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White-tailed deer use of overstory hardwoods in longleaf pine woodlands

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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 relative 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. During fall and winter, deer selection increased with increasing upland hardwood overstory until reaching an upper threshold (12% and 7%; respectively) where increasing cover of upland hardwoods no longer increased selection. Also, in the fall and winter, deer selected areas with greater bottomland hardwood overstory until an upper threshold of 33% bottomland hardwood overstory was reached. In the spring, deer selected areas with < 22% upland hardwood overstory. The effect size of understory cover, defined as lidar-classified vegetation with height < 2 m, was larger than any other variable, regardless of season, and deer consistently selected areas with 20–75% understory cover. When managing longleaf pine woodlands for white-tailed deer, our results indicate maintaining a well-developed woody understory with 20–50% canopy closure is important, ideally with mature upland hardwood overstory cover between 4 and 12% to ensure mast production in fall and winter.

1. Introduction

The longleaf pine (*Pinus palustris*) ecosystem harbors some of the highest biodiversity on the North American continent and once covered nearly 37 million ha (Frost et al., 2006). Widespread logging, forest conversion to agriculture, and fire suppression reduced the longleaf pine ecosystem to ~600,000 ha (Frost, 1993, Gilliam and Platt, 1999; Brockway et al., 2005). As a result, restoration of the longleaf pine ecosystem is a priority for managers across the southeastern United States. Restoration efforts commonly reintroduce fire to the landscape to combat mesophication and hardwood encroachment and return sites to a historical reference condition (Jose et al., 2006). Indeed, the season, frequency, and technique of burning employed by managers of longleaf pine woodlands is one of the most important factors determining the distribution and mast productivity of upland hardwoods (Glitzenstein et al., 1995; Sparks et al., 1999; Jose et al., 2006; Lashley et al., 2014). However, without a clearly articulated reference condition in dynamic fire-climax systems, restoration efforts may be ineffective (Chapman, 1932; Hobbs and Harris, 2001; Van Lear, 2005). Restoring the longleaf pine ecosystem requires more than a static picture of homogeneous "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., 2014, 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 can serve as nursery species for longleaf pine, mitigating the effects of low precipitation and facilitating longleaf pine seedling survival (Loudermilk et al., 2016, although see Willis et al., 2019). In addition, upland hardwoods alter the realized fire regimes of their

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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. Fox squirrels (*Sciurus niger*) 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; Prince et al., 2016). Hardwood mast is an important food source for rodent populations, including white-footed mice (*Peromyscus leucopus*) and deer mice (*Peromyscus maniculatus*), which are prey for raptors, snakes, and other mesopredators (Clotfelter et al., 2007). Cavity-nesting birds, many of which are known to excavate or use hardwoods for nesting or foraging, represent a significant portion of the avian biodiversity present in the longleaf pine ecosystem (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 distribution 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 many longleaf pine woodlands for white-tailed 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 et al., 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 woodlands. We hypothesized that deer would consistently select areas with a greater proportion of hardwood overstory and that the strength of selection for hardwood overstory would increase in fall and winter with availability of hard mast but decrease in spring and summer when forbs and palatable browse are more available.

2. Materials and methods

2.1. Study area

Fort Bragg Military Installation (hereafter Fort Bragg) is located 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 or loblolly pine (*P. taeda*) 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 and pond pine (*P. 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 a relatively open 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 at 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. > 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).

2.2. Capture and field locations

We captured female white-tailed deer ≥ 1.5 years old using tranquilizer guns with 2-cc transmitter darts 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). At 80 min 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 North Carolina Wildlife Resources Commission and the Institutional Animal Care and Use Committee (#10–143-O) at North Carolina State University. The GPS collars calculated and transmitted location data every 2.5 h 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).

2.3. 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 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 Core Team, 2019, version 3.6.0). 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 et al., 2002; D'Eon and Delparte, 2005; Cargnelutti et al., 2007). 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 h (i.e., 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 100,175 steps from 31 individuals, collected from 9 March 2011–31 July 2013.

2.4. 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). We included variables in addition to hardwood overstory because we wanted to determine the amount of explanation that came from hardwood overstory when those other variables were included. One continuous variable represented understory cover, and three continuous variables described overstory composition, including bottomland hardwood overstory, upland hardwood overstory, and pine overstory. The categorical variable described the general topographic position of points (e.g., uplands and bottomlands) and 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 (0.3 m) 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 neighborhood averages of the proportion of each overstory type using the focal statistics tool in ArcMap. Lastly, using the focal statistics tool in ArcMap, we calculated a 36-m radius circular neighborhood average of understory cover using the presence/absence of lidar returns classified as vegetation with height < 2 m. 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 estimated the error of our GPS units by leaving them in known locations and comparing the recorded coordinates with the known points. Thus, we used a 36-m radius because we considered 36 m to be a reasonable range to account for differences between recorded and actual deer locations because of GPS error (Moen et al., 1996; Frair et al., 2010).

Table 1
Parameters 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[a]	Uplands, Bottomlands	n/a	n/a	n/a
Understory cover (%)[b]	0–99.70	8.02	18.67	21.42
Pine overstory (%)[c]	0–96.82	32.95	33.60	18.93
Upland Hardwood Overstory (%)[d]	0–46.14	1.21	2.24	3.18
Bottomland Hardwood Overstory (%)[e]	0–70.92	0	2.75	6.78

[a] Topographic class was calculated from lidar-derived slope and elevation.
[b] Understory cover was a 36-m neighborhood average of lidar returns classified as vegetation with height < 2 m.
[c,d,e] Overstory variables were 36-m neighborhood averages derived from aerial imagery classified as pine, upland hardwood, or bottomland hardwood.

2.5. Statistical analysis

We began by splitting the data into 8 subsets by season and activity. We first designated deer steps as active (step length > 36 m) or inactive (step length < 36 m), as we believed deer step-selection would vary according to whether or not the deer was actively moving (Armstrong et al., 1983; Pollock et al., 1994; Gallina et al., 2010). We used 36 m 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 (Lay, 1965; Korschgen, 1962; Moen, 1978; Warren et al., 1981; Weckerly and Nelson, 1990; Johnson et al., 1995; Hewitt, 2011). 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 mean-centered and scaled all continuous variables prior to running the models. 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 refit the overall optimized model using REML to ensure accurate estimates of coefficients and standard errors (Zuur et al., 2009; Arnold et al., 2010).

Table 2
Model specifications used for white-tailed deer step selection. All quadratic and interaction terms contain their respective main effects. Fort Bragg Military Installation, North Carolina, USA, 2011–2013.

Model	Range/levels
Fall – Active	Topographic Class:Understory Cover^2 + Upland Hardwood^2 + Bottomland Hardwood^2 + Pine
Winter – Active	Topographic Class:Understory Cover^2 + Upland Hardwood^2 + Bottomland Hardwood + Topographic Class:Pine^2
Spring–Active	Topographic Class:Understory Cover^2 + Upland Hardwood^2 + Bottomland Hardwood + Topographic Class:Pine^2
Summer – Active	Topographic Class:Understory Cover^2 + Upland Hardwood^2 + Bottomland Hardwood^2 + Topographic Class:Pine^2
Fall – Inactive	Topographic Class + Understory Cover^2 + Pine + Upland Hardwood + Bottomland Hardwood
Winter – Inactive	Topographic Class + Understory Cover^2 + Pine + Upland Hardwood + Bottomland Hardwood
Spring – Inactive	Topographic Class:Understory Cover^2 + Pine^2 + Upland Hardwood + Bottomland Hardwood
Summer – Inactive	Topographic Class:Understory Cover^2 + Pine + Upland Hardwood + Bottomland Hardwood

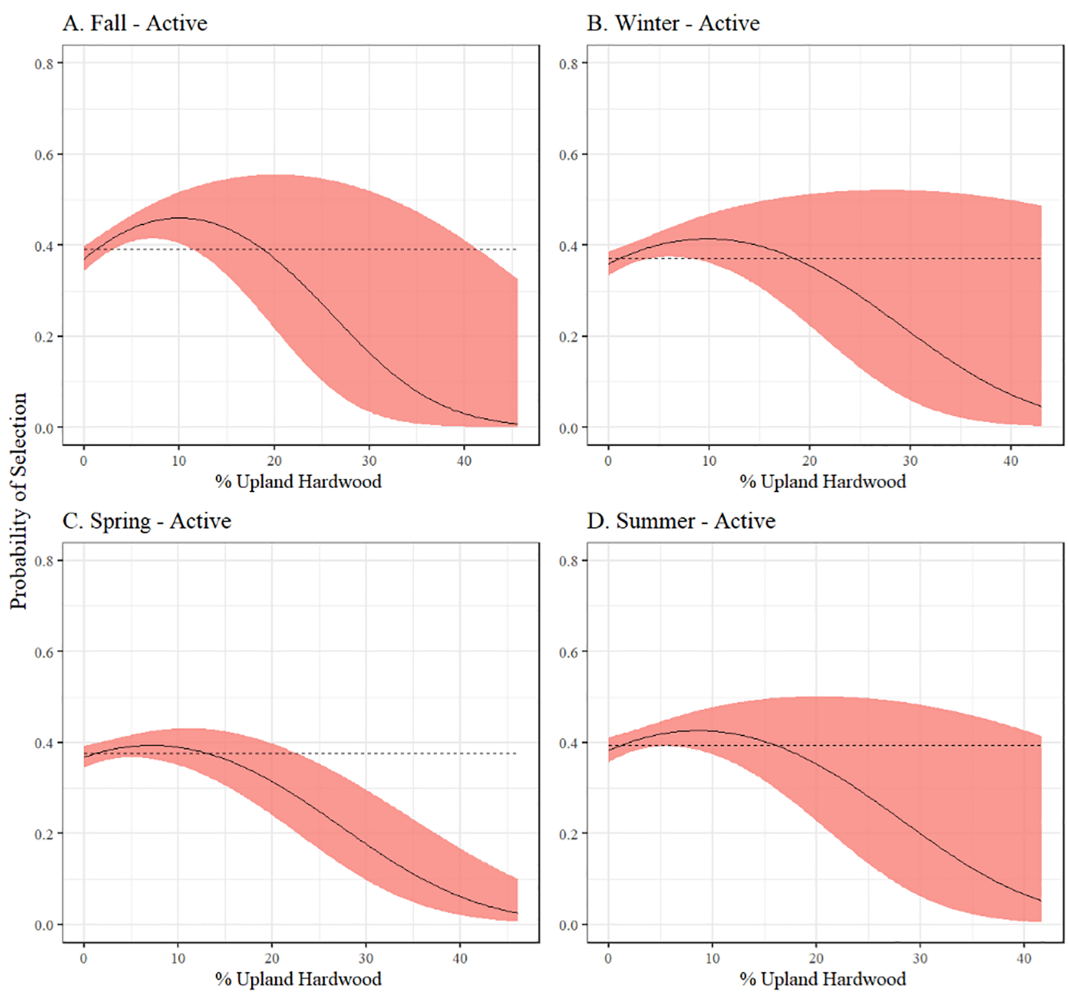

Fig. 1. Probabilities and 95% CI for active white-tailed deer step selection based on upland hardwood overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance), respectively, for the variable of interest.

3. Results

Throughout this section we use the terms “selection” and “avoidance” to reflect deer use of an area where the lower or upper confidence limits (respectively) of the variable did not overlap with the overall probability of selection with all other variables held at median values. Model specifications are in Table 2, whereas parameter coefficients and standard errors are in Appendix A, Tables A1–A8.

3.1. Active deer step selection

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

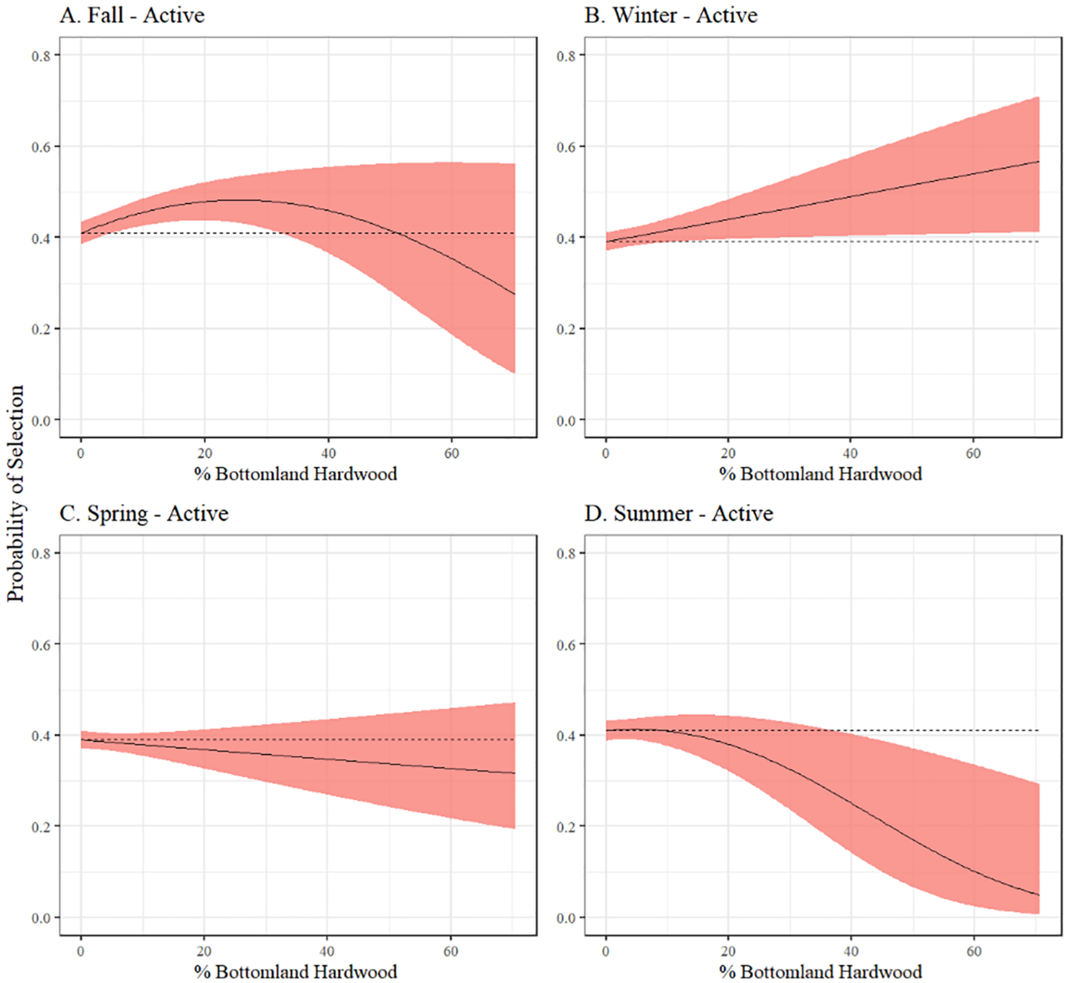

Fig. 2. Probabilities and 95% CI for active white-tailed deer step selection based on bottomland hardwood overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance), respectively, for the variable of interest.

overstory exceeded 10% canopy coverage. Consequently, deer selected areas with 3–12% upland hardwood overstory and avoided areas with > 41% upland hardwood overstory (Fig. 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 (Fig. 2A). Pine overstory was positively associated with selection, and deer avoided areas with < 22% pine overstory (Fig. 3A). Greater understory cover was positively associated with selection in bottomlands and uplands, and the effect was more than 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 cover in uplands (Fig. 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 2). Upland hardwood overstory was positively associated with selection, and deer selected areas with 4–8% upland hardwood overstory (Fig. 1B). Bottomland hardwood overstory was positively associated with selection, and deer selected areas with > 12% bottomland hardwood overstory (Fig. 2B). Deer selected areas with > 80% pine overstory in bottomlands and avoided areas with < 22% pine overstory in uplands (Fig. 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 uplands, respectively (Fig. 4B). In addition, the effect size of understory cover was considerably larger than any other variable.

The model for active deer during 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 2). 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 (Fig. 1C). Bottomland hardwood overstory did not affect selection in spring (Fig. 2C). Deer avoided uplands with < 14% or > 58% pine overstory, but pine overstory did not affect selection in bottomlands (Fig. 3C). The probability of

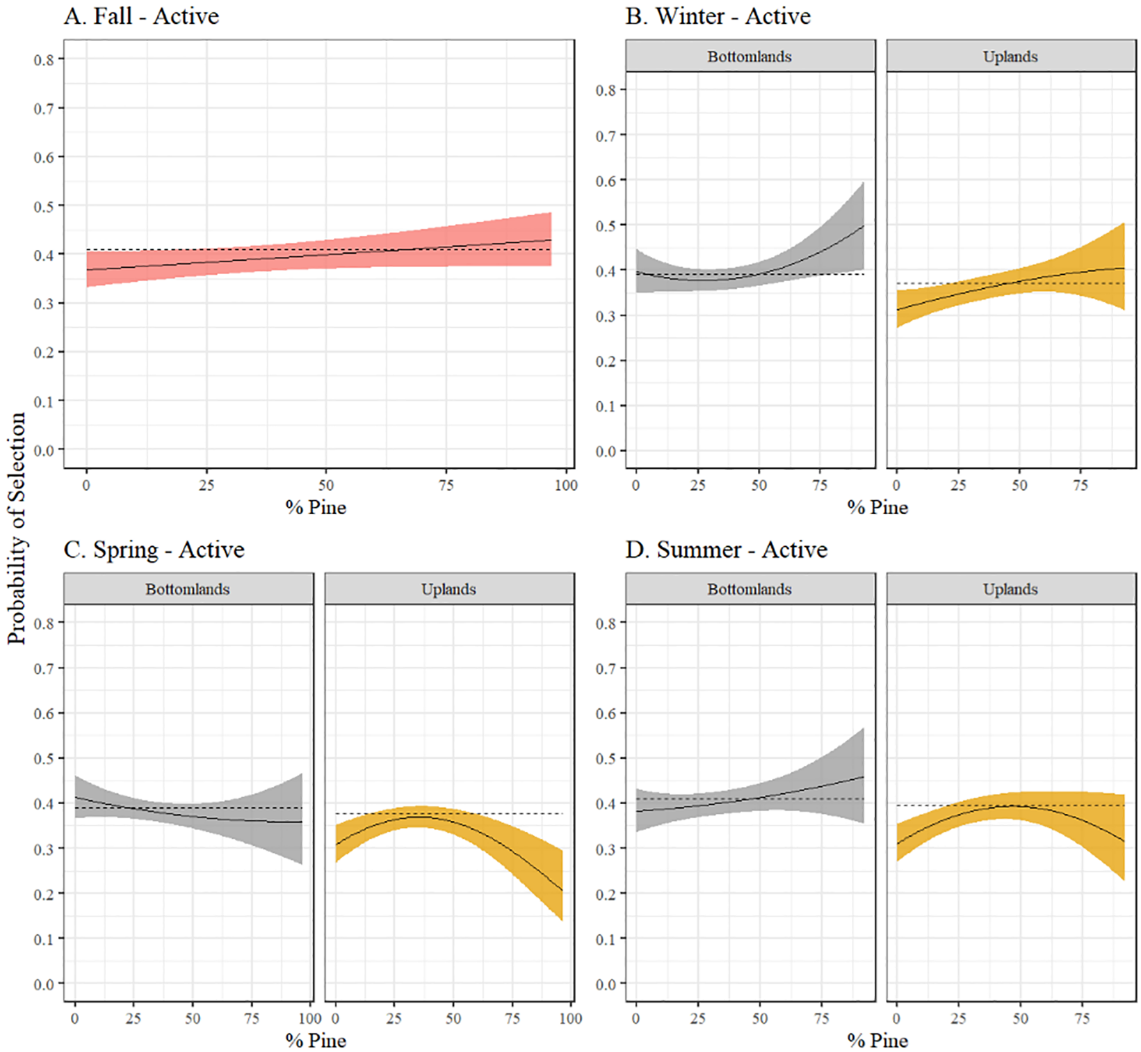

Fig. 3. Probabilities and 95% CI for active white-tailed deer step selection based on pine overstory. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance), respectively, for the variable of interest.

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 (Fig. 4C). In addition, the effect size of understory cover was considerably larger than any other variable.

The model for active deer during 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 2). Selection increased as upland hardwood overstory approached 9%, but uncertainty around the estimate limited our ability to make specific inferences regarding this relationship (Fig. 1D). Finally, increased bottomland hardwood overstory was negatively associated with selection, and deer avoided areas with > 37% bottomland hardwood overstory (Fig. 2D). In addition, deer avoided uplands with < 20% pine overstory, but pine overstory did not affect selection in bottomlands (Fig. 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 (Fig. 4D). Lastly, the effect size of understory cover was considerably larger than any other variable.

3.2. Inactive deer step selection

The model for inactive deer during fall included a quadratic term for understory vegetation (Table 2). 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 (Fig. 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 (Fig. 6A and B).

The model for inactive deer during winter included a quadratic term for understory cover (Table 2). The probability of selection was positively associated with understory cover of up to 50% but began to

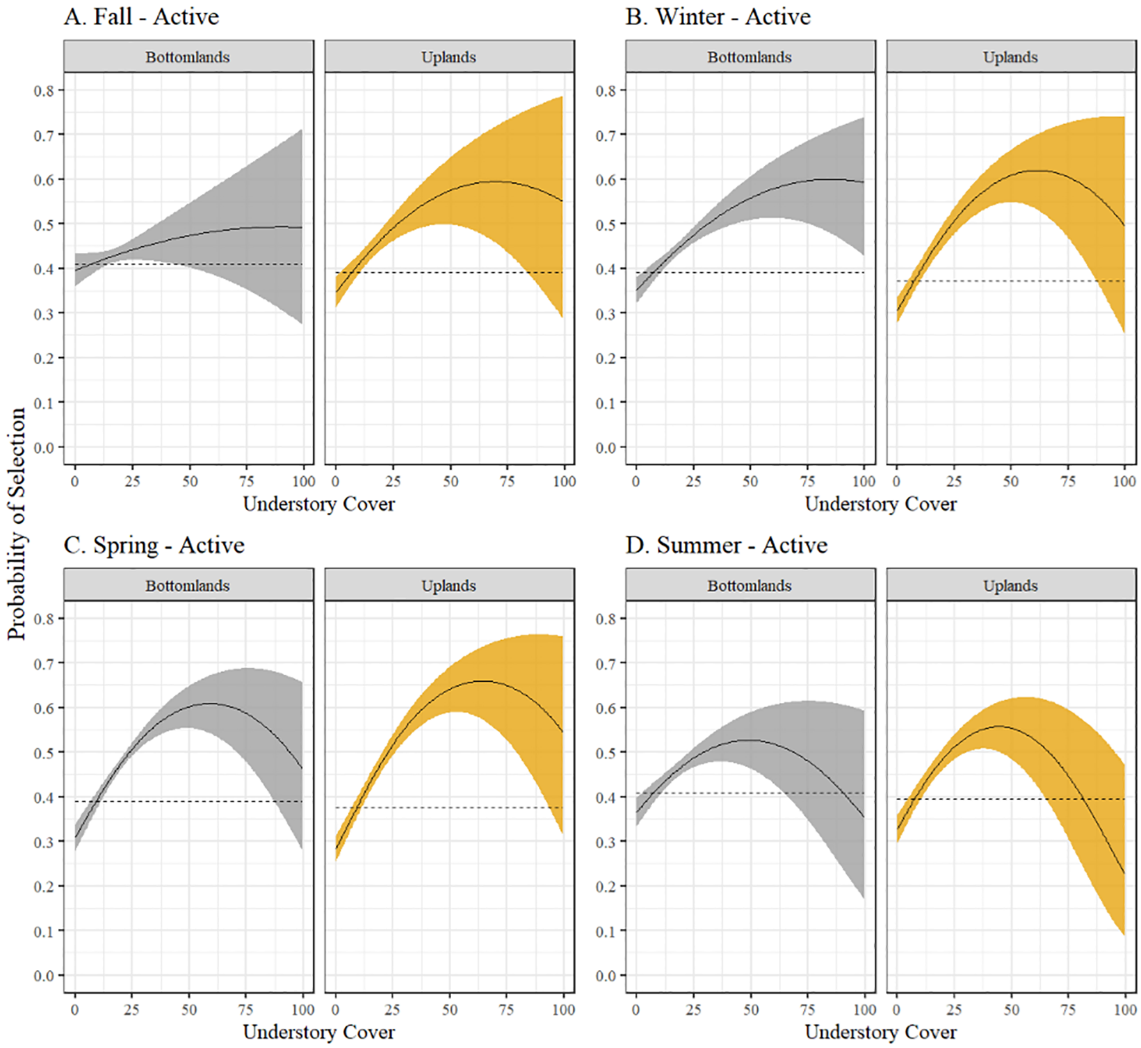

Fig. 4. Probabilities and 95% CI for active white-tailed deer step selection based on understory cover. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal line represents the overall probability of selection, with probabilities above and below this line indicating positive and negative selection (avoidance), respectively, for the variable of interest.

plateau with further increases in understory cover, and deer selected areas with > 14% understory cover and avoided areas with < 2% understory cover (Fig. 5B). The effect size of understory cover was considerably larger than any other variable. In addition, deer selected areas with > 45% bottomland hardwood overstory (Fig. 6C).

The model for inactive deer during spring included quadratic terms for understory cover and pine overstory, and an interaction between understory cover and topographic position (Table 2). 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 (Fig. 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 (Fig. 6D).

The model for inactive deer during summer contained a quadratic term for understory cover as well as an interaction between understory cover and topographic positions (Table 2). 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 (Fig. 5D). The effect size of understory cover was considerably larger than any other variable.

4. Discussion

Upland hardwood overstory was a stronger driver of active deer habitat selection than other overstory types 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 (55% total canopy closure) shading at those areas was sufficient to suppress the understory forb community (Kirkman et al., 2001; Pecot et al., 2007). Deer selected areas with 3–12% upland hardwood overstory in fall, and 4–8% upland hardwood overstory in winter, likely because of mast production, especially oaks and common persimmon (Korschgen, 1962; Lay, 1969; Nixon et al., 1970; Sotala and Kirkpatrick, 1973; Johnson et al., 1995). In particular, turkey oak and other red oak acorns do not germinate until after the dormant season, persisting on the landscape longer than

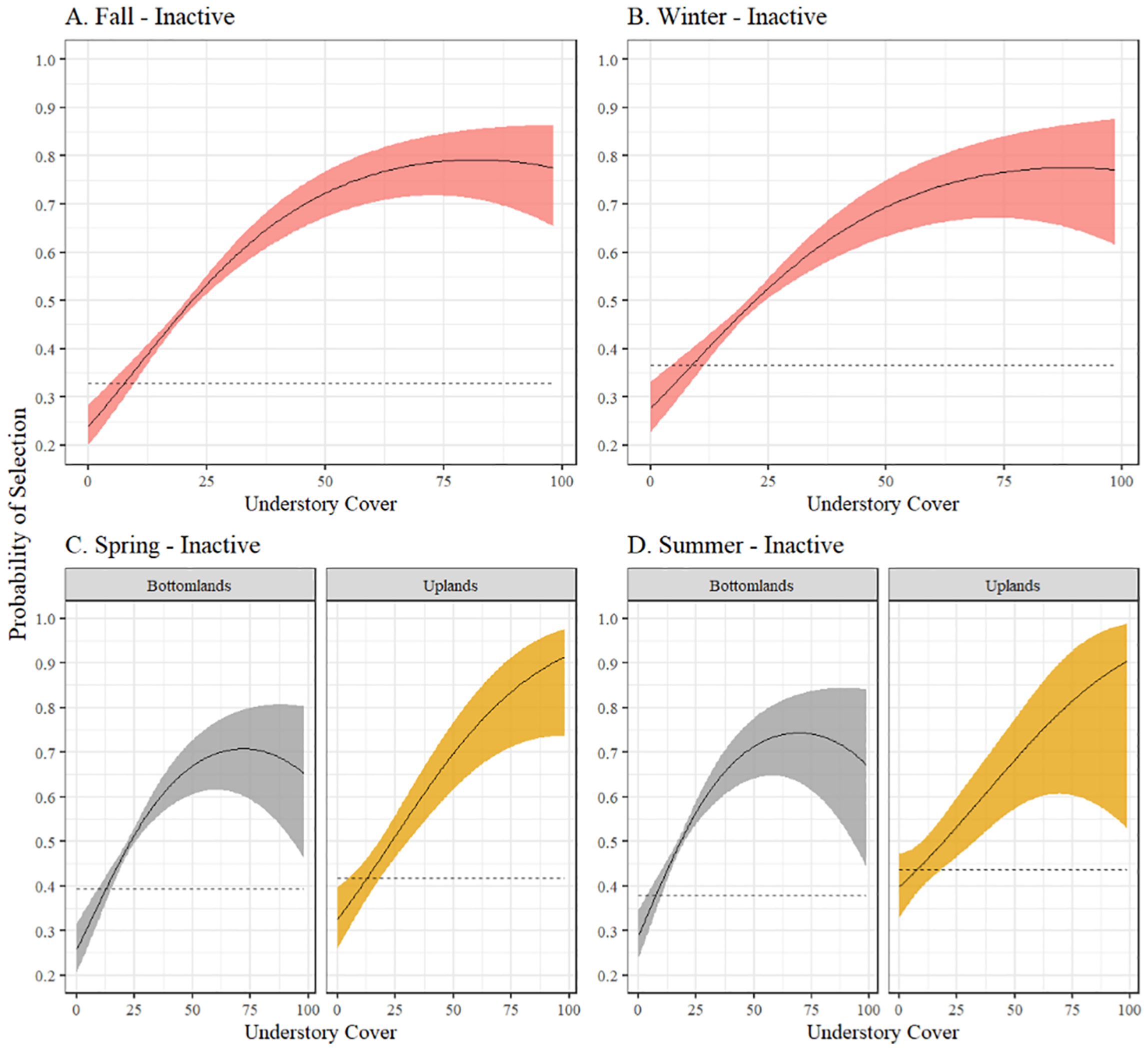

Fig. 5. Probabilities and 95% CI for inactive white-tailed deer step selection based on understory cover. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal line represents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

white oak acorns and represent a significant component of white-tailed deer diets when available 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 initially surprising given that hardwood mast, especially acorns, forms a seasonally important component of white-tailed deer diets when available (Korschgen, 1962; Lay, 1965; 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 Fig. 1), and the actual thresholds may be greater. 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 with a relatively dense hardwood overstory were highly concentrated around the centers of artillery impact areas, which deer may avoid because of frequent anthropogenic disturbance such as shelling. Alternatively, hard mast is likely not a limiting factor to deer in longleaf pine woodlands even when only a small proportion of the overstory is comprised of mature oaks, because of the availability of browse. 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. Habitat selection of inactive deer was driven by understory cover throughout the year, as inactive deer primarily select areas with adequate cover that provides protection from predation and thermal extremes (Armstrong et al., 1983; Pollock et al., 1994; Gallina et al, 2010). Understory cover was most important for active deer in the spring, when deer forage extensively on the tender buds of woody

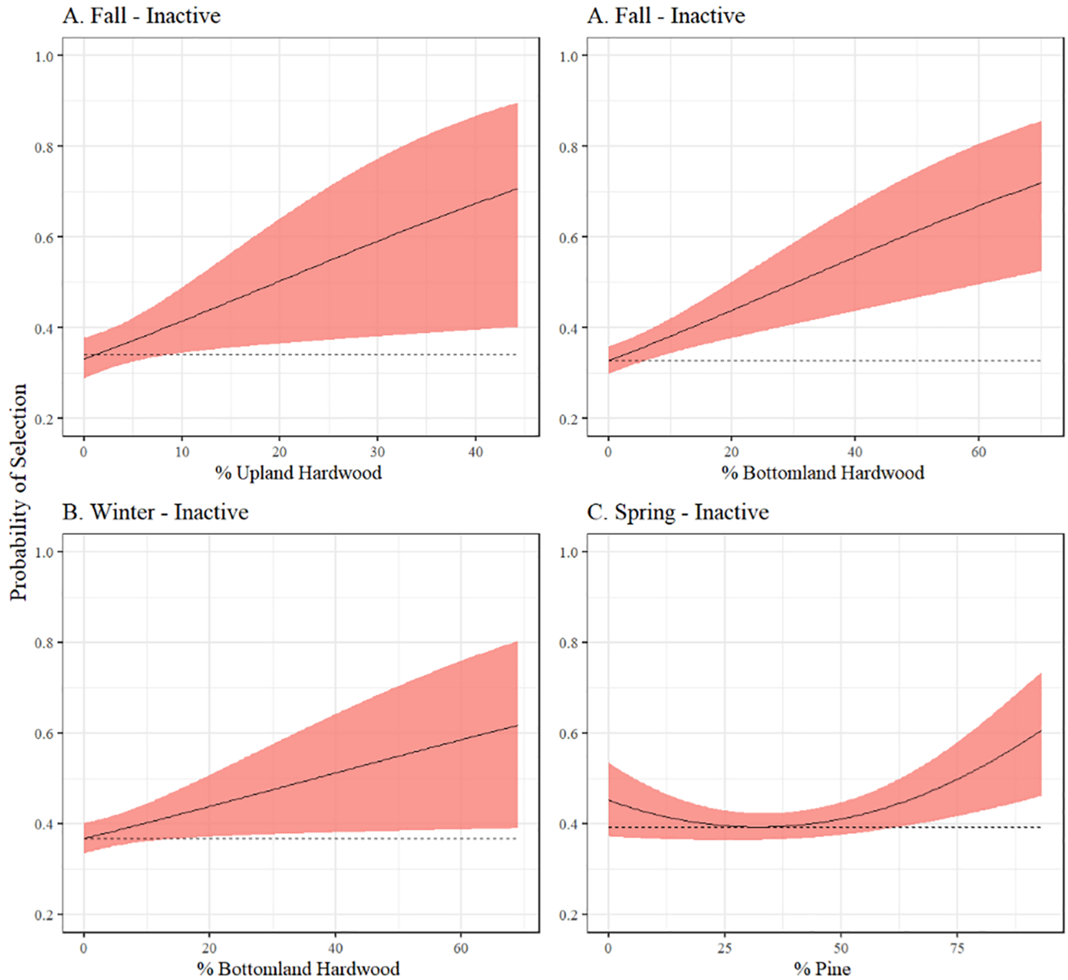

Fig. 6. Probabilities and 95% CI for inactive white-tailed deer step selection based on significant overstory predictors. Fort Bragg Military Installation, North Carolina, USA, 2011–2013. All figures were generated with all other variables held at their respective median values. The dashed horizontal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

species and freshly sprouted forbs (Lay, 1965; Lay, 1969; Short et al., 1975; 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 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 shown to make excursions beyond their normal home range during the breeding season (Kolodzinski et al., 2010). Regardless of variation from season, deer activity, or topographic position, deer consistently selected 20–75% understory cover. Importantly, the resolution of our metric of understory cover precluded the detection of wiregrass, the predominant groundcover species in uplands, which provides no food or cover for white-tailed deer (Ramírez et al., 1997). Consequently, management for white-tailed deer must ensure adequate understory cover and forage other than wiregrass, regardless of overstory composition.

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. 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 reported 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 forb growth (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). Conversely, pine overstory had little effect on selection in bottomlands, but deer consistently avoided uplands with < 13% pine overstory. However, the largest proportion of areas lacking pine overstory on our study site were large, open areas lacking understory cover and subject to frequent anthropogenic disturbance such as drop zones, landing strips, artillery firing points, or the central areas of artillery impact zones denuded of vegetation by repeated shelling.

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 (*Phytolacca* spp.), or *Eupatorium* spp.

rather than the evergreen browse of swamp bay (*Persea palustris*), dwarf huckleberry (*Gaylussacia dumosa*), inkberry, or gallberry common in bottomlands (Lashley et al., 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, 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, likely because these areas contained dense woody understory that provides critical cover, even at high levels of overstory cover.

5. 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 managers can improve habitat quality for white-tailed deer in longleaf pine woodlands by maintaining 20–50% canopy closure of which 4–12% represents important mast-bearing hardwoods. However, managers should remain cognizant that > 50% canopy closure will suppress understory cover and influence composition, especially at sites with low-quality soils. In addition, we suggest 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 managers interested in white-tailed deer conservation consider altering fire regimes and allowing longer intervals between fire (≥ 3 years) in some burn units to allow for greater woody understory development, persistence of mature upland hardwoods, and overall heterogeneity across the landscape (Lashley et al., 2014; Lashley et al., 2015a).

CRediT authorship contribution statement

Anthony J. Kroeger: Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization. **Christopher E. Moorman:** Conceptualization, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Marcus A. Lashley:** Methodology, Resources, Data curation, Writing - review & editing. **M. Colter Chitwood:** Methodology, Resources, Data curation, Writing - review & editing. **Craig A. Harper:** Conceptualization, Validation, Writing - review & editing, Supervision. **Christopher S. DePerno:** Conceptualization, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1
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 A2

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 A3

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 A4
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 A5
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 A6
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 A7
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 A8
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

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