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Home Ranges and Habitat Selection by Black Bears in a Newly Colonized Population in Florida

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Abstract - Understanding how animals use space and resources in newly colonized, anthropogenically altered habitats is important for species management because animals in fragmented habitats may use the landscape differently than conspecifics in contiguous habitats. We collected GPS-location data for 16 individuals (6 females, ages 1–9 y; 10 males, ages 2–8 y) from the summer of 2011 to the summer of 2013 to study space and habitat use by a recently established population of *Ursus americanus floridanus* (Florida Black Bear) in a fragmented landscape of north-central Florida. Average (± 1 SE) female and male home-range sizes estimated using the kernel density method were 31.16 ± 8.23 km^2 and 220.93 ± 28.48 km^2, respectively. Average 95% minimum convex polygon estimates were 34.49 ± 12.76 km^2 for females and 226.04 ± 45.32 km^2 for males. Home ranges in our study area were generally larger than those reported for Black Bears inhabiting the nearby contiguous forested habitat of Ocala National Forest, indicating that fragmentation may influence home-range size. Compositional analysis and generalized linear mixed models revealed that Black Bears selected most strongly for riparian forests; urban areas were generally avoided. These results suggest that large carnivores that inhabit fragmented landscapes may require more space than conspecifics in habitats with better connectivity, and highlight the importance of riparian forests for Black Bears.

Introduction

Many carnivore populations have suffered precipitous declines due to habitat loss and fragmentation (Crooks 2002, Ripple et al. 2014, Woodroffe 2000), but some have responded positively to conservation efforts and begun to recolonize portions of their historic range (Chapron et al. 2014, Gompper 2015, Linnell et al. 2001). Examples of rebounding species include *Pteronura brasiliensis* Gmelin (Giant River Otter; dos Santos Lima 2014), *Canis lupus* L. (Wolf; Pletscher et al. 1997), *Gulo gulo* L. (Wolverine; Flagstad et al. 2004), *Puma concolor* L. (Cougar; Larue et al. 2012), *Ursus arctos* L. (Brown Bear; Bjornlie et al. 2014, Hagen et al. 2015, Swenson et al. 1998), and *Ursus americanus* Pallas (American Black Bear; Bales et al. 2005, Frary et al. 2011, Onorato et al. 2004, Unger et al. 2013). The theory of ideal free-distribution assumes that animals colonizing new areas will distribute themselves among the best-quality habitat available (Fretwell 1972).

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Therefore, understanding how species use space and habitat as they naturally expand their range can help prioritize land-management practices and aid in corridor design for species of conservation concern (Beier et al. 2008, Bocedi et al. 2014, Marcelli et al. 2012), help identify suitable habitat for future population expansions (Mladenoff et al. 1999), and possibly help reduce human–wildlife conflicts (Wilton et al. 2014). Few studies have examined space- and resource-use patterns of recently established populations of native carnivores.

Researchers have concluded that Black Bear populations are increasing throughout the range of the species (Hristienko and McDonald 2007, Scheick and McCown 2014). As populations grow, Black Bears that establish in new areas should select the highest-quality habitats (Fretwell 1972). Habitat productivity and spatial arrangement of resources affect how Black Bears use the landscape (Mitchell and Powell 2007). Black Bears living in particularly productive habitats with rich nutritional resources should require a smaller home range than those living in lower-quality sites (Lindzey and Meslow 1977, Oli et al. 2002). The patchy distribution of resources in anthropogenically or naturally fragmented landscapes should require Black Bears to travel farther and thus to have larger home ranges than those inhabiting unfragmented natural habitats (Hellgren and Maehr 1992, Mitchell and Powell 2008). The increased travel needed to secure sufficient resources in anthropogenically fragmented landscapes could also increase the risk of vehicular mortality and conflict with humans (Baruch-Mordo et al. 2008, Evans et al. 2014, McCown et al. 2004).

The size of a Black Bear home range varies seasonally due to the species' annual physiological cycles and fluctuations in food availability (Baruch-Mordo et al. 2014, Hellgren et al. 1989, Powell et al. 1997). Black Bears may use larger home ranges in the fall while foraging more actively to prepare for winter denning (Hellgren et al. 1989, Moyer et al. 2007). Due to the high variability in space and resource use among Black Bear populations, investigating the seasonal differences in home-range size and habitat selection can provide details that may otherwise be obscured.

Black Bear habitat must include 3 main resources—food, escape cover, and sufficient vegetation or trees for denning sites (Powell et al. 1997, Reynolds-Hogland et al. 2007). The diet of Black Bears consists mainly of plant matter (soft and hard masts); in the Southeast, *Serenoa repens* (Bartram) Small (Saw Palmetto) is a particularly important food source where available (Dobey et al. 2005, Maehr and Brady 1984). Also, Black Bears in the Southeast generally prefer riparian forests and wetland habitats (Hellgren et al. 1991, Stratman et al. 2001, Wooding and Hardisky 1994) to conifer forests and open areas (Moyer et al. 2008, Powell et al. 1997, Stratman et al. 2001). Intensively managed conifer forests often have relatively little understory and therefore fewer sources of food than riparian and wetland habitats, and do not provide adequate cover for denning sites. Black Bears in Florida typically use ground nests for denning and require dense understory vegetation for protection from disturbance (Garrison et al. 2012). Roads may also influence space and habitat use by Black Bears, but responses vary among populations and among individuals, depending on traffic volume, presence of human activities, and habitat and vegetation along the road (Costello et al. 2013, Gaines et al. 2005, Hellgren et al. 1991, Reynolds-Hogland and Mitchell 2007, Switalski and Nelson 2011).

The subspecies of Black Bear in Florida, *Ursus americanus floridanus* Merriam (Florida Black Bear; hereafter Black Bear), occurs in 7 relatively disconnected populations across the state, but the overall population is growing and its occupied range is expanding (FFWCC 2012). The largest population inhabits Ocala National Forest and surrounding areas in central Florida (FFWCC 2012). A patchwork of public and private lands, including the Camp Blanding Joint Training Center (hereafter Camp Blanding; operated by the Florida National Guard), connects Ocala National Forest with Osceola National Forest (hereafter referred to as the corridor), which harbors another sizable Black Bear population (Fig. 1; Hoctor et al. 2000). Extensive sampling during 2002–2003 using hair snares revealed the presence of Black Bears in the corridor, but there was no evidence for the presence of females with cubs, and thus no evidence of a population reproducing within the corridor (Dixon et al. 2006). However, based on increased bear sightings and recovery of females killed on the road, a reproductive population of Black Bears was suspected to have settled at Camp Blanding and the adjacent corridor area (J. Walter McCown, FFWCC, Gainesville, FL, unpubl. data).

Our objectives were to investigate space use and habitat selection by the recently colonized population of Black Bears in the Camp Blanding area of north-central Florida. We hypothesized that Black Bears at our fragmented study site would (1) have larger home ranges than those residing in nearby contiguous forests because they would have to travel farther to acquire sufficient resources; (2) have larger home ranges in fall than in summer, similar to other Black Bear populations, because Black Bears often forage more intensively before winter denning; (3) select for riparian forests, which provide the most cover and food sources; and (4) avoid habitats closer to major roads (but not necessarily minor roads) because of disturbance and the risk of road-related mortality (McCown et al. 2009).

Field-site Description

We conducted our study at the 295-km^2 Camp Blanding Joint Training Center and adjacent private lands located in north-central Florida. Camp Blanding is located near the center of the corridor between the Black Bear populations in Ocala National Forest and Osceola National Forest (Fig. 1). The area is fragmented by agricultural, rural, and urban land-uses and by several roads. The largest urban zones occur in the cities of Starke and Keystone Heights and the unincorporated area of Middleburg. *Pinus* spp. (pine) plantations further fragment the natural vegetation communities and are the dominant landcover at the study site. Natural habitats consist of mesic flatwoods, sandhill uplands, and scrub, as well as hardwood swamps and hammocks that occur near the creeks and drainages that traverse the area. Prevalent understory species include Saw Palmetto, *Myrica cerifera* L. (Wax Myrtle), *Ilex glabra* (L.) Gray (Gallberry), and *Smilax* L. spp. (greenbriers).

Camp Blanding hosts military training activities several times per year that result in an increased use of the training center property by several hundred to

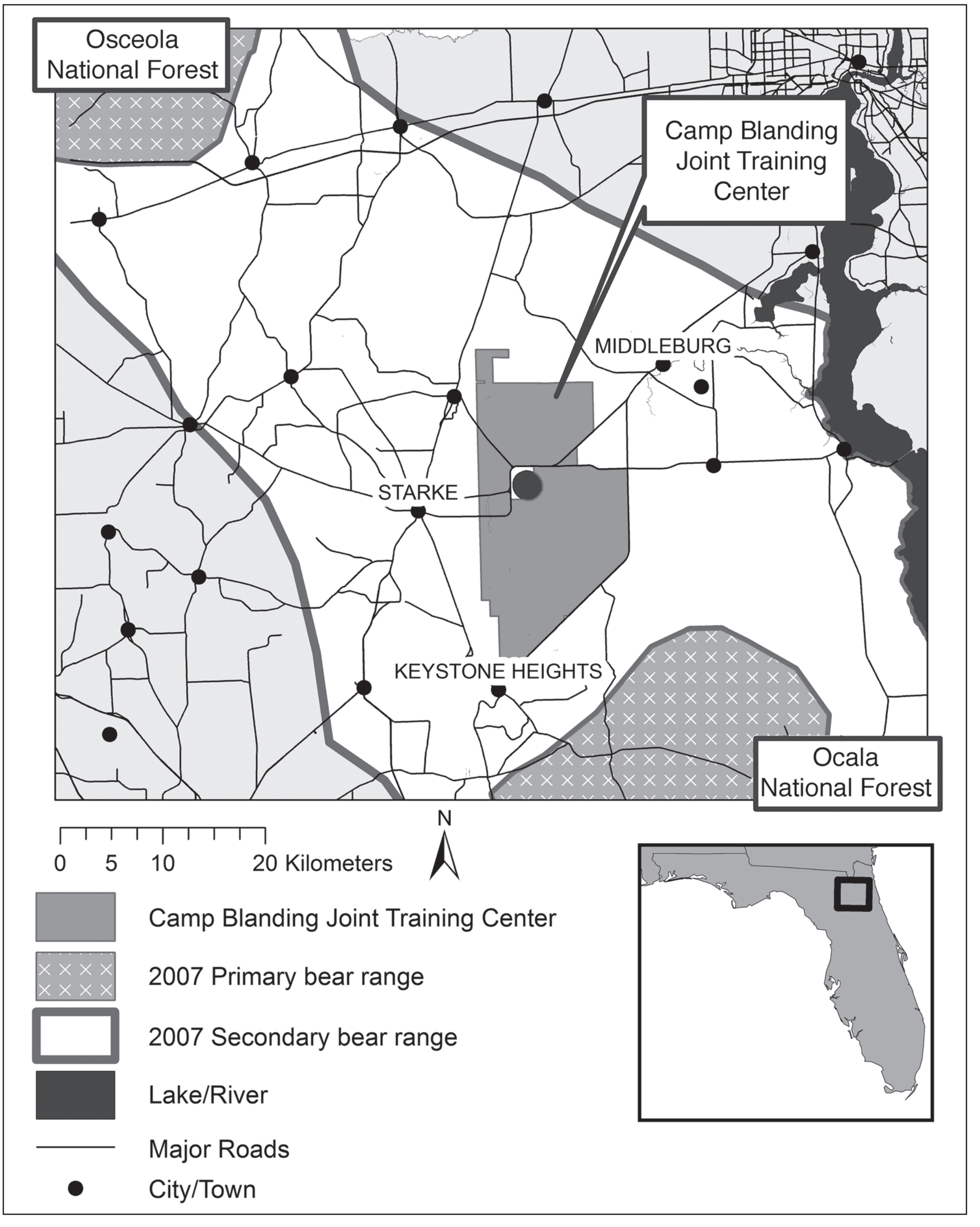

Figure 1. Map showing the location of the Camp Blanding Joint Training Center and the closest designated primary Florida Black Bear ranges, the Ocala Black Bear population to the south and the Osceola Black Bear population to the northwest. The area between the 2 populations has been thought to act as a bear corridor and coincides with what is designated as secondary Black Bear range in this area. Major roads are shown, and the largest human settlements in the corridor are labeled.

several thousand troops. When training activities are not in progress, Camp Blanding remains closed to the general public but allows controlled hunting and fishing by permit. Black Bear hunting in Florida was illegal during our study.

Methods

We captured Black Bears in the summers of 2011 and 2012 at baited sites using Aldrich spring-activated foot snares with a double-anchor cable set (Scheick et al. 2009). The double anchor prevented Black Bears from reaching either anchor tree, thus preventing injury to the animal from becoming wrapped around a tree or limb while ensnared. We set traps during dawn and dusk hours and attached a sentinel VHF collar to the anchor cable of each trap to monitor the snares. We remained ≤2 km from trap sites and continuously monitored the VHF signals; we responded within an hour of a Black Bear's capture. We anesthetized each captured Black Bear with Telazol® (3.5–5 mg/kg) and weighed, measured, and fit the animal with a collar housing a GPS tracking device (Lotek WildCell MG, Lotek Wireless, Inc., Newmarket, ON, Canada), then released each individual at its capture site. We programmed each collar to obtain locations every 2 h and to use a built-in mechanism to drop off after 2 y, but some collars fell off sooner. When winter locations of females indicated the possibility of denning, we visited the site to document reproduction.

Animal handling was performed by FFWCC biologists following agency policy; they needed no permits.

Landcover categories

We used the raster format of the Florida Vegetation and Land Cover 2014 GIS layer to classify landcover (Redner and Srinivasan 2014); the layer had a resolution of 10 m × 10 m. The study area contained 51 landcover types which we grouped into 6 categories: marsh/wetland, rural/agricultural, urban, forested wetlands, wood/scrub, and tree plantations (Table 1). We based groupings on similarity of landscape and vegetation (e.g., we combined all landcover categories of marshes and wetlands that had open canopy cover) using the R package raster (Hijmans

Table 1. Percentage of each landcover category composing the 99% minimum convex polygon constructed using locations from all Black Bears in the study (% Composition) and the percentage of Florida Black Bear GPS locations found in each landcover category (% Black Bear locations) in the Camp Blanding area in north-central Florida. See Supporting Information S1 for details (in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2261-Karelus-s1 and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2261.s1).

Landcover category	% composition	% bear locations (n = 46,922)
Marsh/wetland	6.90	7.75
Rural/agricultural	7.46	1.69
Urban	14.08	0.85
Forested wetlands	16.36	56.08
Wood/scrub	24.94	15.41
Tree plantations	30.25	18.21

2015; see Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2261-Karelus-s1 and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2261.s1). Urban areas consisted of medium- to high-density residential, commercial, and industrial areas. We obtained shapefiles for creeks and roads from the Florida Geographic Data Library (http://www.fgdl.org/). We classified roads as major roads (Class 1: primary routes, including interstates and US highways; and Class 2: secondary routes, including state roads) or minor roads (Class 3: larger roads or streets in residential areas; and Class 4: smaller roads or streets in residential areas) using ArcMap (version 10.3; ESRI 2015).

Home ranges

We prepared the Black Bear location data by excluding all but the highest quality GPS fixes, manually removing obviously erroneous location data, and excluding duplicate fixes resulting from dropped collars and bear mortalities. For further details on our data preparation, see Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2261-Karelus-s1 and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2261.s1.

We estimated home-range size for each Black Bear based on the bihourly locations as 95% utilization distribution using the kernel density estimator (KDE; Worton 1989) with bivariate normal kernels. To determine appropriate bandwidth, we estimated overall KDE home ranges for each individual with the ad hoc bandwidth for the smoothing parameter. We averaged the ad hoc bandwidth separately for females (0.389 km) and males (1.39 km) because females have smaller home ranges (Dobey et al. 2005, Hellgren and Vaughan 1990) and then re-estimated KDE home ranges for each individual using the sex-specific estimate of bandwidth. The bandwidths were biologically reasonable (Powell et al. 1997) and larger than the estimated location error (20.3 m). For comparison, we also estimated home ranges using 95% minimum convex polygon (MCP; Mohr 1947).

We estimated home ranges for 2 active seasons based on Black Bear biology: summer (1 May–31 August) and fall (1 September–31 December). We designated the beginning of the fall season as September because this month corresponds to the end of the breeding season as well as the beginning of acorn availability (Maehr and Brady 1984, Moyer et al. 2007). We included an individual in a seasonal analysis if its collar had been functional for at least 1 month during that season. We excluded location data collected during January–April because female Black Bears den during that period (Moyer et al. 2007). We estimated seasonal home ranges using the same methods and average bandwidths as described previously.

We used the R package adehabitatHR (Calenge 2006) to estimate home ranges and nonparametric Wilcoxon rank sum tests (Conover 1999) to compare home-range sizes between males and females and between summer and fall. All statistical tests were performed in R (version 3.1.0; R Core Team 2013).

Habitat selection

We performed compositional analysis of habitat selection (Aebischer et al. 1993) at both 2^{nd}-order (selection of a home range within the study area) and 3^{rd}-

order (selection of landcover categories within a home range) scales (Johnson 1980). For 2nd-order habitat-selection analysis, we estimated availability as the proportion of area comprised by each landcover category in the study area, defined as the 99% MCP calculated from all Black Bear locations. For 2nd-order selection analysis, we estimated use as the proportion of area comprised by each landcover category within the 99% MCP for each individual. For 3rd-order selection analysis, we designated the proportion of area occupied by different landcover categories within each individual's 99% MCP as available, and the proportion of each individual's locations within each landcover category as usage. If a landcover category was not available to an individual, we combined it with similar categories so that all were available for all Black Bears. We replaced any cases of 0 usage by 0.1 to avoid problems associated with log transformation of 0, which is not defined (Aebischer et al. 1993).

We used Wilks' Λ to test the null hypothesis that Black Bears used landcover categories in proportion to the categories' availability. If the null hypothesis was rejected, we computed the ranking matrix and used a randomization test (10,000 repetitions) to determine significance of preference of 1 landcover category over another (Aebischer et al. 1993). We performed seasonal analyses in the same manner. We conducted compositional analysis of habitat selection in the R package adehabitatHS (Calenge 2006).

Habitat selection by animals is often influenced by measurable features on the landscape, such as distance to nearest water source, road, or to an area of high human activity. Compositional analysis does not permit the testing of how continuous covariates might influence the pattern of habitat selection by animals. Thus, we used mixed-effects logistic regression (MELR) with a binary response variable (1 = observed GPS locations; 0 = random location; Gillies et al. 2006, Godvik et al. 2009, Klar et al. 2008, Nielsen et al. 2006). Random locations were represented by 5000 randomly generated locations within each Black Bear's 99% MCP. Individual Black Bears were treated as a random effect, which accounted for variation among individuals and the nested structure of the data (Gillies et al. 2006). We considered landcover category and distances to creek, major road, and minor road, as well as the biologically relevant additive effects of these covariates, as fixed effects. We calculated the distances using the R package rgeos (Bivand et al. 2016). We standardized distances to creeks and roads by subtracting the mean of the respective category from each value and then dividing by the standard deviation; this method centered the mean on 0.

We fitted MELR models using the R package lme4 (Bates et al. 2015) with the function glmer. For model comparison and statistical inference, we used an information-theoretic approach using Akaike's information criterion (AIC; Burnham and Anderson 2002, Klar et al. 2008) and considered models to have support if the difference in AIC score was less than 2.0 from the highest-ranked model. We used the conditional coefficient of determination ($R^2_{\mathrm{GLMM}(c)}$; Nakagawa and Schielzeth 2013) to assess the fit of the MELR model; $R^2_{\mathrm{GLMM}(c)}$ was calculated using the R package MuMIn (Barton 2015).

Results

We fitted 16 Black Bears (6 females, ages 1–9 y; 10 males, ages 2–8 y) with a GPS collar and tracked them for a total of 5362 bear-days, from June 2011 to August 2013. Tracking yielded 46,922 bihourly, 3D-validated GPS locations (2932.6 ± 88.4 per Black Bear; SD = 1415.1). All values reported indicate mean ± SE unless otherwise indicated.

Home ranges

Females had smaller home ranges than males (MCP: $W = 2$, $P < 0.005$, KDE: $W = 0$, $P < 0.005$; Fig. 2). Overall, 95% home-range size for females estimated using KDE (bandwidth $h = 0.39$ km) ranged from 12.53 km^2 to 68.22 km^2 and

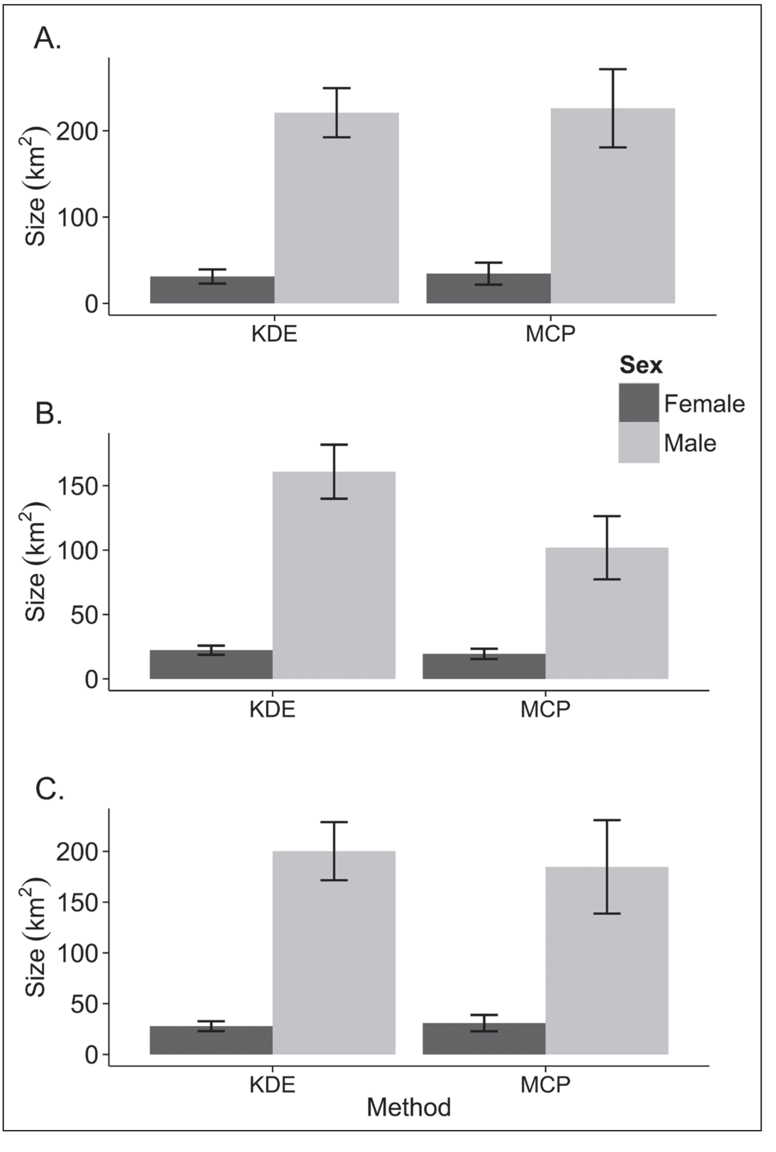

Figure 2. Average Florida Black Bear home-range sizes in the Camp Blanding area based on bihourly GPS telemetry data. Home ranges were estimated using the minimum convex polygon (MCP) and kernel density estimator (KDE) methods for: (A) the entire study period (females: $n = 6$; males: $n = 10$), (B) summer (females: $n = 8$; males: $n = 10$), and (C) fall (females: $n = 10$; males: $n = 8$). Vertical bars represent standard error.

averaged 31.16 ± 8.23 km^2 (SD = 20.15 km^2), and female home ranges estimated from 95% MCP ranged from 10.07 km^2 to 95.57 km^2 and averaged 34.49 km^2 ± 12.76 km^2 (SD = 31.26 km^2). Home ranges for males estimated using 95% KDE (h = 1.39 km) ranged from 106.28 km^2 to 387.65 km^2 and averaged 220.93 ± 28.48 km^2 (SD = 90.07 km^2), and male home ranges from 95% MCP ranged from 55.76 km^2 to 528.06 km^2 and averaged 226.04 km^2 ± 45.32 km^2 (SD = 143.33 km^2). Annual KDE home-range estimates from Camp Blanding and from other studies of nearby Black Bear populations are presented in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2261-Karelus-s1 and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2261.s1.

Female home-range sizes estimated using KDE ranged from 8.45 km^2 to 38.22 km^2 with an average of 22.27 ± 3.57 km^2 (SD = 11.28 km^2) for summer and ranged from 15.12 km^2 to 59.31 km^2 with an average of 27.78 ± 4.85 km^2 (SD = 13.72 km^2) for fall. Male home-range sizes estimated using KDE ranged from 59.02 km^2 to 287.81 km^2 with an average of 160.88 ± 20.96 km^2 (SD = 59.29 km^2) for summer and ranged from 89.30 km^2 to 409.42 km^2 with an average of 200.22 ± 28.60 km^2 (SD = 90.45 km^2) for fall. Summer and fall home-range sizes were not significantly different for females (KDE: W = 49, P = 0.46) or males (KDE: W = 53, P = 0.27) (Fig. 2).

Habitat selection

We concluded that 2nd-order habitat selection occurred over the entire study period (Wilks' Λ = 0.414, P = 0.04) and for each season (summer: Λ = 0.136, P = 0.003; fall: Λ = 0.326, P = 0.024). We observed a significant preference by Black Bears for forested wetlands compared to marsh/wetland, rural/agricultural, or urban habitats for all 3 time-periods. Urban areas were significantly the least preferred by Black Bears of all landcover categories except rural/agricultural areas over the entire study period and for fall. In summer, there was no significant difference in preference among urban areas, wood/scrub, and rural/agricultural landcover categories (Table 2).

Selection also occurred at the 3rd-order scale over the entire study period (Wilks' Λ = 0.063, P < 0.001), in summer (Λ = 0.050, P < 0.001), and in fall (Λ = 0.032, P < 0.001). Black Bears preferred forested wetlands to all other landcover categories for the entire study period and during the fall, but differences between preference for forested wetlands and marsh/wetland were greatly reduced in the summer. Generally, Black Bears avoided habitat in rural/agricultural and urban landcover categories (Table 3).

The most parsimonious MELR model included an additive effect of landcover category, distance to creeks, distance to major roads, and distance to minor roads (Model 1; Table 4). The conditional R^2 ($R^2_{GLMM(c)}$) was 0.281, suggesting no evidence for the lack of fit of the MELR model to data. The next-closest model differed from the top model by >250 ΔAICc (Model 2; Table 4), indicating a substantial decrease in model fit. Based on the most parsimonious model (Model 1, Table 4), Black Bears favored forested wetlands and avoided urban areas (Table 5). The effect of distance to creeks and distance to major roads indicated that Black Bears used areas closer to these features than expected at random. The effect of distance to minor roads indicated that the Black Bears selected areas farther from these roads than expected at random (Table 5). The variance (± SD) of the random effect was 0.397 ± 0.630.

Discussion

Although the presence of males in the Camp Blanding area had been reported, previous studies, including Dixon et al. (2006), found no evidence of the presence of females or a locally breeding population of Black Bears in the area. The earliest available map of Black Bear distribution in Florida does not designate Camp Blanding within the range (Brady and Maehr 1985). During our study, we radio-collared 6 female Black Bears and documented the birth of 5 cubs from 3 litters. These findings provide evidence that female Black Bears recently colonized the area and a locally breeding population of Black Bears currently inhabits the Camp Blanding area. Presence of these animals provided us with the opportunity

Table 2. Ranking matrix from compositional analysis for 2nd-order habitat selection (selection of a home range within the study area) by Florida Black Bears in north-central Florida for (A) the entire study period (1 August 2011–31 July 2013), (B) fall seasons, and (C) summer seasons. Signs indicate preference, with a (+) indicating that the row landcover category is preferred over the column landcover category and a (−) indicating the opposite. Triple signs represent a significant preference for (+++) or avoidance (---) ($P < 0.05$). Rank represents the order of preference for the land cover categories, in order of most-strongly preferred (1) to least-strongly preferred (6).

	Forested wetlands	Marsh/ wetland	Woods/ scrub	Tree plantations	Rural/ agricultural	Urban	Rank
A. Overall							
Forested wetlands	0	+	+	+++	+++	+++	1
Tree plantations	-	0	+	+	+	+++	2
Woods/scrub	-	-	0	+	+	+++	3
Marsh/wetland	---	-	-	0	+	+++	4
Rural/agricultural	---	-	-	-	0	+	5
Urban	---	---	---	-	-	0	6
B. Fall							
Forested wetlands	0	+	+	+++	+++	+++	1
Tree plantations	−	0	+	+++	+++	+++	2
Woods/scrub	−	−	0	+	+++	+++	3
Marsh/wetlands	---	---	-	0	+	+++	4
Rural/agricultural	---	---	---	-	0	+	5
Urban	---	---	---	---	−	0	6
C. Summer							
Forested wetlands	0	+	+	+++	+++	+++	1
Tree plantations	-	0	+	+++	+++	+++	2
Woods/scrub	-	-	0	+++	+	+++	3
Marsh/wetland	---	---	---	0	+	+	4
Rural/agricultural	---	---	-	-	0	+	5
Urban	---	---	---	-	-	0	6

Table 3. Ranking matrix from compositional analysis for 3rd-order habitat selection (selection of landcover categories within a home range) by Florida Black Bears in north-central Florida for (A) the entire study period (1 August 2011–31 July 2013), (B) fall seasons, and (C) summer seasons. Signs indicate preference, with (+) indicating that the row landcover category is preferred over the column landcover category and (-) indicating the opposite. Triple signs represent significant preference for (+++) or avoidance (---) ($P < 0.05$). Rank represents the order of preference for the landcover categories, in order of most strongly preferred (1) to least strongly preferred (5 or 6). For (A) overall and (C) summer, at least 1 bear lacked availability in rural/agricultural or urban areas. Therefore, the test was repeated by combining these 2 landcover categories into 1 category.

	Forested wetlands	Marsh/ wetland	Woods/ scrub	Tree plantations	Rural/ agricultural	Urban	Rank
A. Overall							
Forested wetlands	0	+++	+++	+++	+++		1
Marsh/wetland	---	0	-	+++	+++		2
Woods/scrub	---	---	0	+	+++		3
Tree plantations	---	---	-	0	+++		4
Rural/agricultural and Urban	---	---	---	---	0		5
B. Fall							
Forested wetlands	0	+	+++	+++	+++	+++	1
Marsh/wetland	-	0	+	+++	+++	+++	2
Woods/scrub	---	-	0	+++	+++	+++	3
Tree plantations	---	---	---	0	+	+	4
Rural/agricultural	---	---	---	-	0	-	6
Urban	---	---	---	-	+	0	5
C. Summer							
Forested wetlands	0	+	+++	+++	+++		1
Marsh/wetland	-	0	+	+	+++		2
Woods/scrub	---	-	0	+	+++		3
Tree plantations	---	-	-	0	+++		4
Rural/agricultural and urban	---	---	---	---	0		5

Table 4. Model selection results from mixed-effects logistic regression testing for factors influencing habitat selection by Florida Black Bears in north-central Florida from 2011 through 2013. Models are sorted based on the ΔAICc (Akaike information criterion corrected for small sample size) values in an ascending order. Landcover categories: wood/scrub, marsh wetlands, rural/agricultural, urban, tree plantations, and forested wetlands. Major roads, Minor roads, and Creeks all represent distances to the nearest respective feature. The number of parameters in each model is indicated by *K*. The weight indicates the Akaike weight or model probability. Only the top 10 models, out of 16 total, are shown.

Rank	Candidate model	*K*	Log-likelihood	ΔAICc	Weight
1	Landcover + Major roads + Minor roads + Creeks	10	–70155.96	0.00	1
2	Landcover + Minor roads + Creeks	9	–70303.89	293.85	0
3	Landcover + Major roads + Minor roads	9	–70462.44	610.95	0
4	Landcover + Minor roads	8	–70608.92	901.92	0
5	Landcover + Major roads + Creeks	9	–70645.31	976.69	0
6	Landcover + Creeks	8	–70752.50	1189.07	0
7	Landcover + Major roads	8	–70876.29	1436.67	0
8	Landcover	7	–70985.09	1652.25	0
9	Major roads + Minor roads + Creeks	5	–76413.07	12,504.20	0
10	Minor roads + Creeks	4	–76573.32	12,822.72	0

to investigate space and resource use by a newly colonized population of Black Bears in a human-dominated landscape with substantial anthropogenic habitat fragmentation. Compared with relatively unfragmented habitats in Ocala and in Osceola National Forests, the Camp Blanding area exhibited a lower proportion of suitable habitat, which was less aggregated, more dispersed, and more patchily distributed across the landscape (see Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s15-2-S2261-Karelus-s1 and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2261.s1). Therefore, we expected the Black Bears at our study site to have larger home ranges than those inhabiting relatively unfragmented habitats.

We could not statistically compare our estimates of home-range sizes with those reported from other studies. This comparison would require a consistent bandwidth among the studies that used KDE and the same or a comparable number of locations among studies that used either KDE or MCP (Börger et al. 2014, Kie 2013, Laver and Kelly 2008, Seaman and Powell 1996). The home-range studies of nearby Black Bear populations did not report bandwidths, and the number of locations varied widely among studies. Qualitatively, overall and seasonal Black Bear home ranges in the Camp Blanding area were larger than those for Black Bears in Ocala National Forest, except for females in 2000 (Moyer et al. 2007). An extreme, prolonged drought occurred in Florida from 1998 to 2001 that resulted in a forest-wide mast failure in Ocala National Forest (McCown et al. 2004), likely causing the Black Bears to use substantially larger home ranges in 2000 to meet their resource needs. Black Bear home ranges in Osceola National Forest and Okefenokee National Wildlife Refuge (Dobey et al. 2005) were comparable to or larger than those in the Camp Blanding area. However, much of the data used in Dobey et al.'s (2005) study were also collected during the drought years, which could have led to their observation of larger home ranges. Like Camp Blanding, Eglin Air Force Base (Valparaiso, FL) and the landscape surrounding it are fragmented and receive substantial military use (e.g., as airfields,

Table 5. Estimates (± SE) of slope parameters and 95% confidence intervals for the fixed-effect variables included in the most parsimonious mixed-effects logistic regression model (Model 1; Table 4). Negative coefficients indicate that the respective landcover category is less strongly preferred than the reference category, forested wetlands. Positive coefficients would indicate that the category is preferred over the reference category. All slope parameters are significantly different from 0 at $P \leq 0.001$.

Variable	Estimate ± SE	Confidence interval
Landcover category		
Marsh/wetland	-0.300 ± 0.027	(-0.354, -0.247)
Woods/scrub	-1.231 ± 0.019	(-1.268, -1.193)
Tree plantation	-1.559 ± 0.017	(-1.593, -1.526)
Rural/agriculture	-1.879 ± 0.041	(-1.960, -1.798)
Urban	-2.697 ± 0.055	(-2.804, -2.590)
Distance to creeks	-0.199 ± 0.008	(-0.215, -0.183)
Distance to major roads	-0.131 ± 0.008	(-0.146, -0.116)
Distance to minor roads	0.241 ± 0.008	(0.226, 0.257)

test ranges, and sewage-spray fields), which likely causes resources in that area to be more dispersed and thus may explain the fairly large Black Bear home ranges reported by Stratman (1998). In addition to fragmentation, the quality of habitat also influences home-range size. The smallest American Black Bear home ranges in the southeastern US have been reported for highly productive habitats in the Mississippi Delta region (Benson and Chamberlain 2007, Oli et al. 2002); the Black Bears in the Camp Blanding area used much larger home ranges. Therefore, our results are generally consistent with the expectation that Black Bears inhabiting less productive or fragmented habitats, or a combination of the two, would use larger home ranges than those in unfragmented or more productive habitats.

Most of the Black Bears at our study site exhibited larger home ranges in fall than in summer, although the differences were not significant. This tendency for larger home ranges in fall is attributed to the increased foraging area during fall hyperphagia experienced by Black Bears in preparation for winter denning and is consistent with findings for the Ocala Black Bear population and several other populations (Hellgren et al. 1989, Moyer et al. 2007, Powell et al. 1997). Therefore, our failure to detect a significant difference between summer and fall was most likely due to our small sample sizes.

Black Bears in the Camp Blanding area consistently preferred forested wetlands compared to all other types of landcover at both 2^nd^- and 3^rd^-order scales during the entire study period as well as in the summer and fall. Black Bears also selected for areas close to creeks. Together, these results suggest that riparian forests represent the best-quality habitat for Black Bears in the area. This result is not surprising because forested wetlands include relatively abundant mast from oaks and palmettos, a thick understory for ground-den sites and cover, and connectivity with other habitats (Hellgren et al. 1991, Stratman et al. 2001, Wooding and Hardisky 1994). Black Bears generally avoided agricultural, rural, and urban landcover at both scales of selection in all seasons, most likely due to the lack of cover and higher levels of human disturbance. However, this finding does not indicate that Black Bears will always tend to avoid agricultural landscapes or urban areas. Black Bears can become habituated to humans and alter their behavior to exploit food sources found in neighborhoods, especially when resources are scarce (Bateman and Fleming 2012, Beckmann and Berger 2003b, Johnson et al. 2015). Securing garbage and other food sources early in the Black Bear's recolonization could help mitigate potential human–bear conflict.

There are many challenges inherent in the use–availability design of habitat-selection studies (Beyer et al. 2010, Garshelis 2000). For example, criteria used to partition habitat types are usually arbitrary, distinction between habitat and non-habitat is often blurred, measuring habitat units that are available to study animals is difficult, and unbiased and error-free quantification of habitat use is rarely possible (Garshelis 2000). Although we cannot rule out the possibility that some of our results may have been influenced by aforementioned challenges, the concurrence between the results of compositional analyses and mixed-effect logistic regression models lead us to believe that that our results are robust.

Black Bears at our study site used habitats closer to major roads and farther away from minor roads than would be expected at random. These results may be a consequence of the presence of 2 major roads that cross large blocks of forested habitat in the Camp Blanding area, rather than Black Bears showing preference for areas closer to a major road. Several home ranges spanned both sides of those roads, and 3 radio-collared Black Bears were killed while crossing major roads. Reynolds-Hogland and Mitchell (2007) and Coster and Kovach (2012) reported similar results. Black Bears may have stayed farther away from minor roads more than expected due to high levels of disturbance during military training exercises, deer-hunting season, and land-management activities (Morrison et al. 2014, van Manen et al. 2012), but more data on human use of the area would be required to determine whether that was the case.

Our findings suggest that Black Bears occupying fragmented habitats generally require larger home ranges to acquire sufficient resources and reinforced the importance of riparian forests. Conservation planning that focuses on preserving and restoring riparian habitats and maintaining or increasing the distribution and abundance of soft- and hard-mast-producing plants in adjacent uplands will help ensure the availability of essential resources for Black Bears. These management actions would help increase the likelihood of colonization and persistence of stepping-stone populations, and would facilitate greater connectivity among Black Bear populations.

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