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Microhabitat features influencing habitat use by Florida black bears

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ABSTRACT

Understanding fine-scale habitat needs of species and the factors influencing heterogeneous use of habitat within home range would help identify limiting resources and inform habitat management practices. This information is especially important for large mammals living in fragmented habitats where resources may be scarcer and more patchily distributed than in contiguous habitats. Using bihourly Global Position System (GPS) location data collected from 10 individuals during 2011–2014, we investigated microhabitat features of areas within home ranges that received high vs. low intensity of use by Florida black bears (*Ursus americanus floridanus*) in north-central, Florida. We identified areas receiving high and low levels of use by bears based on their utilization distributions estimated with the dynamic Brownian bridge movement model, and performed vegetation sampling at bear locations within high- and low-use areas. Using univariate analyses and generalized linear mixed models, we found that (1) canopy cover, visual obstruction, and hardwood density were important in defining high-use sites; (2) the probability of high use was positively associated with principal components that represented habitat closer to creeks and with high canopy and shrub cover and higher hardwood densities, likely characteristic of forested wetlands; and (3) the probability of high use was, to a lesser extent, associated with principal components that represented habitat with high canopy cover, high pine density, and low visual obstruction and hardwood density; likely representing sand pine and pine plantations. Our results indicate that the high bear-use sites were in forested wetlands, where cover and food resources for bears are likely to occur in higher abundance. Habitat management plans whereby bears are a focal species should aim to increase the availability and quality of forested wetlands.

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1. Introduction

Habitat selection studies often focus on selection of home ranges from within the larger geographic area or selection of habitat types within a home range (second- and third-order selection, respectively; Johnson, 1980). However, even within those habitat types, an animal may select certain areas more than others based on the microhabitat features (fourth-order

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selection; Johnson, 1980). Investigating a species' habitat requirements at multiple scales may have important management implications because animals may select for certain habitat features at fine scale that could be obscured at larger spatial scales (and vice versa; George and Zack, 2001). Therefore, an understanding of the fine-scale structural features that influence animal-use of habitat could provide information pertinent to management of forested habitats for the conservation of forest-dependent wildlife. Indeed, management plans that provide specific information about habitat requirements at multiple scales are likely to be successful (Freemark et al., 1995). With the technological advances (e.g., Global Positioning System [GPS] tracking), we now have the capability to investigate how animals use the landscapes in more detail (e.g., Rayl et al., 2014).

An animal's memory of, and selection for, microhabitat features may explain the formation of their home ranges (Spencer, 2012). Because large carnivores often occur at low densities and require relatively large home ranges, an understanding of microhabitat features that influence the areas that they use most often may have important management implications, especially in fragmented landscapes where resources tend to be scarce and patchily distributed (Gittleman and Harvey, 1982; Noss et al., 1996).

It is well known that black bears (*Ursus americanus*), like many other animal species, use habitat within their home-ranges heterogeneously (Horner and Powell, 1990; Hellgren et al., 1991; Benson and Chamberlain, 2007; Moyer et al., 2008). However, studies examining the microhabitat features that influence selective use of certain areas within their home ranges are rare. Our objective was to discern the structural and compositional features of the microhabitat associated with areas of high- and low-use by a population of Florida black bears (*U. a. floridanus*) in a fragmented landscape of north-central Florida (Florida Fish and Wildlife Conservation Commission, 2012; Karelus, McCown, Scheick, van de Kerk, and Oli, 2016). We expected that areas of high bear-use would be characterized by greater canopy cover, more visual obstruction, greater density of hardwoods, and more shrub cover of food plants than low-use sites. We also expected that high-use sites would typically be closer to creeks and farther from major roads than low-use sites.

2. Methods

2.1. Study area

Our study site was located in north-central Florida, U.S.A. at Camp Blanding Joint Training Center and the surrounding private lands, encompassing a total area of approximately 315 km². The area contains a diverse array of natural land cover types, including forested wetlands, mesic flatwoods, mixed hardwood hammocks, sand hill uplands, and scrub. The north and south forks of Black Creek begin in the area. The north fork is an outflow from Kingsley Lake on Camp Blanding, and the south fork is formed from several small streams from sandhill seepages and wetlands on Camp Blanding and the surrounding private lands. Black Creek is a tributary to the St. Johns River. Natural land-cover types are fragmented by roads, tree plantations, agriculture, and rural and urban land-use. Land-cover types in the area are described in detail by Karelus et al. (2016).

Camp Blanding lands were jointly managed by the Florida Department of Military Affairs and Florida Fish and Wildlife Conservation Commission. The area is managed for several species, including gopher tortoises (*Gopherus polyphemus*), the federally endangered red-cockaded woodpecker (*Picoides borealis*) (Gregory et al., 2006), and, more recently, for Florida black bears (Karelus, McCown, Scheick, van de Kerk, and Oli, 2016). Camp Blanding also supports several other wildlife species, including the endemic Black Creek crayfish (*Procambarus pictus*), the federally threatened eastern indigo snake (*Drymarchon couperi*), Sherman's fox squirrel (*Sciurus niger shermani*), and the federally threatened wood stork (*Mycteria americana*) (Gregory et al., 2006). Additionally, white-tailed deer (*Odocoileus virginianus*) and turkey (*Meleagris gallopavo*) are popular game species throughout the study site.

2.2. Bear captures and GPS data collection

We trapped bears with Aldrich spring-activated foot snares using a double anchor cable set (Scheick et al., 2009) in the summers of 2011 and 2012. We anesthetized bears with Telazol[®] (3.5–5 mg/kg), fit them with Lotek WildCell MG GPS collars and released them on site. All animals were captured and handled by Florida Fish and Wildlife Conservation Commission biologists, consistent with agency protocols and with the American Society of Mammalogists guidelines (Sikes et al., 2016). We set the collars to collect GPS coordinates of the bears' location every 2 h. The collars were accurate to a 20.3-m radius for 95% of the locations (Karelus, McCown, Scheick, van de Kerk, and Oli, 2016).

2.3. Identification of high- and low-use areas within home ranges

To identify the areas of high- and low-use by bears, we used each bear's bihourly GPS locations to estimate their respective utilization distributions (UD) using a dynamic Brownian bridge movement model (DBBMM; Kranstauber et al., 2012). We used DBBMM because it incorporates the temporal structure of GPS data and estimates utilization distributions based on the animal's movement trajectory (Dray et al., 2010; Kranstauber et al., 2012; Byrne et al., 2014). We defined the 50% contour of each bear's DBBMM as that bear's high-use area and the area between the 75% and 99% contours of each bear's DBBMM as their low-use area (Fig. 1). We then randomly chose 10–13 of the respective bear's GPS locations from within their high-use area and 10–13 of their GPS locations from within their low-use area. If two randomly chosen locations were within 50 m from each other, either from the same bear or two different bears, we randomly selected a different location to avoid sampling

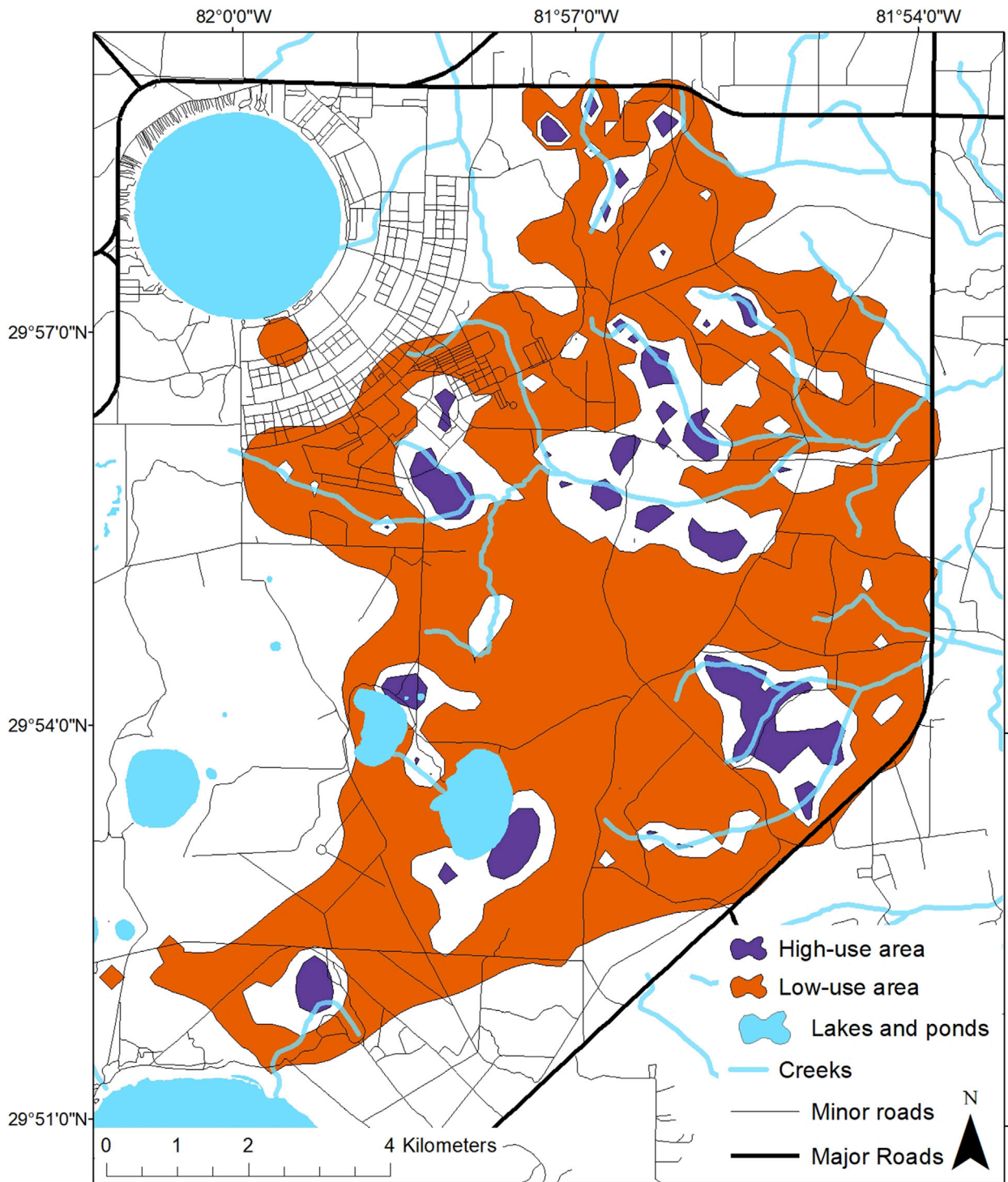


Fig. 1. Map of the dynamic Brownian Bridge movement model utilization distribution for a representative female Florida black bear (*Ursus americanus floridanus*) at different levels of utilization, indicated by percent contours. Bear GPS locations within the 50% contours were designated as high-use and the locations in the area between the 75% and 99% contours were designated as low-use.

the same area twice. If the area around the initial bear location had been burned or cleared since the time the GPS location was obtained, we selected a new bear location randomly from the respective bear's locations and use-category.

We estimated the DBBMMs with the R package 'move' (Kranstauber and Smolla, 2016) and converted the UD contours to GIS shapefiles for visualization in ArcMap (Version 10.4; ESRI, 2016) using the R package 'mapproj' (Bivand and Lewin-Koh,

2016). Additionally, randomly selected bear locations were chosen using R software (Version 3.3.1; R Core Team, 2016. <http://www.r-project.org/>).

2.4. Vegetation sampling

At each selected location, we performed detailed vegetation sampling to collect data on canopy cover, visual obstruction, tree density, and understory vegetation. Sampling occurred during March–July 2016. Given the mild climate in Florida, seasonal variation in vegetative characteristics was insubstantial. We measured canopy cover in each cardinal direction with a spherical densiometer (Lemmon, 1956). We measured the visual obstruction in each cardinal direction using a 2-m-tall cover board that was divided into 4 sections, each 0.5 m tall (Coulloudon et al., 1999). The cover board was vertically held 15 m away from the central point and the proportion of visible space on the board was estimated while kneeling to approximate bear-eye level. To quantify tree density, we used the point center quarter method (PCQ; Cottam and Curtis, 1956; Mueller-Dombois and Ellenberg, 1974) and measured the distance from the center point to the nearest pine and hardwood in each of the 4 cardinal quadrants (northeast, southeast, southwest, northwest). We recorded the tree species and measured its diameter at breast height (DBH at 130 cm from the ground) if ≥ 4 cm DBH. If no tree was located within 65 m of the point within a quadrant, we treated it as a missing value for that quadrant. To investigate understory vegetation composition, we made a 4 × 4 m plot at each site, using the point as the southwest corner of the plot. We recorded each plant species present inside the plot and estimated the percent cover and maximum height (excluding height for vines) of each respective species in the plot. We did not distinguish among species within the families of *Cyperaceae* (sedges), *Poaceae* (grasses), or *Juncaceae* (rushes), and instead grouped these into one category of Poales.

We calculated the distance from each sampling location to the nearest major road, minor road, and creek using the R package rgeos (Bivand and Rundel, 2016) and shapefiles obtained from the Florida Geographic Data Library (<http://www.fgdl.org/>). Major roads included Class 1 roads (interstates and U.S. highways) and Class 2 roads (state roads). Minor roads included Class 3 roads (larger roads or streets in residential areas) and Class 4 roads (smaller roads or streets in residential areas).

2.5. Statistical analyses

For the measures of canopy cover and visual obstruction, we averaged the estimates from each cardinal direction for each site. Using the DBH data, we calculated the absolute tree density per hectare for conifers and hardwoods using the Cottam et al. (1953) method and the correction factor proposed by Warde and Petranka (1981) (Mitchell, 2015). We transformed percent canopy cover, percent visual obstruction, and the percent cover for each species in the plot with an arcsine square root transformation (Sokal and Rohlf, 2011). We classified shrub species into two categories, food and non-food shrubs, based on species that have been found in bear diets (Maehr and Brady, 1984; Dobey et al., 2005) or those with fleshy fruits likely eaten by bears (e.g., *Asimina* spp. [paw paw], *Diospyros virginiana* [persimmon], *Prunus umbellata* [wild plums]).

We calculated summary statistics for each covariate and compared them between high- and low-use sites with nonparametric Wilcoxon rank sum tests (Conover, 1999). Using generalized linear mixed effect models (GLMM; Zuur et al., 2009) with binomial distribution, we tested for the effect of individual habitat covariates on the probability of high-use. Because of multi-collinearity among several covariates, we could not use the original habitat variables to test for the additive and interactive effects of habitat variables. Thus, we used principal components analysis (PCA) to reduce data dimensionality and to combat problems associated with correlated explanatory variables (Graham, 2003; Manly and Alberto, 2017). We used the first four principal components (PCs) as explanatory variables in GLMM with a binomial response (high-use = 1, low-use = 0), a random effect of individual bear, and fixed effect of PC1–PC4, and their additive effects. We selected the most parsimonious model using an Information Theoretic approach with Akaike's information criterion (AIC; Burnham and Anderson, 2002). We used the conditional coefficient of determination ($R^2_{\text{GLMM}(c)}$; Nakagawa and Schielzeth, 2013) for assessing the fit of the resulting most parsimonious model. To test for seasonal differences, we repeated the GLMMs with PCs as covariates for bear locations obtained in the summer (May 01–August 31) and the fall (September 1–December 31) separately; data were insufficient data to perform similar analysis using winter locations. We used R (Version 3.3.1; R Core Team. <<http://www.r-project.org/>>, 2016) and the package 'lme4' for fitting GLMMs (Bates et al., 2015) and $R^2_{\text{GLMM}(c)}$ was calculated using the package MuMIn (Barton, 2015).

3. Results

We used GPS location data collected from 10 bears (5 females; 5 males; ages 1–9 years) during 2011–2014 for our analysis. The average size of an individual's high-use area (50% DBBMM contour \pm SE) spanning a timeframe of ca. 10–22 months was 5.10 ± 1.63 km² (range: 0.93–16.26) and contained an average of 1976.60 ± 229.52 bear-locations (range: 1119.00–3442.00). Together, high-use areas covered 8.16% (43.45 km²) of our study area (Fig. 2). The average high-use area for females was 2.08 ± 0.71 km² (range: 0.93–4.70) and contained an average of 2449.80 ± 297.78 bear-locations (range: 1839.00–3442.00), whereas the average high-use area for males was 8.12 ± 2.64 km² (range: 2.32–16.26) and contained an average of 1503.40 ± 190.85 bear-locations (range: 1119.00–2205.00). The average overall low-use area (99%–75% DBBMM contour) was 82.87 ± 22.02 km² (range: 11.11–202.20) and contained an average of 604.30 ± 42.10 locations (range: 439.00–797.00). Together, low-use areas covered 91.84% (489.33 km²) of our study area (Fig. 2). The average low-use area for females were

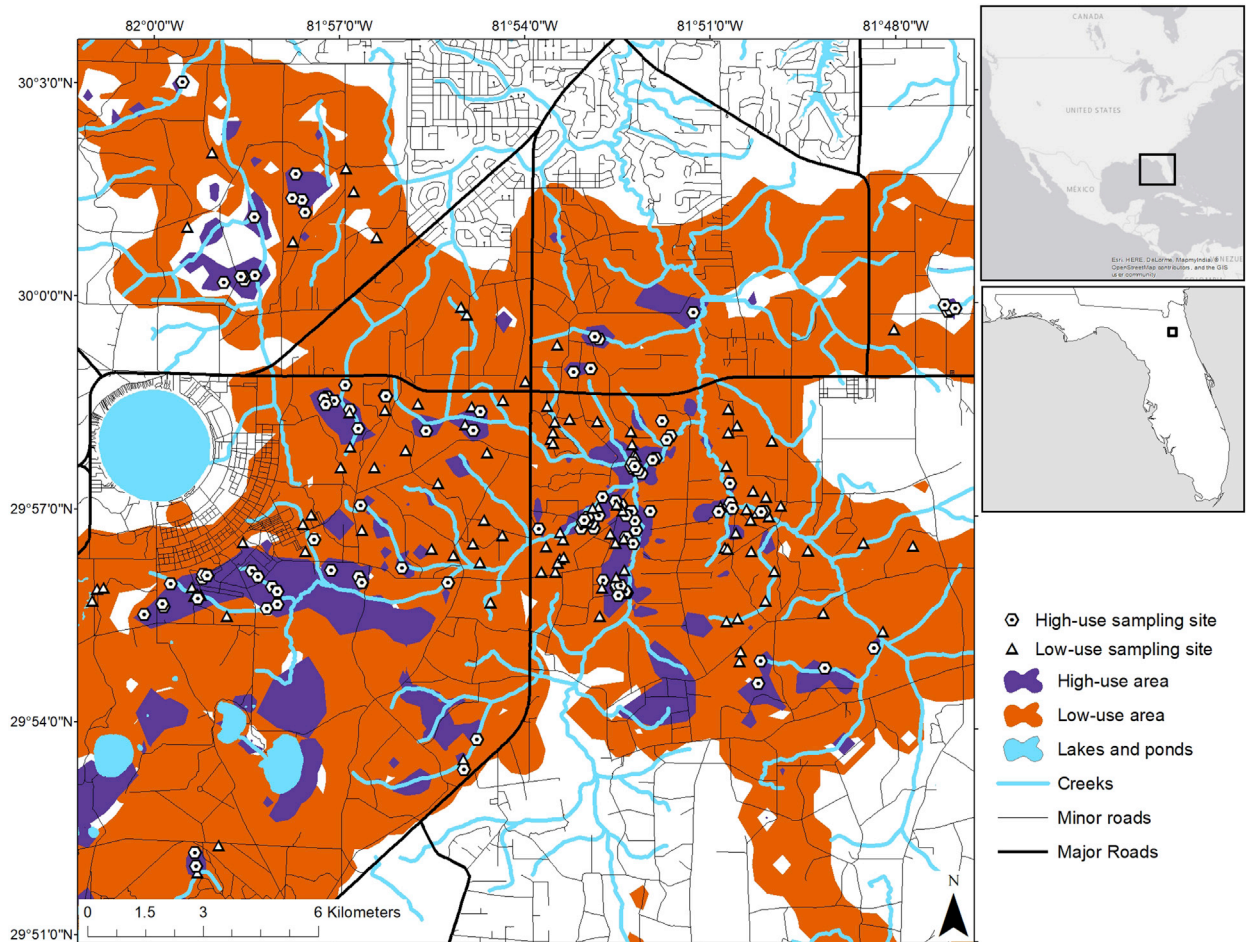


Fig. 2. Locations of vegetation sampling in high- and low-use areas for Florida black bears (5 F, 5 M) at Camp Blanding Joint Training Center and the surrounding private and state forest lands. Black lines indicate major roads. The dots and triangles represent the sampled locations, and the shaded areas represent the combined contours of the bears' utilization distributions estimated using dynamic Brownian Bridge movement models.

$29.72 \pm 8.87 \text{ km}^2$ (range: 11.11–62.98) and contained an average of 577.20 ± 72.03 locations (range: 439.00–764.00); the average low-use area for males was $136.02 \pm 26.27 \text{ km}^2$ (range: 63.22–202.20) and contained an average of 631.40 ± 49.18 locations (range: 519.00–797.00).

We conducted vegetation sampling at 213 sites; 108 of these sites were considered high bear-use (39 in fall, 27 in summer, 42 in winter) and 105 were low bear-use (36 in fall, 52 in summer, 17 in winter; Fig. 2). Canopy cover, visual obstruction, and density of hardwoods and, marginally, of conifers, were greater in areas of high bear-use than in areas of low bear-use ($p \leq .05$ for all; Table 1; Figs. 3 and 4). Additionally, high-use sites were farther from minor roads and closer to creeks than low-use sites ($p \leq .05$; Table 2) but there was no significant difference in distance to major roads between high- and low-use sites ($p \geq .05$; Table 2).

We recorded 41 hardwood species and seven conifer species. Almost all conifers were pines (Table S1). The most common conifer across all sites was *Pinus elliotti* (slash pine; present in 49.77% of all sites, 44.44% of high-use sites, and 55.24% of low-use sites) but the most common conifer in high-use sites was *Pinus taeda* (loblolly pine; present in 35.21% of all sites, 49.07% of high-use sites, and 20.95% of low-use sites); 23.00% of all sites had no pine trees within 60 m (Table S1). The most common hardwood species in high-use sites were *Quercus nigra* (water oak; present in 34.74% of all sites, 33.33% of high-use sites, and 36.19% of low-use sites), *Gordonia lasianthus* (loblolly bay; present in 26.29% of all sites, 32.14% of high-use sites, and 20.00% of low-use sites), and *Nyssa* sp. (tupelo; present in 19.72% of all sites, 25.93% of high-use sites, and 13.33% of low-use sites). A complete list of tree species found in high- and low-use plots is presented in Table S1.

We documented 155 (and another 15- unidentified) understory plant species (not including the unknown number of species within the Poales group; Table S2). The most common understory species found across all sites were *Smilax* spp. (greenbrier; present in 73.24% of all sites, 70.37% of high-use sites, and 73.24% of low-use sites), *Vitis rotundifolia* (muscadine grape; present in 50.2% of all sites, 60.2% of high-use sites, and 40.0% of low-use sites), and *Serenoa repens* (saw palmetto;

Table 1

Averages (\pm SE) of vegetation measures from high and low bear-use sites in the Camp Blanding area. N represents the number of sampled locations. Canopy cover is the percent canopy cover as measured with a spherical densitometer and averaged for each site among measures from the four cardinal directions. Visual obstruction represents the percent of a 2 m tall coverboard obstructed by vegetation and averaged at each site among the four cardinal directions. Absolute density of pines and hardwoods represents the average density of trees as measured by the Point-Center Quartered Method. Wilcoxon Rank Sum tests were used to test for differences between high-to low-sites for the overall measures; *W* indicates the rank-sum and $p < .05$ was considered significant.

		Averages \pm SE					
	N	Canopy cover	Visual Obstruction	Absolute Density Pines (trees/hectare)	Absolute Density Hardwoods (trees/hectare)	Shrub cover food species	Shrub cover non-foods
High	108	0.95 \pm 0.01	0.81 \pm 0.02	355.72 \pm 91.49	1023.75 \pm 91.83	107.86 \pm 5.24	56.82 \pm 3.76
Low	105	0.79 \pm 0.03	0.66 \pm 0.03	346.59 \pm 53.90	872.09 \pm 154.11	82.17 \pm 4.73	58.17 \pm 4.10
		<i>W</i>	7434	4804	6962	7034.5	6376
		<i>p</i>	<0.0001	0.05	0.004	0.002	0.12
Female							
High	53	0.94 \pm 0.02	0.83 \pm 0.02	180.59 \pm 59.70	1128.71 \pm 134.89	112.94 \pm 7.62	59.58 \pm 4.90
Low	50	0.84 \pm 0.02	0.67 \pm 0.04	334.40 \pm 64.87	1132.72 \pm 301.86	84.34 \pm 6.67	65.20 \pm 5.72
Male							
High	55	0.96 \pm 0.01	0.80 \pm 0.03	524.48 \pm 167.89	922.61 \pm 124.65	102.96 \pm 7.22	54.16 \pm 5.69
Low	55	0.74 \pm 0.05	0.65 \pm 0.04	357.68 \pm 84.89	635.15 \pm 99.85	80.20 \pm 6.74	51.78 \pm 5.76

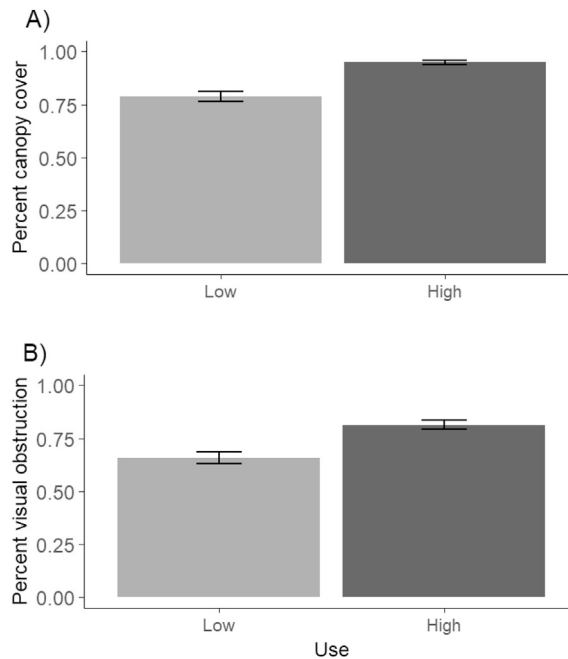


Fig. 3. Average (\pm SE) A) percent canopy cover and B) visual obstruction from sites of high and low black bear-use in the Camp Blanding area. A value of 1 represents 100% cover and a value of 0% indicates no cover.

present in 46.5% of all sites; 52.8% of high-use sites, and 40% of low-use sites; Table S2). Of the most commonly occurring understory species, those that were more abundant in high-use areas were saw palmetto, *Lyonia lucida* (fetterbush), *Ilex coriacea* (sweet gallberry), muscadine grape, *Persea* spp. (bays), and *Vaccinium corymbosum* (highbush blueberry; Fig. 5; Table S2). Understory plant species that were more abundant in low-use sites included the group of species in the order Poales and *Ilex glabra* (bitter gallberry; Fig. 5; Table S2). Cover of food plants was greater in high-use sites than in low-use sites ($W = 7034.5$, $p = .002$; Fig. 6; Table 1), whereas cover of non-food plants did not differ between high- and low-use sites ($W = 5594$, $p = .87$; Fig. 6; Table 1).

Examining the effect of the individual habitat variables, the probability of high-use was positively influenced by canopy cover, visual obstruction, food shrub cover, and distance to minor roads; it was negatively influenced by distance to creek. Other variables did not significantly influence the probability of high-use black bears (Table 3).

Several of the habitat covariates were significantly correlated with each other (Table 4). Principal components (PC) analysis (Table 5) indicated that: (1) PC1 was positively correlated with canopy cover, visual obstruction, shrub cover (both food and non-food plants), hardwood density, and negatively correlated with pine density and distance to creeks; (2) PC2 was

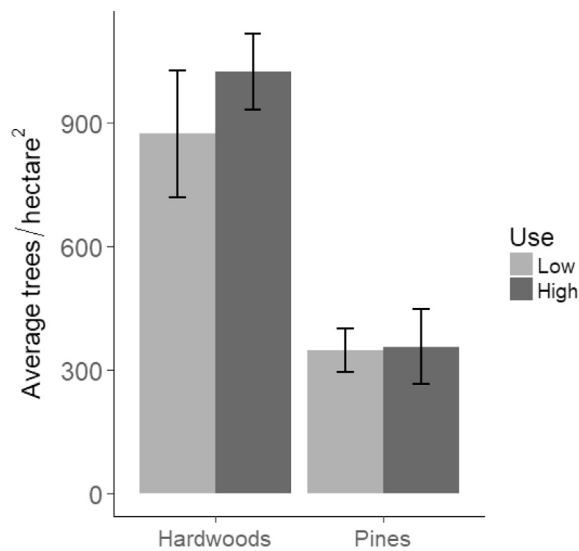


Fig. 4. The absolute density (\pm SE) of hardwood and pine trees in high- and low-bear-use sites in the Camp Blanding area. Density was calculated from measures of diameter at breast height of trees collected using the Point Center Quartered Method.

Table 2

Average distances (\pm SE) from the sampled bear locations to major roads, minor roads, and creeks for high and low bear-use sites in the Camp Blanding area. *N* represents the number of locations sampled. Wilcoxon Rank Sum tests were used to test for differences between high-to low-sites for the overall measures; *W* indicates the rank-sum and $p < .05$ was considered significant.

		<i>N</i>	Average distances \pm SE (m)		
			Major roads	Minor roads	Creeks
	High	108	2481.68 \pm 154.53	306.93 \pm 16.84	222.56 \pm 22.17
	Low	105	2327.16 \pm 141.42	232.87 \pm 18.89	346.47 \pm 29.90
			<i>W</i>		
			6128	7253	4143
			<i>p</i>	<0.001	<0.001
Female	High	53	2036.87 \pm 138.04	326.80 \pm 21.35	150.35 \pm 18.75
	Low	50	2245.70 \pm 199.99	216.39 \pm 22.02	307.70 \pm 33.73
Male	High	55	2910.31 \pm 230.64	287.77 \pm 25.83	292.15 \pm 37.45
	Low	55	2401.21 \pm 233.65	247.86 \pm 30.05	381.72 \pm 47.97

positively correlated with visual obstruction, pine density, cover of food and non-food plants, and distance to creeks and was negatively correlated with canopy cover and hardwood density; (3) PC3 was positively correlated with visual obstruction and was negatively correlated with canopy cover, hardwood density, and pine density; (4) PC4 was positively correlated with canopy cover and pine density, and was negatively correlated with visual obstruction and hardwood density. PC1-PC4 cumulatively explained 70% of variance in the data (Table 5).

The GLMMs using 1 PC at a time as a predictor variable indicated that the probability of high-use of an area by bears was positively affected by PC1, PC2, and PC4, and negatively affected by PC3 (Tables 6 and 7). The most parsimonious GLMM testing for the singular and additive effects of PCs included an additive effect of PC1 and PC4 and had an $R^2_{GLMM(C)}$ of 0.226. Based on this model, both PC1 and PC4 positively affected the probability of high-use. The second ranked model included an additive effect of PC1, PC3, and PC4. Based on coefficients from this model, the effect of PC1 and PC4 remained the same but PC3 negatively influenced the probability of high-use (Tables 6 and 7). Repeating the GLMM models seasonally, we found that the most parsimonious model for summer included an additive effect of PC1 and PC3, whereas that for fall included an additive effect of PC1 and PC4 (Table 6). The pattern of influence of the PCs was similar to that reported for the overall analyses.

4. Discussion

Bears are expected to forage optimally for resources and to use some patches within their home ranges more than others because resources are temporally and spatially isolated across the landscape (Mitchell and Powell, 2012). However, why bears

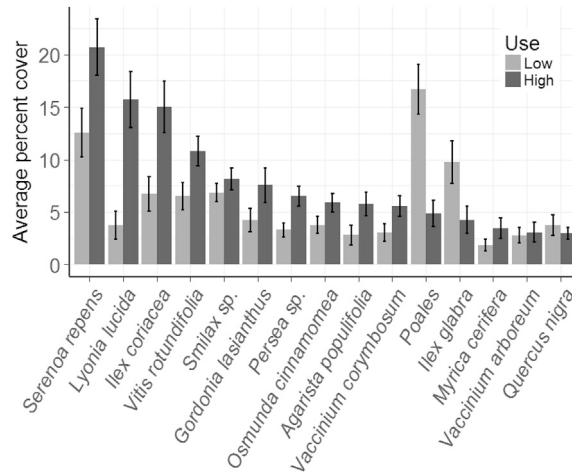


Fig. 5. The average (\pm SE) percent cover by 15 of the most common species found in the shrub layer in 4×4 m plots in high- and in low-use sites used by bears in the Camp Blanding area. If a species was not present in the shrub layer in a plot, we inserted a value of 0 for the cover within the plot for that species; therefore, the averages were calculated including a large number of zeros and do not represent a measure of the actual amount of cover found when a species was present. A list of all species, total percent cover, percent cover when present, and percent of plots where they were present is provided in [Supplemental Information Table 1](#).

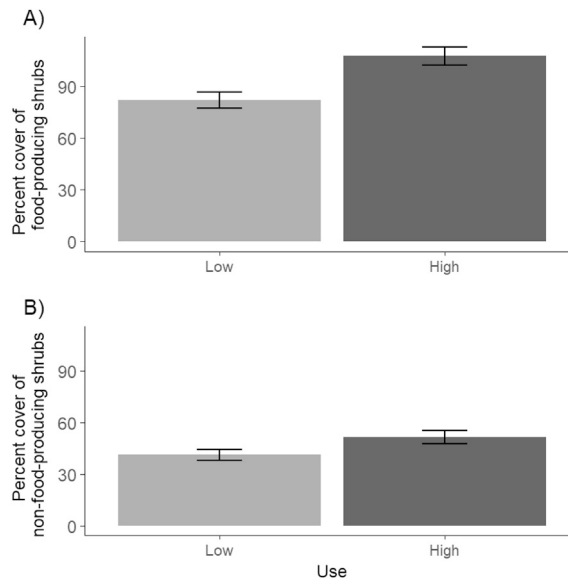


Fig. 6. The average percent cover (\pm SE) of A) food producing shrubs and B) non-food producing shrubs within 4×4 m plots at high- and low-use bear sites in the Camp Blanding area of north-central Florida. Values amounted to more than 100% because cover of individual species was estimated within the plot and these were then added together when concatenating data into food-producing shrubs and non-food producing shrubs.

use some areas within their home ranges more than others of the same habitat type remains unclear, but the structural and compositional aspects of the habitat driving these patterns may help identify limiting resources for bears. Thus, we sought to discern structural and compositional microhabitat features of habitat patches receiving high bear-use. We expected that high-use sites would have more canopy cover, more visual obstruction, and a higher density of hardwood trees because of the importance of escape cover, saw palmetto across all seasons, and mast producing tree species for bears. Our results supported these expectations. Consistently, high-use sites had greater than 90% closed canopies and greater than 80% visual obstruction; both much greater than in low-use sites. Cover is an important component of bear habitat (Brady and Maehr, 1985; Wooding and Hardisky, 1994; Stratman et al., 2001; van Why, 2003; Mitchell and Powell, 2012) and is likely important to reduce disturbance from other bears or humans (Mitchell and Powell, 2012) and possibly to aid in thermoregulation (Stratman et al., 2001; Fecske et al., 2002; Lyons et al., 2003).

Table 3

Results of generalized linear mixed models testing for the effect of individual habitat covariates on the probability of high-use by black bears (*Ursus americanus floridanus*) in north-central Florida. Regression coefficients testing for the effect of each habitat covariate on the probability of high-use are presented along with the associated significant level (*P*).

Variable	Coefficient ±SE	<i>P</i>
Canopy cover	3.37 ± 0.68	<.001
Visual obstruction	1.73 ± 0.44	<.001
Creek	−0.002 ± 0.001	.003
Food shrub cover	0.490 ± 0.16	.002
Minor roads	0.002 ± 0.001	.005
Non-food shrub cover	0.29 ± 0.18	.09
Hardwood density	0.96 ± 1.15	.405
Major roads	0.001 ± 0.001	.459
Pine density	0.15 ± 1.77	.932

Table 4

Pairwise correlation between habitat variables. Significance levels (*p* values) are given in parenthesis. Bold type face indicates significant correlation.

	Canopy cover	Visual obstruction	Hardwood density	Pine density	Food shrub cover	Non-food shrub cover	Major roads	Minor roads	Creeks
Canopy cover									
Visual obstruction	0.29 (< 0.001)								
Hardwood density	0.34 (< 0.001)	0.17 (0.0122)							
Pine density	−0.01 (0.92)	−0.08 (0.255)	−0.13 (0.051)						
Food shrub cover	0.36 (< 0.001)	0.47 (< 0.001)	0.19 (0.006)	−0.11 (0.098)					
Non-food shrub cover	0.16 (0.021)	0.14 (0.035)	0.08 (0.224)	−0.08 (0.257)	0.17 (0.013)				
Major roads	0.03 (0.62)	0.09 (0.196)	−0.03 (0.646)	−0.09 (0.188)	0.06 (0.405)	0.12 (0.089)			
Minor roads	0.29 (<0.001)	0.28 (< 0.001)	0.11 (0.107)	−0.11 (0.106)	0.13 (0.052)	0.16 (0.023)	0.16 (0.020)		
Creeks	−0.35 (< 0.001)	−0.30 (< 0.001)	−0.17 (0.011)	0.25 (<0.001)	−0.19 (0.004)	−0.16 (0.022)	−0.15 (0.026)	−0.33 (< 0.001)	

Table 5

Principal component (PC) loadings from microhabitat variables measured at 213 Florida black bear locations in the Camp Blanding area. Only the first 4 principal components are shown here from 9 total PCs. Positive values indicate a positive loading of the variable on the PC and negative values indicate a negative loading on the PC. The amount of variance in the data explained by each PC is given as the Proportion of variance. The combined total of variance explained by the PCs in order is given by the Cumulative proportion.

Variables	PC1	PC2	PC3	PC4
Canopy cover	0.34	−0.21	−0.42	0.36
Visual obstruction	0.48	0.41	0.11	−0.10
Hardwood density	0.23	−0.28	−0.55	−0.13
Pine density	−0.15	0.47	−0.21	0.75
Distance to major roads	0.12	−0.22	0.60	0.27
Distance to minor roads	0.30	−0.28	0.19	0.42
Distance to creeks	−0.34	0.41	−0.10	−0.05
Cover of food shrubs	0.37	0.21	−0.17	−0.15
Cover of other shrubs	0.47	0.39	0.17	−0.11
Proportion of variance	0.33	0.13	0.13	0.11
Cumulative proportion	0.33	0.47	0.59	0.70

High-use sites were closer to creeks than low-use sites; this result was consistent with our expectation because bears move shorter distances when closer to creeks (Karelus, McCown, Scheick, van de Kerk, and Oli, 2016), and often select for forested wetland habitats within their home ranges (Weaver and Pelton, 1994; Stratman et al., 2001; Dobey et al., 2005; Takahata et al., 2014; Lewis et al., 2015; Duquette et al., 2017). Hardwood densities were greater in high-use sites than in low-use sites, indicating that the bears preferentially used forested habitats over other land-cover types. Additionally, several of the hardwood species that we recorded, such as oaks and tupelos, likely provide the bears with important sources of food from soft or hard mast. Tupelo drupes (more specifically, black gum, *N. sylvatica*) were important early fall foods for bears in the populations just north of the Camp Blanding area, in Osceola and Okefenokee National Forests (Dobey et al., 2005) and

Table 6

Model selection from generalized linear mixed models testing for the effect of principal components (PC) 1 through 4 on the probability of high-use by black bears (*Ursus americanus floridanus*) in north-central Florida for the A) the entire study period, B) and results using bear locations obtained during summer, and C) results using bear locations obtained in the fall. PC loadings are provided in Table 5. Models appear in order of the difference in the Akaike Information Criterion corrected for small sample sizes (ΔAICc). The difference in the log-likelihood from the top model (ΔLL), model probability (Weight), and the number of parameters (K) are also given.

	Rank	Model	K	ΔLL	ΔAICc	Weight
A) Overall	1	PC1 + PC4	4	0.00	0	0.43
	2	PC1 + PC3 + PC4	5	0.46	1.17	0.24
	3	PC1 + PC2 + PC4	5	0	2.09	0.15
	4	PC1 + PC2 + PC3 + PC4	6	0.47	3.29	0.08
	5	PC1	3	-3.39	4.7	0.04
	6	PC1 + PC3	4	-2.86	5.72	0.02
	7	PC1 + PC2	4	-3.39	6.77	0.01
	8	PC1 + PC2 + PC3	5	-2.86	7.82	0.01
	9	PC4	3	-15.44	28.8	0.00
	10	PC3 + PC4	4	-14.99	29.97	0.00
	11	PC2 + PC4	4	-15.41	30.82	0.00
	12	PC2 + PC3 + PC4	5	-14.94	31.97	0.00
	13	PC3	3	-17.66	33.25	0.00
	14	PC2	3	-18.04	34.01	0.00
	15	PC2 + PC3	4	-17.66	35.32	0.00
B) Summer	1	PC1 + PC3	4	0.00	0.00	0.24
	2	PC1	3	-1.15	0.08	0.23
	3	PC1 + PC2 + PC3	5	0.21	1.86	0.09
	4	PC1 + PC4	4	-1.01	2.02	0.09
	5	PC1 + PC3 + PC4	5	0.04	2.20	0.08
	6	PC1 + PC2	4	-1.11	2.22	0.08
	7	PC3	3	-2.75	3.28	0.05
	8	PC1 + PC2 + PC3 + PC4	6	0.29	4.05	0.03
	9	PC1 + PC2 + PC4	5	-0.92	4.12	0.03
	10	PC4	3	-3.74	5.25	0.02
	11	PC2 + PC3	4	-2.63	5.26	0.02
	12	PC2 + PC3	3	-3.79	5.36	0.02
	13	PC3 + PC4	4	-2.74	5.49	0.02
	14	PC12 + PC4	4	-3.71	7.42	0.01
	15	PC2 + PC3 + PC4	5	-2.63	7.54	0.01
C) Fall	1	PC1 + PC4	4	0.00	0.00	0.42
	2	PC1 + PC3 + PC4	5	0.38	1.54	0.20
	3	PC1 + PC2 + PC4	5	0.21	1.88	0.17
	4	PC1 + PC2 + PC3 + PC4	6	0.77	3.11	0.09
	5	PC1	3	-3.46	4.68	0.04
	6	PC4	3	-4.24	6.24	0.02
	7	PC2 + PC4	4	-3.27	6.55	0.02
	8	PC1 + PC2	4	-3.30	6.61	0.02
	9	PC1 + PC3	4	-3.44	6.88	0.01
	10	PC2 + PC3 + PC4	5	-2.96	8.23	0.01
	11	PC3 + PC4	4	-4.16	8.33	0.01
	12	PC1 + PC2 + PC3	5	-3.28	8.86	0.01
	13	PC3	3	-8.47	14.71	0.00
	14	PC2	3	-8.52	14.81	0.00
	15	PC2 + PC3	4	-8.47	16.94	0.00

Table 7

Estimates ($\pm\text{SE}$) of slope parameters, as well as 95% confidence intervals, for the fixed effects of the principal component loadings that were included in select generalized linear mixed models as indicated by their rank (Table 5).

Rank	Model	PC1	PC2	PC3	PC4
1	PC1 + PC4	0.52 \pm 0.10 (0.31, 0.72)	–	–	0.41 \pm 0.17 (0.09, 0.74)
2	PC1 + PC3 + PC4	0.52 \pm 0.10 (0.31, 0.72)	–	-0.14 \pm 0.15 (-0.44, 0.15)	0.41 \pm 0.17 (0.08, 0.75)
3	PC1 + PC2 + PC4	0.52 \pm 0.10 (0.31, 0.72)	-0.01 \pm 0.14 (-0.28, 0.26)	–	0.41 \pm 0.17 (0.08, 0.74)
4	PC1 + PC2 + PC3 + PC4	0.52 \pm 0.11 (0.31, 0.73)	-0.01 \pm 0.14 (-0.28, 0.27)	-0.14 \pm 0.15 (-0.44, 0.15)	0.41 \pm 0.17 (0.08, 0.74)
5	PC1	0.48 \pm 0.10 (0.29, 0.67)	–	–	–
9	PC4	–	–	–	0.35 \pm 0.16 (0.03, 0.66)
13	PC3	–	–	-0.11 \pm 0.13 (-0.37, 0.14)	–
14	PC2	–	0.01 \pm 0.12 (-0.23, 0.26)	–	–

for bears in other populations as well (Hellgren and Vaughan, 1988). In our study area, tupelos were more common at high-use sites than in low-use sites, so it is likely that bears in this area also rely on the tupelo drupes in the fall for sustenance. Acorns are an important food source for bears across their range (Dobey et al., 2005; Benson and Chamberlain, 2006; Reynolds-Hogland et al., 2007), but density of oaks did not differ substantially between high- and low-use sites. Whereas tupelos occur in forested wetlands, oaks occur in several different habitat types, including those with more open canopies and less visual obstruction, such as scrub. Several other hard- and soft-masting hardwood species occurred in our study area (e.g. *Carya* spp. [hickory species], *Cornus* spp. [dogwood species], persimmons, plums). Although bears eat fruits and nuts when available (Hellgren, 1993; Stratman and Pelton, 1999; Dobey et al., 2005; Inman and Pelton, 2011; Simek et al., 2012), these trees occurred infrequently in our study site. Densities of conifers, mostly loblolly pines, were marginally greater in high-use sites. Loblolly pines occur in a variety of habitats, including forested wetlands. However, a large portion of our study area is managed as slash pine plantation and thus, overall, slash pine was the most common species. Depending on how they are managed, stands of pine plantation typically provide only scattered food sources, but they do provide ample cover.

Several understory plant species that likely provide bears with food occurred more frequently in high-use sites, including saw palmetto, sweet gallberry, muscadine grape vine, and high bush blueberry. Bears in Florida rely heavily on saw palmetto for food throughout the year; they eat the fruits in the fall and winter and they eat the hearts of the palm in the spring (Maehr and Brady, 1984; Stratman and Pelton, 1999; Dobey et al., 2005). Indeed, we often found evidence of bears eating the hearts of the palmettos throughout our study site (D. Karelus, personal observation). Although saw palmettos occurred frequently in both high- and low-use sites in our study area, they were more common in high-use sites. Sweet gallberry, blueberries, and [to a lesser extent] muscadine grapes, were important foods for bears in the Okefenokee-Osceola system (Dobey et al., 2005) and at Eglin Air Force Base in the Florida panhandle (Stratman and Pelton, 1999). Given the frequency of sweet gallberries, high bush blueberries, and muscadine grapes in our high-use sites, they are likely important for bears in the Camp Blanding area as well. Throughout our study site, we also found several other species of berry-producing shrubs, including several other species of blueberry (*V. arboreum*, *V. myrsinites*, *V. stamineum*), huckleberries (*Gaylussacia dumosa* and *G. frondosa*), and blackberries (*Rubus* sp.) and also berry-producing vines of greenbrier species. These also species may have provided important food sources for bears (Maehr and Brady, 1984; Stratman and Pelton, 1999; Dobey et al., 2005; Belant et al., 2006; Mosnier et al., 2008; Baldwin and Bender, 2009; Hertel et al., 2016), but they were generally equally as common in both high- and low-use sites. We expected that the amount of shrub cover by potential food plants would be important for characterizing high-use sites (e.g., Mitchell and Powell, 2012). Indeed, we found that high-use sites had a greater amount of shrub cover by food-producing plants but that cover of non-food producing plants did not differ between high- and low-use sites.

Results of GLMMs testing for the effect of each habitat variable indicated that high-use sites were generally characterized by high canopy cover, high visual obstruction, high cover of food-producing shrubs, and closer to the creeks but farther away from roads. These results are generally consistent with those obtained from univariate analyses, and thus re-inforce the importance of these habitat features.

When there are many explanatory variables, multicollinearity can cause computational problems and yield results that may be difficult to interpret (Graham, 2003). To avoid these issues, we performed PCA to investigate how the suite of microhabitat features jointly influenced the probability of high-use by bears. Based on the PC loadings, the first PC identified sites with high canopy cover and high visual obstruction, dense hardwoods, proximity to creeks; these are characteristics of forested wetlands. The fourth PC characterized sites with high canopy cover and high pine density, and low shrub cover; this is indicative pine plantation and sand pine forest. Together PC1–PC4 explained 70% of the variation in the microhabitat data.

Using GLMMs with PC1–PC4 as explanatory variables, we modeled the probability of high-use by bears. Considered individually, PC1 and PC4 positively influenced the probability of high-use; the effect of PC2 and PC3 was negligible, but generally negative. The most parsimonious GLMM included PC1 and PC4, both of which positively affected high-use; indicating that, within their home ranges, bears preferentially use forested wetlands, targeting sites with high understory cover and abundance of potential food sources. The fact that PC1 was included in the top model for overall as well as seasonal analyses highlight the fact that black bears in our study site intensively use forested wetlands during all seasons.

Our findings regarding forested wetlands are consistent with conclusions from black bear habitat selection studies at our study site at second- and third-order scales and elsewhere in the southeastern United States (Stratman et al., 2001; Dobey et al., 2005; Karelus, McCown, Scheick, van de Kerk, and Oli, 2016). A previous study showed that bears in this area did not select for pine plantations at the second- or third-order scales (Karelus, McCown, Scheick, van de Kerk, and Oli, 2016). Bears in Ocala National Forest, located south of our study site, selected for sand pine forests in the summer (Moyer et al., 2008). Sand pine forest and pine plantations may afford bears with escape cover; however, we note that all high bear-use sites that were in pine plantations were close to edges of the plantation adjacent to forested wetlands. Therefore, bears' use of pine plantations may potentially reflect the fact that they are generally juxtaposed to forested wetlands (Karelus, McCown, Scheick, van de Kerk, and Oli, 2016), though pine plantations with understory growth may afford bears with some food sources (e.g., blueberries and saw palmettos). Our results show bears in our study site show strong preference for forested wetlands with high canopy and shrub cover and with an abundance of food-producing understory plant species; they use open habitats (e.g., savannas) rather infrequently.

Animals are likely to use different habitats depending on the activity in which they are engaging (Lima and Zollner, 1996; Morales and Ellner, 2002; Nathan et al., 2008; Ordiz et al., 2011; Abrahms et al., 2016). Bears may use low-use areas primarily for traveling and high-use areas for foraging or resting. We tested this idea by comparing step-lengths of bears while in low- vs. high-use areas. The mean (\pm SE) bi-hourly step length while in the high-use sites was 141.61 ± 33.67 m, compared to step

length of 659.20 ± 113.19 m, while in the low-use sites. High-use sites were generally associated with shorter-distance movements and the low-use sites were generally associated with longer-distance movements (Karelus, McCown, Scheick, van de Kerk, Bolker, and Oli, 2017). Therefore, we would expect that high-use sites were generally indicative of resting or intensive foraging sites, whereas the low-use sites were generally indicative of sites obtained while the bear was traveling. Thus, our results can also be considered in terms of the structural and vegetative features that influenced bears to use a site for resting or intensively foraging versus traveling.

5. Conclusions and management recommendations

Demographic parameters of large carnivore populations often reflect healthy habitat (Beschta and Ripple, 2012). It is, therefore, important to identify key habitat components such that management practices can be directed towards promoting the components of habitat that are critical to the target species. Our study showed that the best predictors of high-use of an area by black bears are proximity to creeks, high canopy and escape cover, high densities of hardwoods, and high abundance of potential food plants. Some high use sites were located in pine plantation and sand pine; however, most of these sites were in close proximity to forested wetlands (Fig. 2). Conservation planners should conserve forested wetlands, and enhance the diversity and abundance of hard- and soft-mast producing trees, and berry producing shrubs and vines across all habitat types (Hellgren et al., 1991; Hellgren and Vaughan, 1994). When managing forests for black bears, managers should be particularly mindful to take actions to promote growth and berry production of saw palmettos, especially in or near forested wetlands (Maehr et al., 2001). Additionally, conservation efforts should focus on preserving the linkages among forested wetlands afforded by creeks and riparian forests. Creeks and riparian forests generally have high conservation value in fragmented landscapes because they offer critical resources for many wildlife species, and provide connectivity across the landscapes (Naiman et al., 1993; Taulman and Smith, 2004; Keuroghlian and Eaton, 2008; Lees and Peres, 2008; Kniowski and Gehrt, 2014).

Supporting healthy populations of large carnivores in fragmented, human-dominated landscapes is challenging and will require cooperation among multiple agencies and private land holders. Nonetheless, managing forests for black bears is a worthy conservation goal, given their status as the largest terrestrial carnivore of Florida and their role as an umbrella species for biodiversity conservation (Simberloff, 1999; Karelus et al., 2017).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2017.e00367>.

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