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Adult bobcat (*Lynx rufus*) habitat selection in a longleaf pine savanna

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Abstract

Background: Pine savannas are primarily managed with frequent prescribed fire (≤ 3 years) to promote diversity of flora and fauna, and to maintain open, park-like conditions needed by species such as the endangered red-cockaded woodpecker (*Picoides borealis*). However, a knowledge gap exists in our understanding of bobcat (*Lynx rufus*) habitat selection in longleaf pine savannas and research is warranted to direct our future management decisions.

Methods: We examined bobcat habitat selection in a pine savanna managed with frequent fires at two spatial scales (i.e., study area boundary [hereafter, landscape scale]) and annual area of use [95% kernel density; local scale]), and assessed effects of prescribed fire on bobcat habitat selection. Specifically, we monitored 45 bobcats (16 males and 29 females) during 2001–2007.

Results: We found differential habitat selection by sex. At the landscape scale, female bobcats were closer to mixed pine-hardwoods, young pine, and secondary roads, but farther from mature pine and hardwoods stands relative to males. We found no difference in selection of agriculture, shrub-scrub, and primary roads between sexes. At the annual area of use scale, female bobcats were closer to secondary roads, but farther from agriculture and shrub-scrub relative to males. We found no difference in selection of mature pine, mixed pine-hardwoods, hardwoods, young pine, and primary roads between sexes. Bobcats primarily selected for stands burned ≤ 1.1 years post-fire.

Conclusions: Our results show that bobcats exploit a broad range of habitat types in pine landscapes managed with frequent fire and commonly use recently burned stands (≤ 1.1 year post-fire), suggesting prey in many areas of this system are at risk of bobcat predation. Additionally, we suggest land managers consider scale of selection by bobcats when developing habitat management strategies.

Keywords: Georgia, Habitat selection, *Lynx rufus*, *Pinus palustris*, Prescribed fire

Background

Longleaf pine (*Pinus palustris*) savannas historically occupied over 30 million hectares in the southeastern USA (Brockway et al. 2005, Van Lear et al. 2005). This unique ecosystem is considered one of the most biologically diverse in North America because it supports hundreds of species of flora and fauna (Alavalapati et al. 2002). Longleaf pine savannas were shaped over millennia by frequent, low-intensity fires ignited by man and lightning (Brockway et al. 2005, Van Lear et al. 2005). Today, longleaf pine savannas are primarily managed by frequent prescribed fires (≤ 3 years return interval) to reduce undesirable vegetation while stimulating growth and development of a diverse understory (Waldrop et al. 1992, Cain et al. 1998, Barnett 1999, Steen et al. 2013). Frequent fire enables pine savannas to support an abundant diversity of flora and fauna (Alavalapati et al. 2002, Van Lear et al. 2005). For example, approximately 40% of the 1600+ plant species (including many rare species) found in the Atlantic and Gulf coastal plains are found in longleaf pine savannas (Walker 1998).

Fire is the primary management tool in longleaf pine savannas and can increase understory plant species richness, diversity, and evenness (Brockway and Lewis 1997). Without fire disturbance, hardwood encroachment reduces plant diversity (Landers et al. 1995, Glitzenstein et al. 2012). Fire also benefits fauna found in this system including common game birds (e.g., eastern wild turkey [*Meleagris gallopavo silvestris*], northern bobwhite quail

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[*Colinus virginianus*]) and species of conservation concern (e.g., red-cockaded woodpeckers [*Picoides borealis*], gopher tortoise [*Gopherus Polyphemus*]). Frequent fire can also reduce foraging habitat for common avian nest predators such as raccoons (*Procyon lotor*; Jones et al. 2004), and thus, conservation practices that reduce use by predators may result in increased nest success.

Bobcats are the most widely distributed wild felid in North America, and population abundance is increasing in many regions (Roberts and Crimmins 2010). Additionally, bobcats are a top carnivore and a vital component of most terrestrial ecosystems in the USA. The role bobcats play as a predator of game animals is still poorly understood in many systems. For example, what role do bobcats play in ecosystem function including direct and indirect effects (i.e., predation risk) on game and non-game populations? Additionally, their value as a furbearer requires management attention, especially in the absence of other larger carnivores such as mountain lions (*Felis concolor*) and wolves (*Canis lupus*). Bobcats are also closely tied to their prey and have previously been recommended to serve as indicators of ecosystem health (Conner and Leopold 1996). However, further research is needed to understand bobcat ecology in pine savannas.

Bobcat space use is influenced by prey abundance, season, breeding behaviors, and intraspecific relationships (Chamberlain et al. 2003). Bobcats commonly select mature pine, young pine, hardwood, and agricultural habitat types albeit at different spatial scales (Conner and Leopold 1996, Chamberlain et al. 2003, Godbois et al. 2003a), and prey abundance has been shown to influence bobcat habitat selection (Miller and Speake 1978, Maehr and Brady 1986, Conner and Leopold 1996, Chamberlain et al. 2003, Godbois et al. 2003a). For example, bobcat prey items (e.g., small mammals; hispid cotton rat [*Sigmodon hispidus*]) were most abundant in early successional habitats containing woody debris and significant herbaceous growth, and least abundant in pine stands with high basal area and little ground-level debris (Chamberlain 1999). Coincidently, bobcats often select habitat types that support abundant small mammal communities (Conner and Leopold 1996, Chamberlain 1999). Additionally, hardwood stands are commonly used by bobcats for refugia (i.e., den sites, cover, protection from summer heat; [Hall and Newsome 1976, Godbois et al. 2003a]) or travel corridors between foraging patches (Godbois et al. 2003a), and are particularly important in pine-dominated landscapes (Conner et al. 1992, Conner and Leopold 1996, Chamberlain et al. 2003). Roads and other linear features are also considered important to bobcats as they also serve as travel corridors (Lovallo and Anderson 1996).

Multi-scale studies are important for understanding how patterns and processes interact and operate on the landscape and influence animal behaviors. Previous research has indicated that bobcat habitat selection occurs at multiple spatial scales (Conner and Leopold 1996, Chamberlain et al. 2003, Godbois et al. 2003a). For example, Godbois et al. (2003a) found bobcats selected mixed pine-hardwood habitat at the landscape scale, while selecting for agriculture and hardwoods at the home range scale. Fire can also influence wildlife habitat selection by altering vegetation structure (e.g., Harper et al. 2016); however, little is known about how time-since-fire influences bobcat habitat selection. For example, small mammals (e.g., cotton rats [*Sigmodon hispidus*]) are likely exposed to predation from bobcats following a fire event due to reductions in herbaceous cover (Conner et al. 2011, Morris et al. 2011). However, in a pine savanna ecosystem managed by frequent fire (≤ 3 years) and at small scales (≤ 100 ha), fire may have minimal influence on bobcat selection due to the diversity of cover created by frequent fire. Improving our knowledge of how these fires influence bobcat habitat selection can enable land managers to make informed management decisions, especially in cases where biodiversity management is a primary objective. Therefore, our objective was to examine bobcat habitat selection in a longleaf pine savanna managed by frequent-fire.

Methods

Study area

We conducted our research on the 11,735 ha privately owned Joseph W. Jones Ecological Research Center at Ichauway (hereafter, Jones Center; Fig. 1) located in Baker County, Georgia. The Jones Center contains a diversity of habitat types including a variety of forested cover such as longleaf pine, loblolly pine (*Pinus taeda*), slash pine (*P. elliottii*), mixed-pine and hardwood forests, oak barrens, lowland hardwood hammocks, and cypress-gum (*Taxodium ascendens-Nyssa biflora*) limesink ponds (Boring 2001). The Ichawaynochaway Creek bisects the property and the Flint River borders the property to the southeast. The Jones Center was historically managed as a northern bobwhite quail hunting plantation. Today, the Jones Center is an ecological research site while also serving as a quail hunting plantation. The Jones Center was comprised of approximately 31.2% mixed-pine hardwood, 31.1% mature pine (> 20 years old), 11.2% agriculture/food plot, 9.8% young pine (< 20 years old), 9.8% hardwoods, 2.6% open water, 1.8% wetlands, 1.5% shrub-scrub, and 0.9% urban/barren (Fig. 2). Wiregrass and old-field grasses (e.g., *Andropogon* spp.) were the dominant understory habitat in pine and pine/hardwood stands (Goebel et al. 1997), but > 1000 vascular plant species occur on the site (Drew et al. 1998). Road density was 5.48 km/km^2. Total annual rainfall during the study period ranged from 95.9 to 154.8 cm (Jones Center; Georgia Automated Environmental Monitoring Network, http://georgiaweather.net).

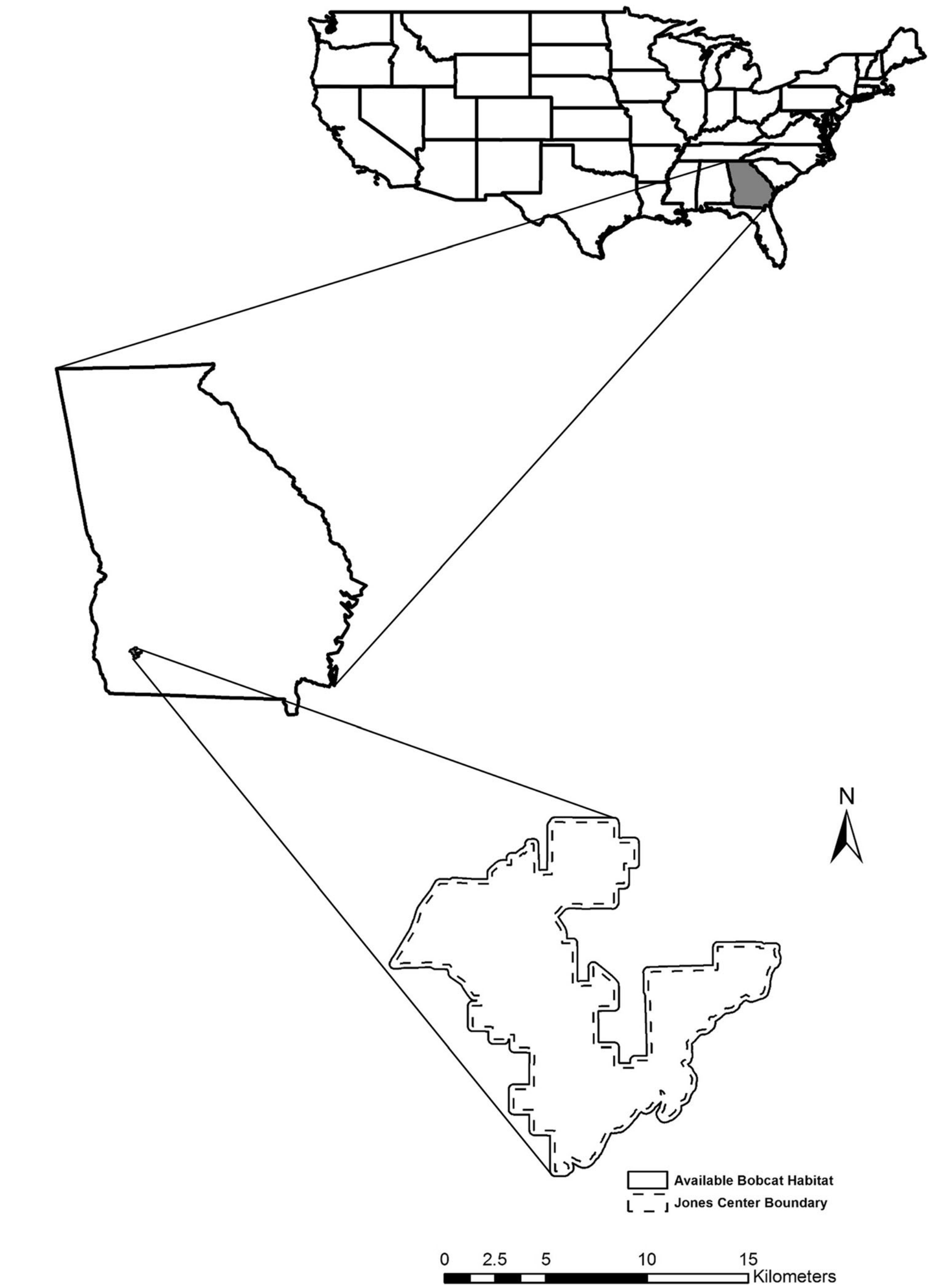

Fig. 1 Study area boundary. The dashed line shows the spatial extent of the Joseph W. Jones Ecological Research Center at Ichauway located in southwestern Georgia, USA, and the solid line shows the spatial extent of available habitat used in the study area scale habitat analysis

We classified stands as pine if they consisted of > 90% loblolly, longleaf, slash, and/or shortleaf (*P. echinata*) pine. We further classified stands as mature pine if trees were > 20 years old and were in large pole (12.6–25.4 cm) or saw timber (>25.4 cm) size classes. We classified stands as young pine if trees were ≤ 20 years old and were considered seedling-sapling or small pole timber (< 12.6 cm).

Mixed pine-hardwood stands contained a variety of species (e.g., loblolly, longleaf, slash pine, southern red oak [*Quercus falcata*], turkey oak [*Q. laevis*], live oak [*Q. virginiana*], laurel oak [*Q. laurifolia*], and sweetgum [*Liquidambar styraciflua*]). We classified stands as mixed pine-hardwoods if they were 50–89% hardwoods or pine. Within these stands, tree sizes ranged from seedling-sapling through saw timber;

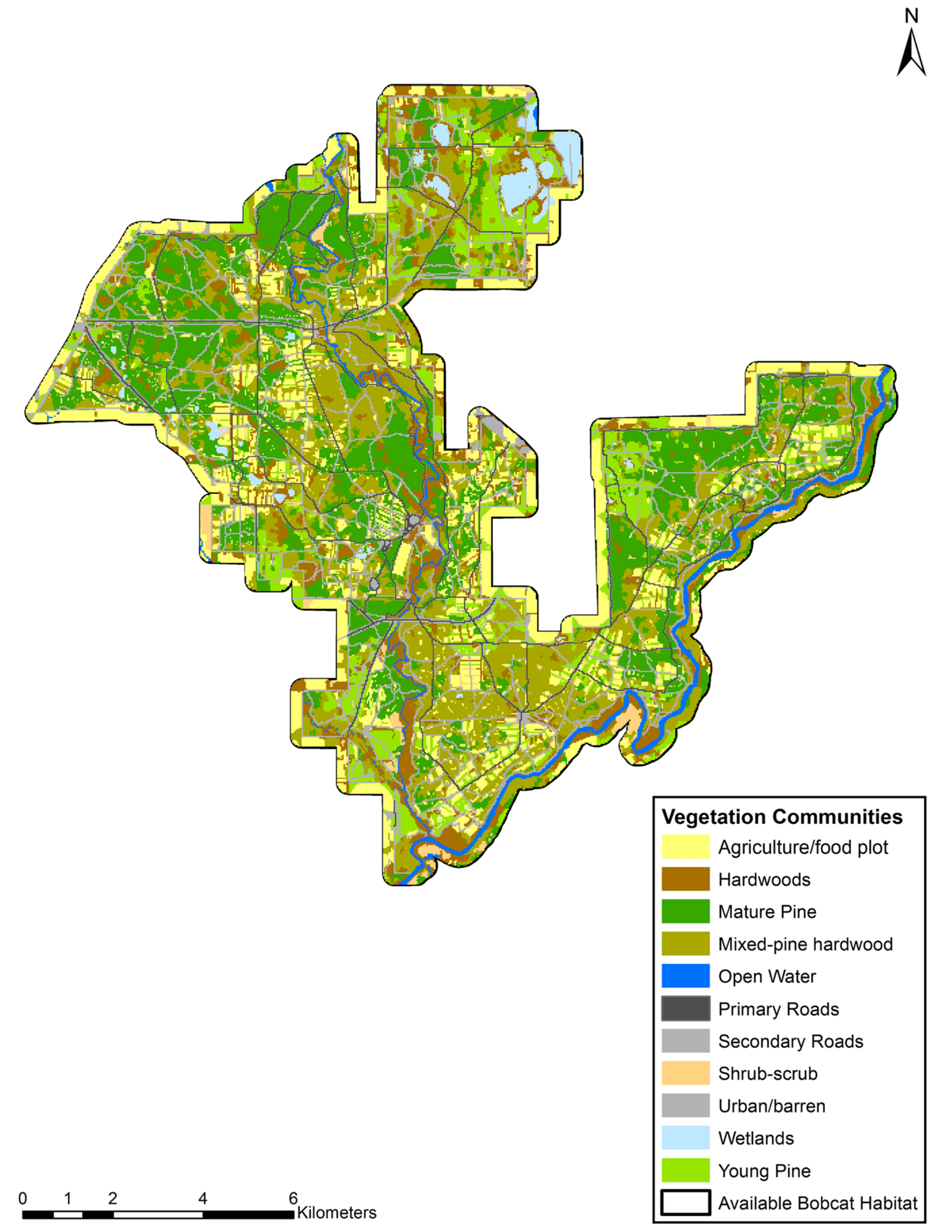

Fig. 2 Vegetation communities located at the Joseph W. Jones Ecological Research Center at Ichauway located in southwestern Georgia, USA

however, most (> 90%) were in the pole to saw timber classes.

We classified stands as hardwoods if they consisted of > 90% hardwood species such as southern red, turkey, live, and laurel oaks, and sweetgum) and trees ranged in size from seedling-sapling to saw timber. The majority of these stands were in pole to saw timber classes (> 90%). Agricultural stands consisted of cropland, pastureland, wildlife food plots, and horticultural crops (e.g., pecan orchard). Shrub-scrub stands consisted of abandoned agricultural fields and pastures, clear-cuts, grassland, and shrubby areas.

To successfully restore and maintain pine savannas on our study sites, land managers used prescribed fire and mechanical hardwood removal. Fire was applied to mature pine, young pine, mixed pine/hardwood, and shrub-scrub habitats. Prescribed fire was conducted throughout the year with > 50% of burns conducted during the growing season (15 April–15 August). Prescribed fire application occurred in a mosaic fashion, which promoted landscape diversity. Average patch size burned at the Jones Center during the study was 35.60 ha (range = 0.01–373.68 ha). Fire-return interval typically ranged from 1 to 3 years with an average fire return interval ≤ 2 years. Land managers often used mechanical removal to remove large off-site hardwoods (e.g., water oak [*Q. nigra*]) from within mature pine stands.

Bobcat capture and monitoring

We captured adult bobcats using Victor No. 1.75 offset and No. 3 Soft Catch traps (Woodstream Corp., Litiz, Pennsylvania) during December 2000–May 2007. We fitted adults with a 180-g VHF radiocollar (Advanced Telemetry Systems, Isanti, MN), and each individual bobcat received a uniquely numbered ear tattoo. Additional information regarding the capture and tagging of bobcats can be found in Godbois et al. (2003a). The Institutional Animal Care and Use Committee at the University of Georgia approved trapping and handling procedures (Animal Use Proposal no. A990159). Georgia Department of Natural Resources–Wildlife Resources Division issued the scientific collection permit (no. 29-WJH-16-190).

We monitored bobcats from 6 times/day to 4–6 times per week depending on the season using a 3-element Yagi antenna (Sirtrack, New Zealand) and hand-held receiver (Wildlife Materials, Carbondale, IL). Our telemetry data set was compiled from five separate research projects on the same study area, which led to the differences in telemetry sampling. Due to potential observer biases, we conducted an accuracy test for all field personnel and the standard deviation associated with bearing accuracy was 7° (Kirby et al. 2010). To reduce additional error with VHF locations, we limited time between consecutive bearings to < 15 min, though most consecutive bearings were taken within 7 min (White and Garrott 1990).

Habitat selection

To investigate bobcat habitat selection, we examined selection at two spatial scales: landscape (i.e., study area boundary) and annual area of use scale (hereafter, AAU). Bobcats frequently moved off the study area during the study period. Therefore, to assess landscape scale habitat selection, we calculated the median linear distance of all bobcat locations occurring outside of the Jones Center boundary to the property boundary line, which resulted in a median distance from the study area boundary of 237 m. We then buffered the Jones Center boundary by 237 m (i.e., available habitat; see Fig. 1) and excluded all bobcat locations occurring outside of this boundary. This resulted in the loss of 5.3% of locations from our master data set, which we felt was an acceptable loss as some of the locations were likely erroneous fixes due to triangulation errors. To assess AAU habitat selection, we calculated 95% fixed kernel utilization distributions (KDE) in Geospatial Modeling Environment (Ver. 0.7.4; Beyer 2012). Due to a lack of defined breeding and kitten rearing seasons on our study area (L. M. Conner, Joseph W. Jones Ecological Research Center, unpublished data), we chose to focus on annual habitat selection. We required each bobcat to have ≥ 40 locations during each year and ≥ 6 months of telemetry locations to calculate AAU. We clipped the 95% AAU to the available study area boundary because we were only interested in bobcat habitat selection in the fire-maintained pine savanna, and we lacked fire data off-site.

To quantify habitat selection, we used a geographic information system (ArcGIS® 10.3.1, Environmental Systems Research Institute Inc., Redlands, CA) to create a vector layer of habitat types available on our study area. We converted the vector layer to a 30-m raster layer and used the Euclidean Distance tool in ArcGIS® 10.3.1 to calculate distance (m) from every 30-m pixel to the nearest patch of each habitat type. To evaluate the influence of roads as travel corridors, we converted a digitized road layer consisting of county (paved), primary (graded and dirt), secondary (harrowed), and tertiary (mowed and firebreaks) roads to a 30-m raster grid. We combined road classes into two categories based on traffic-levels (L.M. Conner, Joseph W. Jones Ecological Research Center, personal observation): (1) primary roads (county and primary; paved or sand/dirt roads); and (2) secondary roads (firebreaks). Primary roads were defined as roads that received vehicle travel daily, whereas, secondary roads (firebreaks) rarely received vehicle travel and served as an edge between vegetation communities. We used a distance-based approach because distance-based metrics are not restricted to linear or point habitat features, require no explicit error handling, and permit extraction of more information than classification-based analyses (Conner et al. 2003). At the landscape scale, we evaluated non-random habitat selection with a ratio of 1 bobcat location to 5 available (random) locations to characterize available habitat at a larger extent (Northrup et al. 2013). At the AAU scale, we characterized available habitat using a ratio of 1 bobcat location to 3 available (random) locations due to the smaller spatial extent. Finally, we extracted values from the raster habitat variables to both used and available locations.

Model development and analysis

We modeled habitat selection at each scale using a generalized linear mixed-effects model (GLMM) implemented in program R (V. 3.3.3, R Core Team 2017) and a use vs. availability habitat selection approach to evaluate non-random habitat selection (Manly et al. 2002). We compared used (bobcat locations) to available (random) locations in a logistic regression framework where used and random locations were represented as a binary response (1 = bobcat location; 0 = random location). We included sex (male and female) as an interaction term with each stand type in the model to evaluate whether habitat selection differed between sexes. Males were the reference group for the interaction. We included bobcat identification and year as random effects to account for variability among individual bobcats and year-to-year variation in habitat selection, respectively (Gillies et al. 2006).

Prior to data analysis, we scaled all distance values for used and available locations by dividing the linear distance by 200 m to reduce model convergence issues. We evaluated pairwise correlations between explanatory variables at each scale using Pearson correlation. We considered any variables that were highly correlated ($|r| > 0.7$) and retained the variable that provided the simplest biological interpretation (Dormann et al. 2013). We then evaluated variance inflation factors of all variables to assess the extent of any remaining collinearity. All variables contained a variance inflation factor ≤ 1.12, which suggested that collinearity was not likely an issue (Zuur et al. 2009). We then constructed a full model for each scale. We made inference to only those variables that were statistically significant ($\alpha = 0.05$). For easier interpretation, we calculated scaled odds ratios (OR) and associated 95% confidence intervals for parameter estimates. We only considered parameter estimates with 95% confidence intervals that excluded 0 to be informative (Miller and Conner 2007). Lastly, we ranked the absolute value of each standardized beta coefficient estimate from largest to smallest to assess relative importance of each landscape variable (Hamilton 1992).

Habitat selection in relation to prescribed fire

To evaluate whether prescribed fire influenced bobcat habitat selection, we used a subset of our radio-telemetry data that included only those bobcat locations occurring on our study area during the growing season (15 April–15 August) and in stands that received frequent fire (i.e., mature pine, young pine, and mixed pine-hardwoods). We chose to focus the analysis during this period because it corresponded to the growing season when most prescribed fire was applied and prescribed fire may be a useful management tool to reduce incidental encounters between bobcats and prey species (e.g., Jones et al. 2004). Additionally, we used only locations within our study area boundary because fire history data were not available outside of this area. We used the union tool in ArcGIS® 10.2 to create a days-since-fire (no. of days) map for the study area. We determined the radius of the buffer by calculating the median 100% daily area of use minimum convex polygon (MCP) for bobcats from 15 April to 15 August using Geospatial Modeling Environment. We required a minimum of six telemetry locations/bobcat/day from 15 April to 15 August to calculate a daily area of use MCP ($n = 9$ males; $n = 14$ females). These 23 individuals were a subset of the larger data set because they met the minimum required number of locations/bobcat/day. We calculated an MCP rather than a KDE because the average number of locations per bobcat/day was 7.6 (range 6–9), which would likely lead to over-smoothing of the kernel density estimate (Seaman and Powell 1996). We placed a buffer (170 m radius) based on the median 100% daily area of use minimum convex polygon (MCP) around each used telemetry location to delineate available habitat. Within each buffer, we generated five random points that intersected with the days-since-fire map. We calculated a days-since fire value for each used and random location by subtracting the day we obtained the location from the day the fire occurred for that patch.

We modeled effect of days-since-fire on habitat selection by using a generalized linear mixed-effects model (GLMM) in program R. We included bobcat identification and year as random effects to account variability among individual bobcats and year-to-year variation in habitat selection, respectively (Gillies et al. 2006).

Results

We monitored 64 adult bobcats (27 males and 37 females) during 2001–2007. We removed 19 bobcats (12 males and 7 females) prior to analysis because they contained less than 40 locations during each year and < 6 months of telemetry locations. Our final dataset contained 45 bobcats (16 males and 29 females; Table 1) and generated 144 AAU. We found no highly correlated variables at landscape and AAU scales; therefore, we retained all variables in our modeling efforts. At the landscape scale, female bobcats were closer to mixed pine-hardwoods ($\beta = -0.172$, $P < 0.001$), young pine ($\beta = -0.083$, $P < 0.001$), and secondary roads ($\beta = -0.165$, $P < 0.001$), whereas

Table 1 Mean number (and SE) of radio-telemetry locations/bobcat/year/sex

Sex	Year	n[a]	$\bar{x}$ number of locations/bobcat	SE
Male	2001	5	104.8	4.4
	2002	7	201.9	23.8
	2003	8	136.9	11.1
	2004	6	116.0	21.6
	2005	5	125.8	6.1
	2006	7	62.6	2.4
	2007	6	60.3	4.1
Female	2001	7	104.7	9.6
	2002	15	222.1	21.0
	2003	16	147.1	10.4
	2004	20	131.1	8.1
	2005	18	118.3	6.3
	2006	14	66.7	1.3
	2007	10	65.1	1.5

[a]*n*, number of radio-marked bobcats
This research was conducted at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, 2001–2007

females were farther from mature pine (β = 0.085, $P < 0.001$) and hardwoods (β = 0.119, $P < 0.001$) relative to males. We found no difference in selection of agriculture (β = 0.011, $P = 0.723$), shrub-scrub (β = 0.001 $P = 0.964$), and primary roads (β = 0.018, $P = 0.284$) relative to males.

Because of differences in habitat selection by sex at the landscape scale, we developed two separate sex-specific models and provided sex-specific parameter estimates (Table 2; Fig. 3a–h). Based on standardized coefficient estimate rankings at the landscape scale, distance to primary road was the most important landscape variable to male bobcats followed by young pine, agriculture, mature pine, mixed pine-hardwood, and shrub-scrub; distance to nearest secondary road was least important (Table 2). Specifically, male bobcats were closer to mature pine (β = – 0.289, SE = 0.026, OR = 0.749), mixed pine-hardwoods (β = – 0.262, SE = 0.035, OR = 0.769), hardwoods (β = – 0.268, SE = 0.024, OR = 0.765), agriculture (β = – 0.349, SE = 0.026, OR = 0.705), shrub-scrub (β = – 0.097, SE = 0.013, OR = 0.907), and primary roads (β = – 0.241, SE = 0.014, OR = 0.786), and farther from young pine (β = 0.139, SE = 0.010, OR = 1.150). Male bobcat selection of secondary roads did not occur ($P > 0.05$; Table 2). At the landscape scale, distance to nearest primary road was the most important landscape variable to female bobcats followed by agriculture, mixed pine-hardwood, mature pine, shrub-scrub, hardwoods, and young pine; distance to nearest secondary road was least important (Table 2). Specifically, female bobcats were closer to mature pine (β = – 0.204, SE = 0.026, OR = 0.816), mixed pine-hardwoods (β = – 0.434, SE = 0.024, OR = 0.648), hardwoods (β = – 0.149, SE = 0.014, OR = 0.862), agriculture (β = – 0.338, SE = 0.017, OR = 0.713), shrub-scrub (β = – 0.097, SE = 0.008, OR = 0.908), primary roads (β = – 0.223, SE = 0.009, OR = 0.800), and secondary roads (β = – 0.139, SE = 0.023, OR = 0.870).

At the AAU scale, female bobcats were closer to secondary roads (β = – 0.122, $P = 0.006$), but farther from agriculture (β = 0.092, $P = 0.003$) and shrub-scrub (β = 0.053, $P = 0.002$) relative to males. We found no difference in selection of mature pine (β = – 0.005, $P = 0.873$), mixed pine-hardwoods (β = – 0.049 $P = 0.309$), hardwoods (β = 0.030, $P = 0.310$), young pine (β = – 0.008, $P = 0.526$), and primary roads (β = – 0.002, $P = 0.930$).

Because of differences in habitat selection by sex at the AAU scale, we developed two separate sex-specific models and provided sex-specific parameter estimates (Table 3; Fig. 3i–p). At this scale, distance to agriculture was the most important landscape variable to male bobcats followed by hardwoods, shrub-scrub, young pine, mature pine, secondary roads, and mixed pine-hardwoods; distance to nearest primary road was least important (Table 3). Specifically, male bobcats were closer to mature pine (β = – 0.079, SE = 0.029, OR = 0.924), hardwoods (β = – 0.140, SE = 0.025, OR = 0.869), agriculture (β = – 0.280, SE = 0.027, OR = 0.756), shrub-scrub (β = – 0.070, SE = 0.015, OR = 0.932), and farther from young pine (β = 0.040, SE = 0.011, OR = 1.041). Selection of mixed

Table 2 Parameter estimates for bobcat habitat selection at the landscape spatial scale

Variable[a]	Sex	β	SE	Z^b	P	Scaled odds ratio[c]	Scaled lower 95%	Scaled upper 95%
Mature pine	Male	– 0.289	0.026	– 11.104	< 0.001	0.749	0.712	0.788
	Female	– 0.204	0.016	– 13.106	< 0.001	0.816	0.791	0.841
Mixed pine/hardwoods	Male	– 0.262	0.035	– 7.463	< 0.001	0.769	0.718	0.824
	Female	– 0.434	0.024	– 18.440	< 0.001	0.648	0.619	0.678
Hardwoods	Male	– 0.268	0.024	– 11.384	< 0.001	0.765	0.731	0.801
	Female	– 0.149	0.014	– 10.334	< 0.001	0.862	0.838	0.886
Young pine	Male	0.139	0.010	14.524	< 0.001	1.150	1.128	1.171
	Female	0.056	0.007	8.590	< 0.001	1.057	1.044	1.071
Agriculture	Male	– 0.349	0.026	– 13.365	< 0.001	0.705	0.670	0.743
	Female	– 0.338	0.017	– 20.251	< 0.001	0.713	0.690	0.737
Shrub/scrub	Male	– 0.097	0.013	– 7.261	< 0.001	0.907	0.884	0.931
	Female	– 0.097	0.008	– 11.433	< 0.001	0.908	0.893	0.923
Primary roads	Male	– 0.241	0.014	– 16.795	< 0.001	0.786	0.764	0.808
	Female	– 0.223	0.009	– 24.755	< 0.001	0.800	0.786	0.815
Secondary roads	Male	0.026	0.036	0.713	0.476	1.026	0.956	1.101
	Female	– 0.139	0.023	– 5.989	< 0.001	0.870	0.831	0.911

[a]Distance to nearest habitat patches (m)
[b]Standardized coefficient estimates
[c]Scalar, 200 m
This research was conducted at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, 2001–2007

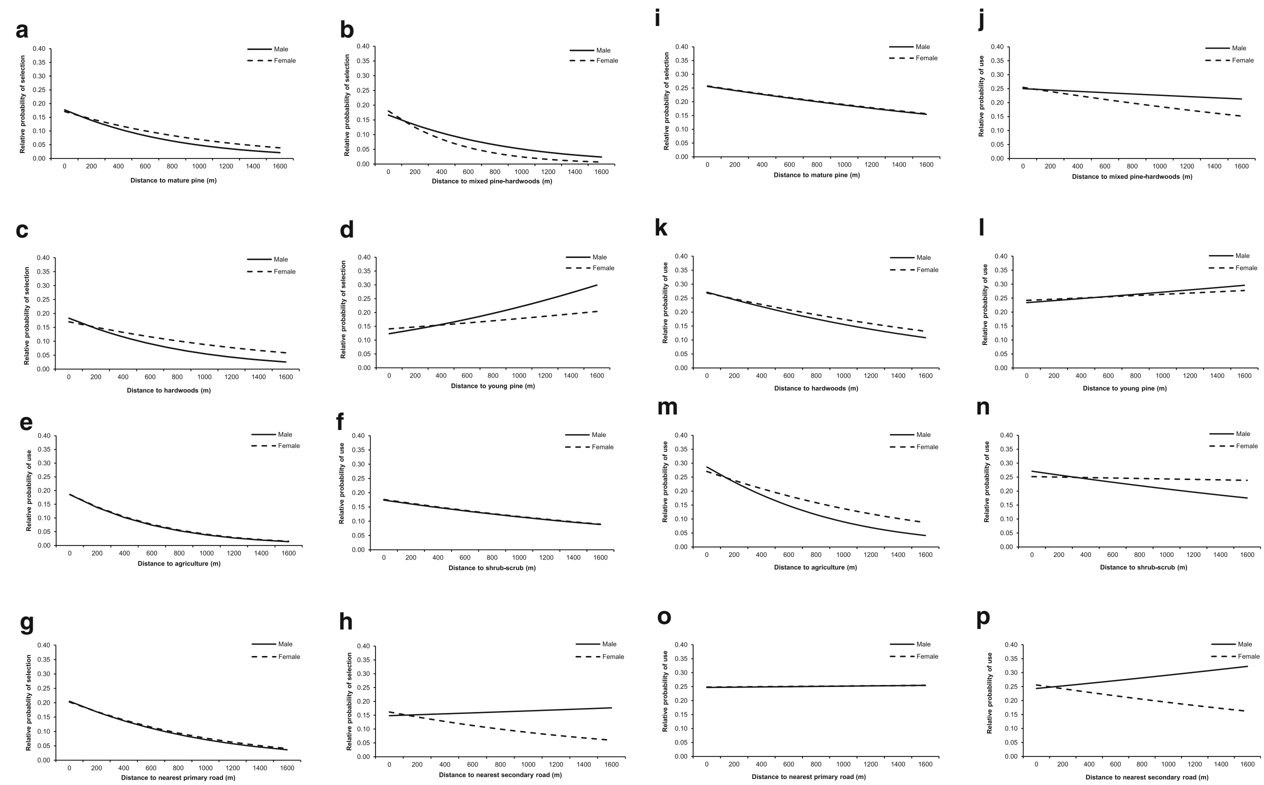

Fig. 3 Relative probability of selection at the landscape and annual area of use spatial scales This research was conducted at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, 2001–2007. Landscape scale predictive probability figures: mature pine (**a**), mixed pine-hardwoods (**b**), hardwoods (**c**), young pine (**d**), agriculture (**e**), shrub-scrub (**f**), primary roads (**g**), and secondary roads (**h**). Annual area of use predictive probability figures: mature pine (**i**), mixed pine-hardwoods (**j**), hardwoods (**k**), young pine (**l**), agriculture (**m**), shrub-scrub (**n**), primary roads (**o**), and secondary roads (**p**)

pine-hardwoods, primary roads, and secondary roads did not differ ($P > 0.05$; Table 3) from expectation. Distance to agriculture was the most important landscape variable to female bobcats followed by hardwoods, mature pine, young pine, mixed pine-hardwoods, secondary roads, and shrub-scrub; distance to nearest primary road was least important (Table 3). Specifically, female bobcats were closer to mature pine ($\beta = -0.078$, $SE = 0.017$, $OR = 0.925$), mixed pine-hardwoods ($\beta = -0.081$, $SE = 0.027$, $OR = 0.923$), hardwoods ($\beta = -0.111$, $SE = 0.015$, $OR = 0.895$), agriculture ($\beta = -0.169$, $SE = 0.017$, $OR = 0.845$), secondary roads ($\beta = -0.072$, $SE = 0.025$, $OR = 0.931$), and farther from young pine ($\beta = 0.023$, $SE = 0.007$, $OR = 1.023$). Selection of shrub-scrub and primary roads did not differ ($P > 0.05$; Table 3) from expectation.

Days-since-fire did not influence male and female bobcat use of pine stands that received frequent fire ($\beta = 1.303$ e-05, $SE = 4.372$ e-05, $P = 0.766$). Median use of stands was 404.0 ± 8.6 days after fire, whereas expected use was 402.0 ± 3.8 days.

Discussion

Male and female bobcats selected vegetation communities differently based on scale. Female bobcats presumably establish their home ranges to ensure sufficient resources for individual survival and survival of their young (Anderson 1987, Sandell 1989) compared to males that likely establish their home range based on breeding opportunities (Sandell 1989). Males and females generally selected mature pine and mixed pine-hardwoods, which is contrary to previous studies in pine-dominated systems (Conner and Leopold 1996, Chamberlain et al. 2003). However, these studies were conducted in systems that were not managed by frequent fire. For example, Conner et al. (1992) reported that mature pine and mixed pine-hardwood stands were not managed by frequent fire, resulting in prominent mid-stories, little herbaceous understory, and few bobcat prey. In a system managed by frequent fire return intervals (≤ 3 years), herbaceous plant communities do not shift to dense hardwood understory communities (Glitzenstein et al. 2012). Therefore, these systems

Table 3 Parameter estimates for bobcat habitat selection at the annual area of use spatial scale

Variable[a]	Sex	β	SE	Z^b	*P*	Scaled odds ratio[c]	Scaled lower 95%	Scaled upper 95%
Mature pine	Male	− 0.079	0.029	− 2.741	0.006	0.924	0.873	0.978
	Female	− 0.078	0.017	− 4.469	< 0.001	0.925	0.894	0.957
Mixed pine/hardwoods	Male	− 0.026	0.040	− 0.646	0.518	0.975	0.902	1.053
	Female	− 0.081	0.027	− 3.019	0.003	0.923	0.876	0.972
Hardwoods	Male	− 0.140	0.025	− 5.671	< 0.001	0.869	0.828	0.912
	Female	− 0.111	0.015	− 7.257	< 0.001	0.895	0.868	0.922
Young pine	Male	0.040	0.011	3.649	< 0.001	1.041	1.019	1.063
	Female	0.023	0.007	3.319	0.001	1.023	1.009	1.037
Agriculture	Male	− 0.280	0.027	− 10.562	< 0.001	0.756	0.717	0.796
	Female	− 0.169	0.017	−9.764	< 0.001	0.845	0.816	0.874
Shrub/scrub	Male	− 0.070	0.015	− 4.783	< 0.001	0.932	0.906	0.960
	Female	− 0.009	0.009	− 1.025	0.305	0.991	0.973	1.009
Primary roads	Male	0.005	0.016	0.290	0.772	1.005	0.973	1.038
	Female	0.004	0.010	0.412	0.680	1.004	0.984	1.025
Secondary roads	Male	0.049	0.037	1.333	0.183	1.051	0.977	1.130
	Female	− 0.072	0.025	− 2.919	0.004	0.931	0.887	0.977

[a]Distance to nearest habitat patches (m)
[b]Standardized coefficient estimates
[c]Scalar, 200 m
This research was conducted at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, 2001–2007

contain diverse understory plant communities (Brockway and Lewis 1997), which can produce abundant small mammal populations (Golley et al. 1965, Schnell 1968, McMurry et al. 1994, Masters et al. 1998). We suspect bobcats selected mature pine and mixed pine-hardwoods due to the availability of prey (see also Sasmal et al. 2017); however, we lack data on prey availability among the vegetation types on our study area.

We found that male and female bobcats were farther from young pines, which is also contrary to previous studies (Conner and Leopold 1996, Chamberlain et al. 2003). We expected bobcats to select for areas with lower basal areas managed by frequent fire that contained an abundance of understory vegetation. Selection of young pines in the Mississippi studies was primarily due to relative abundance of small mammals in young pines (Conner 1991, Conner et al. 1992). Many young pines in our study area contained little herbaceous vegetation and few small mammals (Golley et al. 1965, Schnell 1968, McMurry et al. 1994, Masters et al. 1998), which may explain why bobcats were farther from young pines.

Bobcats were found to be closer to agriculture fields and shrub-scrub vegetation communities at both spatial scales. Our findings were consistent with previous studies that found agricultural areas were important to bobcats (Conner et al. 1992, Conner and Leopold 1993, Godbois et al. 2003a). Hardwoods were also important to bobcats; perhaps because they serve as travel corridors between forage patches (Godbois et al. 2003a). Likewise, hardwood stands may also serve as refugia (i.e., den sites, cover, and protection from summer heat; [Hall and Newsome 1976, Godbois et al. 2003a]) within otherwise pine-dominated systems.

Our interpretation of results differed based on sex and the scale examined, suggesting that scale acts as a hierarchy distinguishing broad-level population questions from more fine-scale activity patterns for bobcats. Our findings suggest that primary roads are important to bobcats at the landscape scale but their use of primary roads was random within the AAU scale. Bobcats commonly use roads as travel corridors (Lovallo and Anderson 1996, Conner and Leopold 1998), and roads provide valuable edge habitats (Frey and Conover 2006, Barding and Nelson 2008). Use of primary roads may provide others benefits to bobcats such as reduction in energetic costs related to space use. The lack of importance of primary roads at the AAU scale may be due to increased risk of mortality (e.g., Benson et al. 2015) or availability of other important habitat types or edge. Secondary roads were of minimal importance at both spatial scales, which is likely due to their structure as these roads were primarily disked roads separating pine stands and serving as firebreaks. These roads received rarely received vehicle traffic and maintenance; therefore, they may not have provided enough edge habitat to benefit bobcats.

Days-since-fire did not appear to influence bobcat habitat selection. However, our results may be partially due to a lack of stands with longer burn rotations (> 3 years). With frequent fire-return intervals, herbaceous plant communities do not shift to dense hardwood understory communities (Glitzenstein et al. 2012). In addition, frequent use of prescribed fire in longleaf pine forests increases understory plant species richness, diversity, and evenness (Brockway and Lewis 1997), which may influence where bobcats search for prey items. Small mammals (e.g., cotton rats [*Sigmodon hispidus*], Conner et al. 2011, Morris et al. 2011) are commonly exposed to predation from bobcats and other predators following a fire event due to reductions in herbaceous cover. Our results may also be due to the scale of fire relative to bobcat home ranges. Bobcat home range size varies from 2.76 to 36.5 km^2 (Conner et al. 1992, Cochrane 2003, Doughty 2004). With the average patch size burned on our study area < 40 ha in size, our findings suggest that small scale (< 40 ha) frequent fires (≤ 3 years) may have minimal influence on bobcat habitat selection. Additionally, Sasmal et al. (2017) found no difference in abundance of *Peromyscus* spp. among five vegetation types and three burn regimes (1, 2, and 3 years post-fire) in pine savannas, suggesting bobcats likely do not have to move far to locate available prey in a system managed by frequent fire. Lastly, bobcats were monitored from 6 times a day to 4–6 times per week depending on the season. The infrequency of locations may have led to biased results in cases where bobcats rapidly exploited a burned area and moved away before the subsequent telemetry location(s). We suggest future research evaluate bobcat foraging strategies in pine savannas to potentially reduce incidental encounters between bobcats and ground-dwelling prey species. For example, Kaufmann et al. (2007) found landscape heterogeneity shaped predation with specific landscape features and vegetation structure influencing the probability of detection between gray wolves (*Canis lupus*) and elk (*Cervus elaphus*). We also suggest future research collect finer-temporal data using GPS technology to improve our understanding of how rapidly bobcats locate and exploit recently burned areas in fire-maintained pine savannas and examine the influence of larger scales of fire (e.g., > 40 ha) on bobcat habitat selection.

Conclusions

Our findings demonstrate the importance of vegetation diversity (e.g., mature pine, mixed pine/hardwoods, hardwoods, agriculture/food plots, shrub-scrub) for bobcats in a forested landscape managed by frequent (≤3 years) and small scale (< 40 ha) fires. We found no apparent fire-associated selection at the smaller spatial scale, which is likely due to frequency of telemetry locations, and scale and frequency of fire return intervals. Interestingly, at larger spatial scales, frequent burns led to selection patterns contrary to our current knowledge of bobcat habitat selection, which are based on studies where frequent fire was absent. For example, bobcats generally selected mature pine and mixed pine-hardwoods, which were managed by frequent fire in our system. However, prior studies found bobcats avoided these vegetation communities primarily due to the absence of herbaceous understory vegetation beneficial to prey species (Conner et al. 1992). Small mammals are the primary prey of bobcats on our study area (Godbois et al. 2003b). Bobcats selected mature pine and mature pine-hardwood stands managed by frequent fire, but also selected other habitat types such as agricultural fields and shrub-scrub. Additionally, fire events facilitate predation of small mammal communities by temporarily reducing cover and exposing prey to predators (Conner et al. 2011, Morris et al. 2011). Therefore, there is a chance that bobcats—and other predators—may be temporarily attracted to recently burned areas, suggesting a tradeoff between managing for prey that may be particularly sensitive to predators following fire (e.g., wild turkey nests) and those species that rely on frequent fire (e.g., gopher tortoise [*Gopherus Polyphemus* and red-cockaded woodpecker (*Picoides borealis*; Alavalapati et al. 2002).

Abbreviations

AAU: Annual area of use; GLMM: Generalized linear mixed-effects models; MCP: Minimum convex polygon; VHF: Very high frequency

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Authors' contributions

ARL designed the study, managed and analyzed the data, wrote the statistical code, and drafted the manuscript. LMC designed the study, managed data collection, provided statistical assistance, and reviewed the manuscript drafts. MJC designed the study and reviewed the manuscript drafts. NPN designed the study, provided statistical assistance, and reviewed the manuscript drafts. RJW designed the study, managed data collection, and reviewed the manuscript drafts. All authors read and approved the final manuscript.

Competing interests

The author(s) declare that they have no competing interests.

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