^2	–0.087	0.017
Random Effect		**SD**
Random Slope|Understory Cover		0.323
Random Slope|Pine Overstory		0.189
Random Slope|Bottomland Hardwood Overstory		0.158
Random Slope|Upland Hardwood Overstory		0.142
Random Slope|Pine Overstory^2		0.064
Random Slope|Understory Cover^2		0.125

Table 5. Model parameters, coefficients and standard errors for active white-tailed deer step selection in summer. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

Parameter	β	SE
Uplands	0.043	0.032
Understory Cover	0.358	0.07
Understory Cover^2	–0.115	0.028
Pine Overstory	0.053	0.035
Bottomland Hardwood Overstory	0.018	0.044
Upland Hardwood Overstory	0.104	0.043
Bottomland Hardwood Overstory^2	–0.023	0.009
Upland Hardwood Overstory^2	–0.03	0.011
Pine Overstory^2	0.007	0.02
Uplands:Understory Cover	0.179	0.039
Uplands:Understory Cover^2	–0.086	0.024
Uplands:Pine Overstory	0.037	0.02
Uplands:Pine Overstory^2	–0.065	0.016
Random Effect		**SD**
Random Slope|Understory Cover		0.355
Random Slope|Pine Overstory		0.163
Random Slope|Bottomland Hardwood Overstory		0.183
Random Slope|Upland Hardwood Overstory		0.212
Random Slope|Pine Overstory^2		0.082
Random Slope|Bottomland Hardwood Overstory^2		0.026
Random Slope|Upland Hardwood Overstory^2		0.039
Random Slope|Understory Cover^2		0.13

Table 6. Model parameters, coefficients and standard errors for inactive white-tailed deer step selection in fall. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

| Parameter	β	SE
Uplands	0.059	0.084
Understory Cover	1.051	0.111
Understory Cover^2	–0.191	0.034
Pine Overstory	0.136	0.093
Bottomland Hardwood Overstory	0.172	0.046
Upland Hardwood Overstory	0.106	0.045
Random Effect		**SD**
Random Slope|Understory Cover		0.247
Random Slope|Pine Overstory		0.337
Random Slope|Upland Hardwood Overstory		0.085
Random Slope|Pine Overstory^2		0.242

Table 7. Model parameters, coefficients and standard errors for inactive white-tailed deer step selection in winter. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

| Parameter	β	SE
Uplands	0.014	0.083
Understory Cover	0.848	0.121
Understory Cover^2	–0.138	0.035
Pine Overstory	0.157	0.055
Bottomland Hardwood Overstory	0.106	0.05
Upland Hardwood Overstory	0.042	0.065
Random Effect		**SD**
Random Slope|Understory Cover		0.354
Random Slope|Bottomland Hardwood Overstory		0.072
Random Slope|Upland Hardwood Overstory		0.199

Table 8. Model parameters, coefficients and standard errors for inactive white-tailed deer step selection in spring. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

Parameter	β	SE
Uplands	0.002	0.087
Understory Cover	0.82	0.122
Understory Cover^2	–0.183	0.033
Pine Overstory	0.026	0.059
Bottomland Hardwood Overstory	0.082	0.048
Upland Hardwood Overstory	–0.02	0.051
Pine Overstory^2	0.088	0.031
Uplands:Understory Cover	–0.13	0.095
Uplands:Understory Cover^2	0.186	0.062
Random Effect		**SD**
Random Slope|Understory Cover		0.453
Random Slope|Pine Overstory		0.106
Random Slope|Bottomland Hardwood Overstory		0.101
Random Slope|Upland Hardwood Overstory		0.093

Table 9. Model parameters, coefficients and standard errors for inactive white-tailed deer step selection in summer. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All random effects are conditioned on deer ID.

| Parameter	β	SE
Uplands	–0.022	0.113
Understory Cover	0.886	0.132
Understory Cover^2	–0.184	0.039
Pine Overstory	–0.005	0.086
Bottomland Hardwood Overstory	–0.005	0.046
Upland Hardwood Overstory	0.011	0.061
Uplands:Understory Cover	–0.405	0.132
Uplands:Understory Cover^2	0.216	0.09
Random Effect		**SD**
Random Slope|Understory Cover		0.417
Random Slope|Pine Overstory		0.322
Random Slope|Upland Hardwood Overstory		0.141
Random Slope|Understory Cover^2		0.064
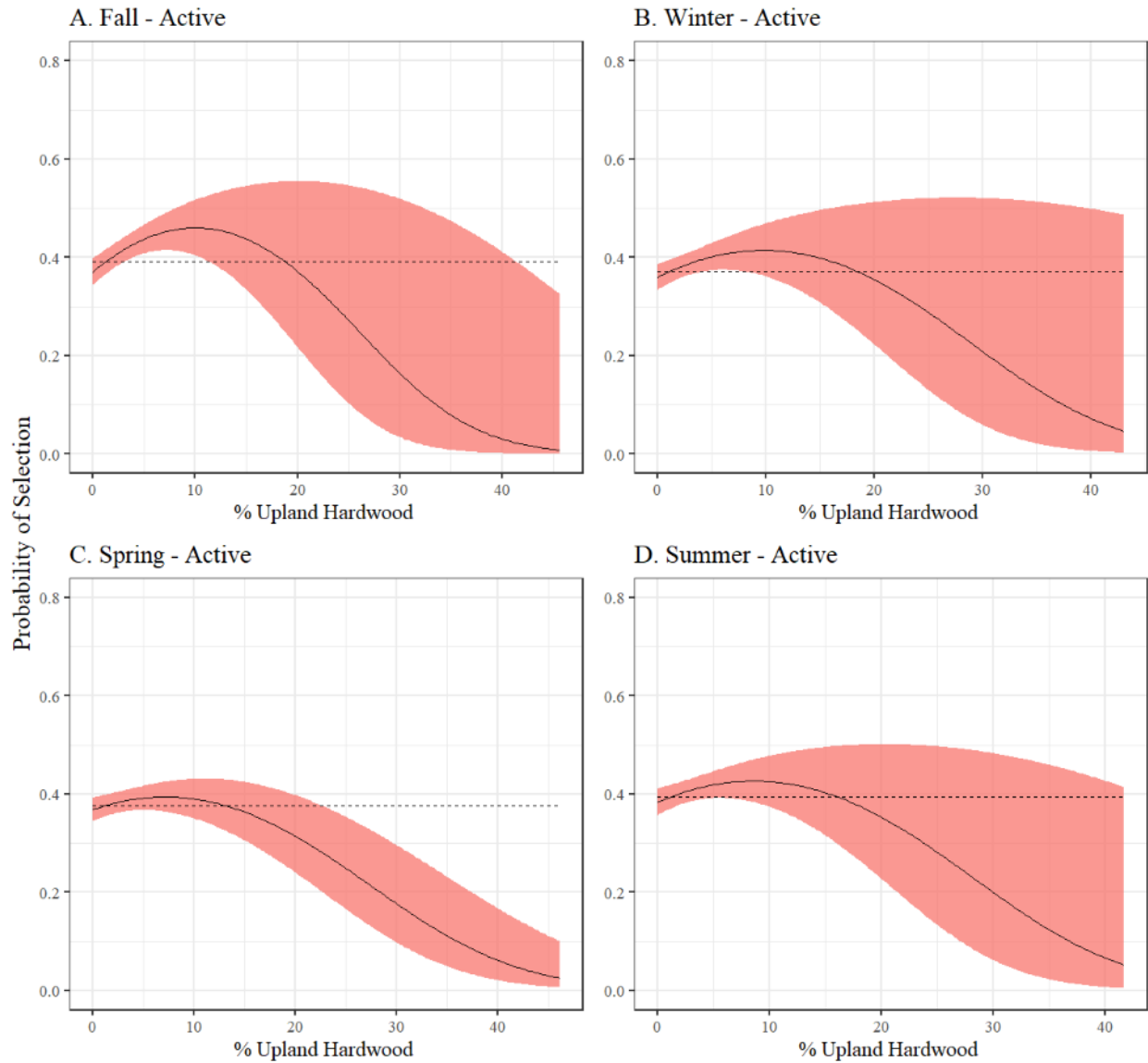
Figure 1. Probabilities and 95% CI for active white-tailed deer step selection based on upland hardwood overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The horizontal plane represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.
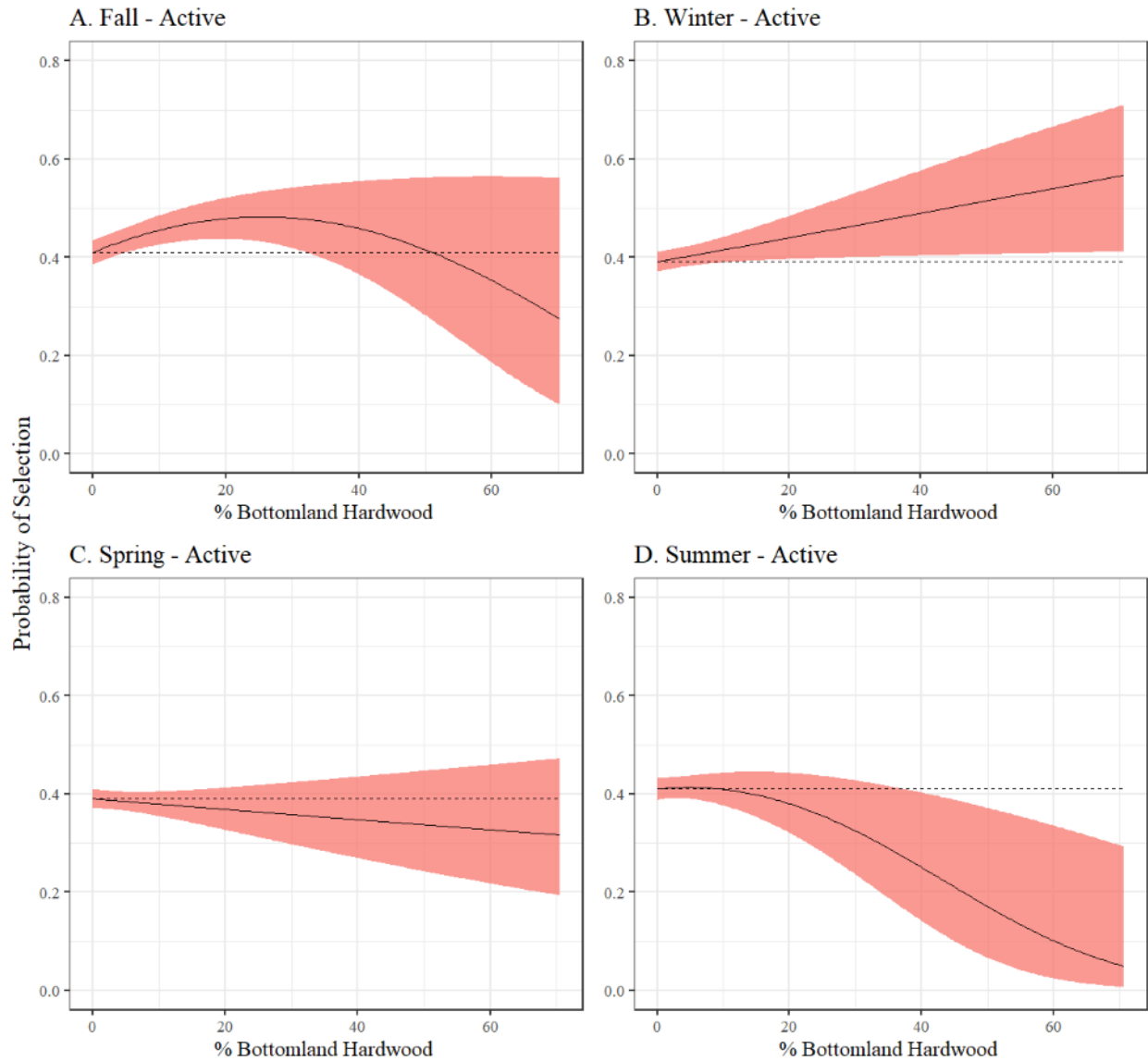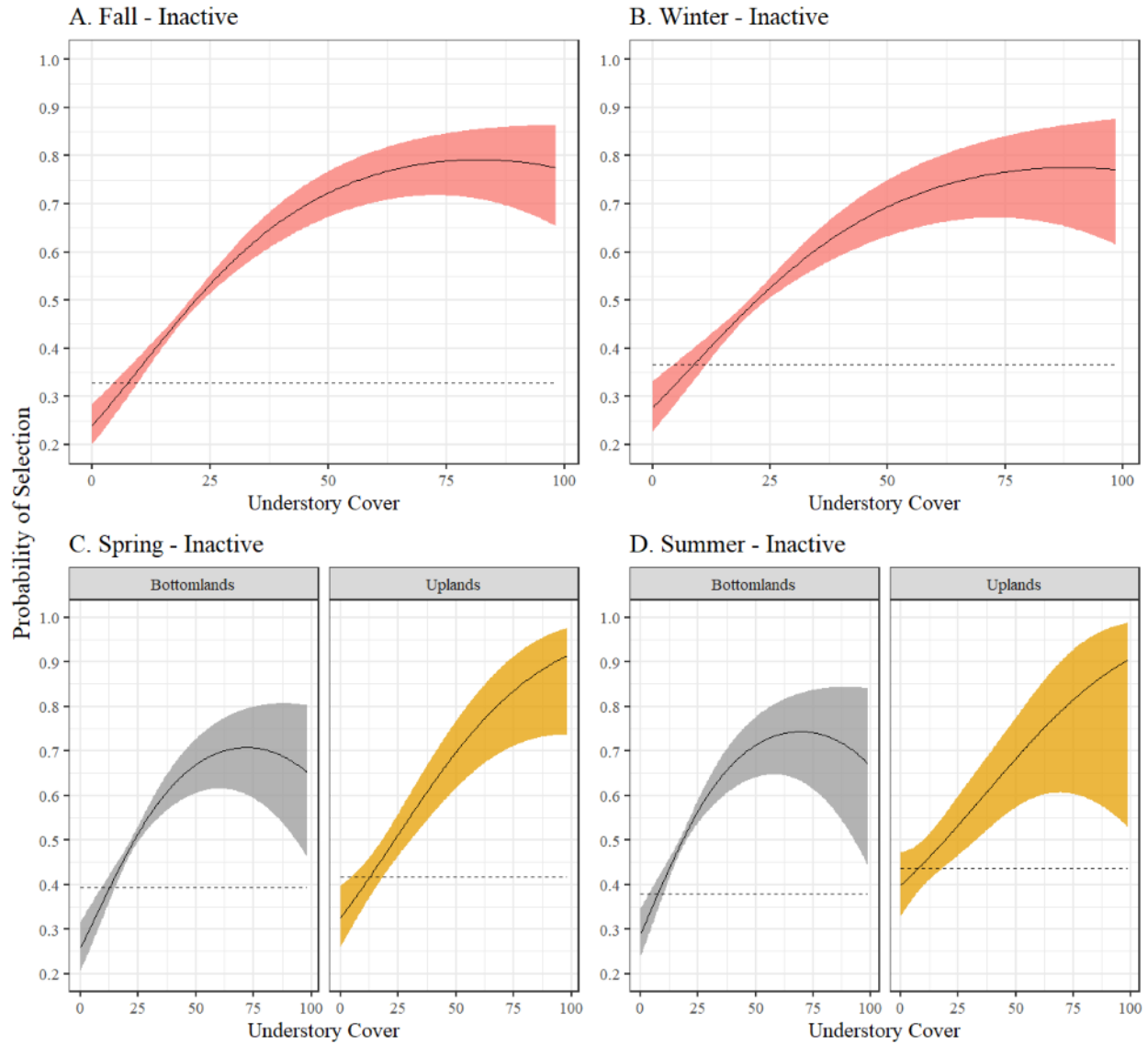
Figure 2. Probabilities and 95% CI for active white-tailed deer step selection based on bottomland hardwood overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The horizontal plane represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.
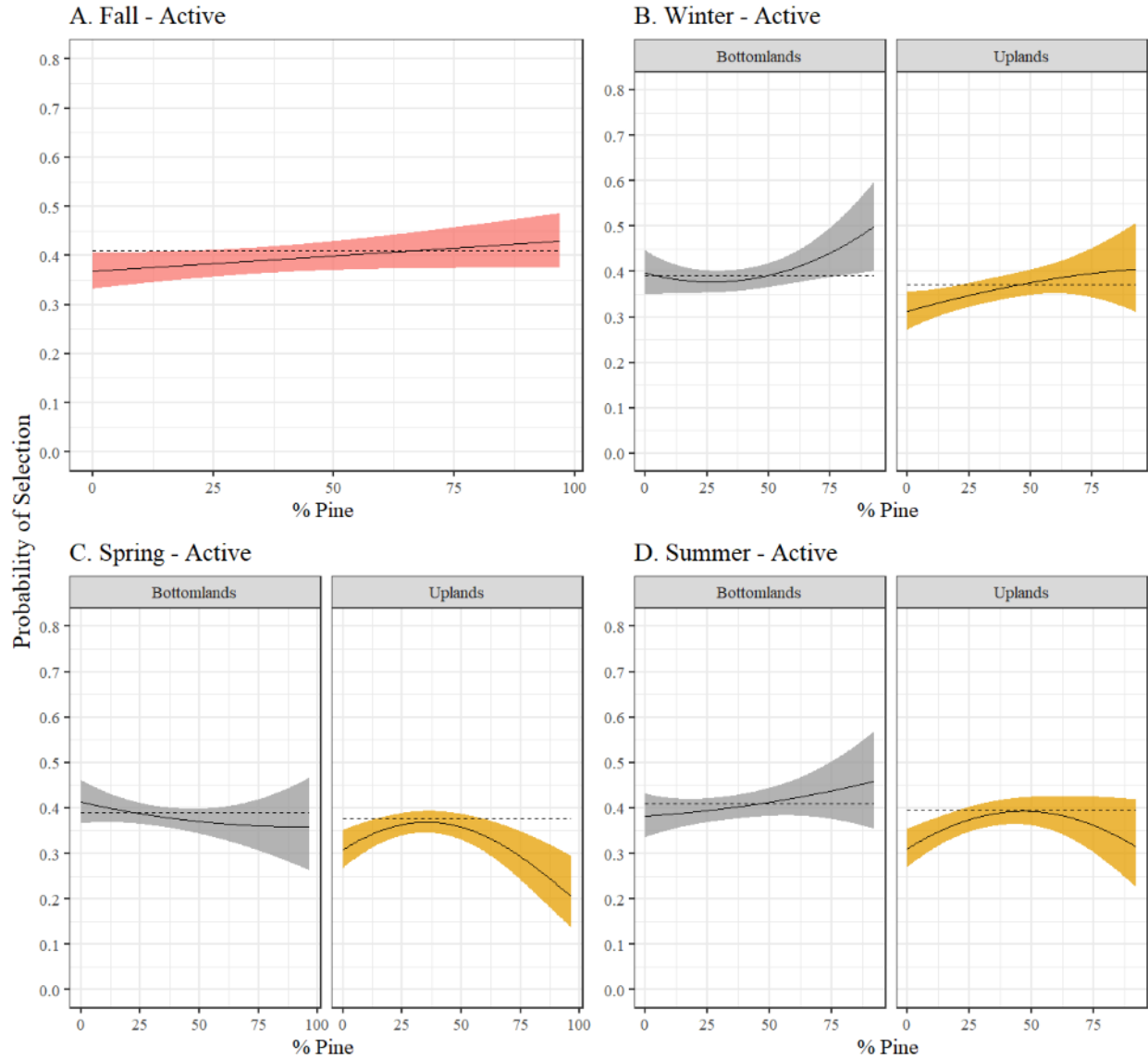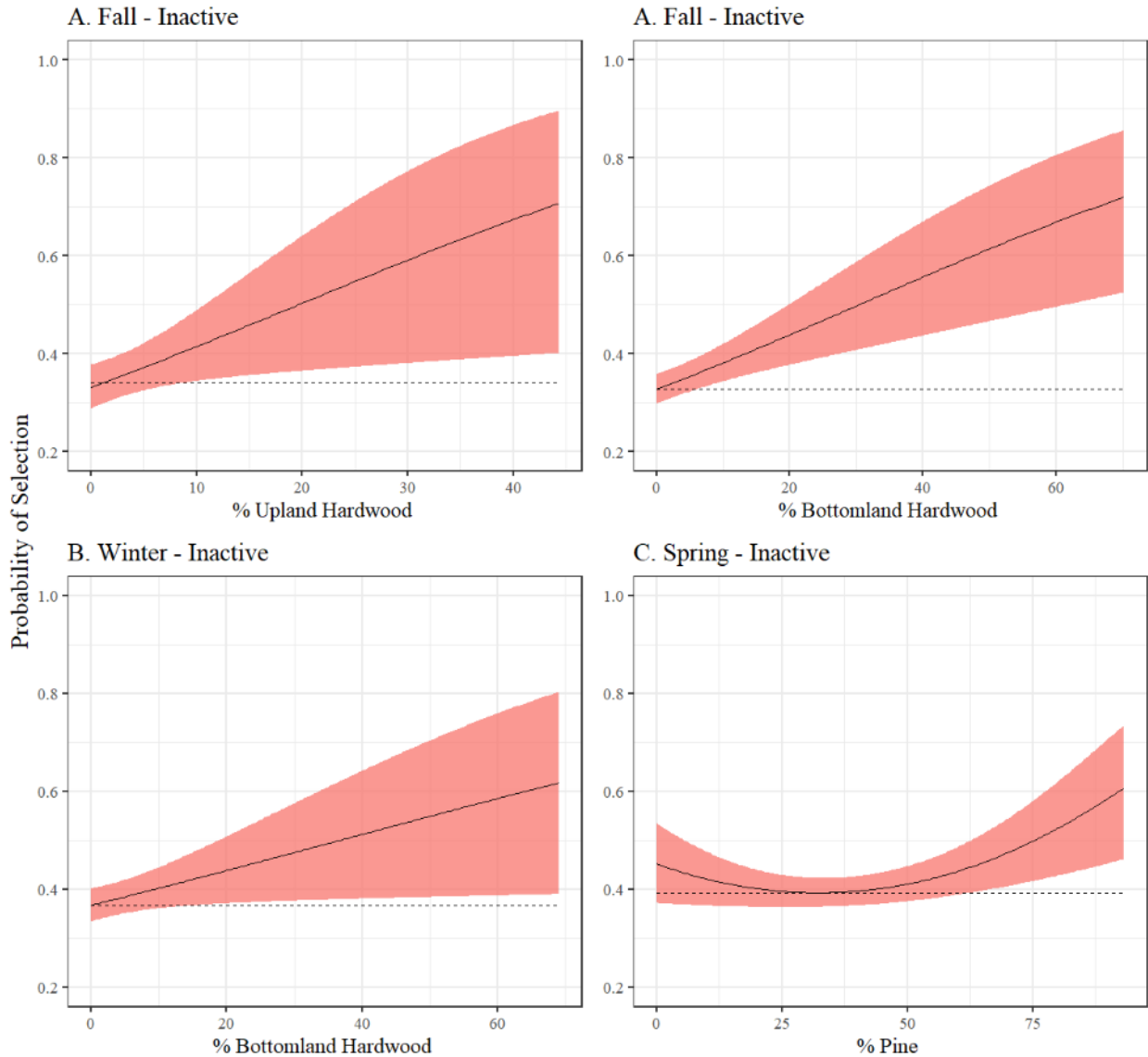
Figure 3. Probabilities and 95% CI for active white-tailed deer step selection based on pine overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The horizontal plane represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.
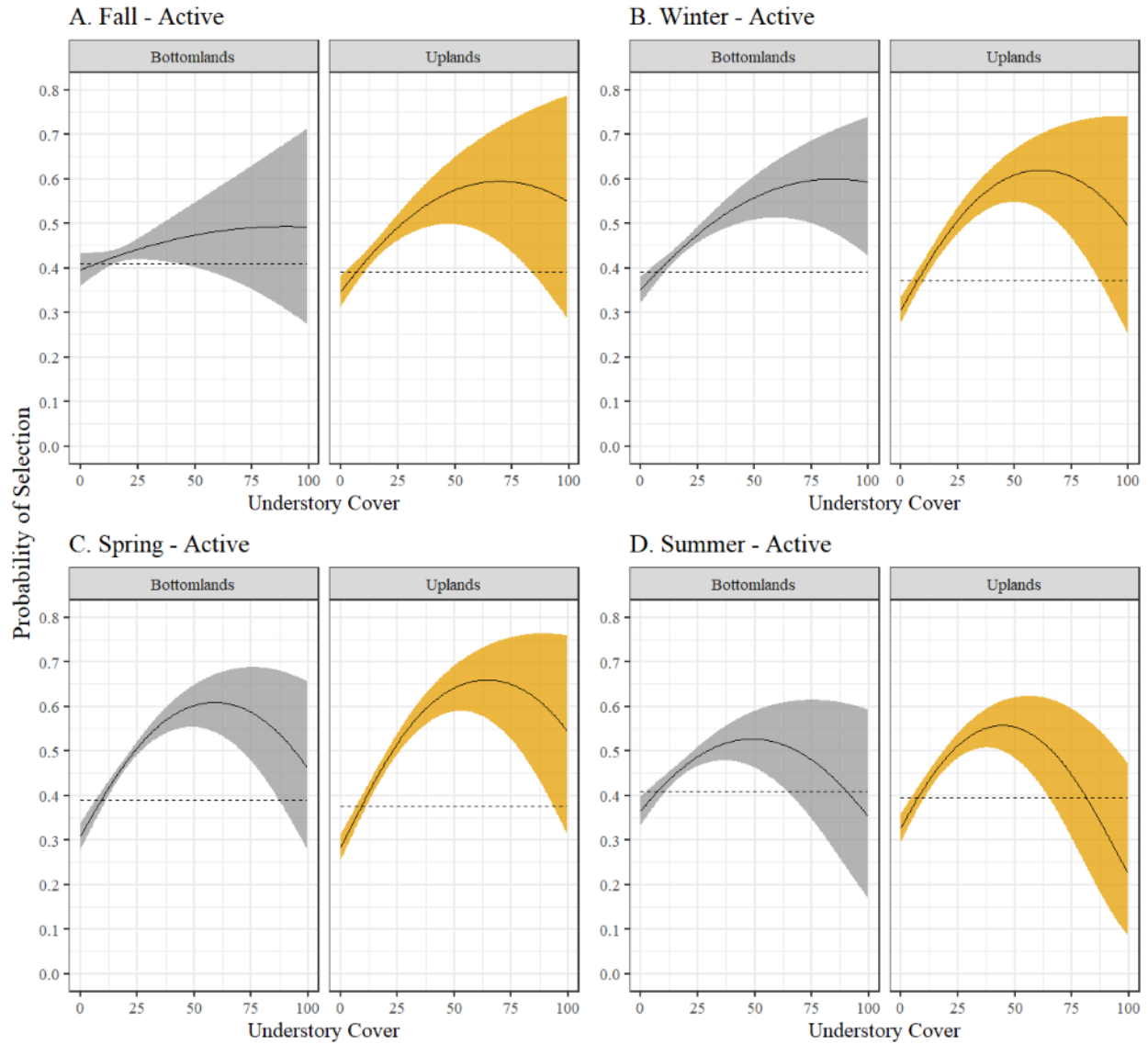
Figure 4. Probabilities and 95% CI for active white-tailed deer step selection based on understory cover. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The vertical dash line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.

Figure 5. Probabilities and 95% CI for inactive white-tailed deer step selection based on understory cover. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The horizontal plane represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.

Figure 6. Probabilities and 95% CI for inactive white-tailed deer step selection based on significant overstory predictors. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The horizontal plane represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance) for the variable of interest, respectively.