Spatially Explicit Population Estimates of the Florida Black Bear

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Dedication

This thesis is dedicated to:

Anyone who ever pushed me to be better than I already was;
To the many influential people in my life who forced me
to realize my potential,

To my parents and my brother especially
for always believing in me,

And to Richard (Jeffers) Frazier,
the first person to show me what it was
to stand up for what you believe in.
I will never forget that day on the playground.

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Abstract

The Florida black bear (*Ursus americanus floridanus*) is currently comprised of 7 isolated subpopulations: Apalachicola, Eglin, Osceola, Ocala/St. Johns, Chassahowitzka, Highlands/Glades, and Big Cypress. The last statewide assessment of Florida black bear population dynamics was conducted by Simek et al. (2005) using traditional capture-mark-recapture methods. The subspecies was removed from Florida's List of State Threatened Species in 2012 contingent upon the formulation of a management plan that would maintain viable subpopulations of black bears in suitable habitat. Accurate population estimates for each of the remaining black bear subpopulations in Florida were needed to achieve the management goals of this plan.

I used spatially explicit capture-recapture (SCR) within a maximum likelihood inference framework to estimate population density (*D*) and abundance (*N*) for the Osceola, Ocala/St. Johns, Eglin, Apalachicola, and Big Cypress subpopulations; these 5 subpopulations constitute the bulk of the statewide population. I constructed genetic capture histories for each subpopulation from genotyped hair samples taken from barbed-wire sampling stations (henceforth referred to in this document as hair snares). I used a 3 × 3 hair snare cluster layout with 2 km between hair snares and 16 km between cluster centers. I created covariates of density from land use/land cover (LULC) data to model heterogeneity in density across study areas. Model-averaged population estimates were 120.3 bears (95% CI = 61.1 – 269.1) or 0.025 bears/km^2 [bears per square kilometer] (95% CI = 0.013 – 0.056) for the Eglin subpopulation, 1,060.3 bears (95% CI = 825.4 – 1,385.9) or 0.082 bears/km^2 (95% CI = 0.064 – 0.107) for Apalachicola, 492.9 bears (95 % CI = 319.5 – 792.4) or 0.127 bears/km^2 (95% CI = 0.082 – 0.203) for Osceola, 1,192.6 bears (95% CI = 950.8 – 1,519.5) or 0.127 bears/km^2 (95% CI =

0.101 – 0.161) for Ocala/St. Johns, and 1,037.4 bears (95% CI = 756.1 – 1,444.6) or 0.131 bears/km^2 (95% CI = 0.096 – 0.183) for Big Cypress. Effects of covariates on density estimates varied among study areas. The total population estimate was 3,908.8 bears (95% CI = 2,916.2 – 5,425.8). The cluster sampling method allowed abundance to be estimated across extensive areas that would not have been possible otherwise.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

Background and Justification

The Florida black bear, *Ursus americanus floridanus*, is 1 of 16 subspecies of the American black bear (*U. americanus*). The historic range of the subspecies included mainland Florida, some of the Florida Keys, the southern borders of Georgia and Alabama, and a small portion of southeastern Mississippi (Hall 1981). The type specimen of the subspecies was taken from Key Biscayne, Florida (Harlow 1961); this is a testament to the surprising adaptability of this large carnivore. Human development of bear habitat and unregulated harvest caused precipitous declines in bear population sizes in the past (Williams 1978). Conditions adversely affecting bear subpopulations in Florida (Harlow 1961) included killings related to bear-human conflict arising from property damage (e.g., hog predation, bee predation); loss of habitat due to rapid development for housing, pasture, roadways (Harlow 1961), and more recently, timber harvest (Hendry et al. 1982); and hunting pressure. Although reports varied and were based on very little statistical data, statewide Florida black bear population estimates in the mid-20th century were all low. Five-hundred (500) bears were estimated statewide in 1949 (Frye et al. 1950), 860 bears in 1960 (Harlow 1961), and 500 bears in 1972 (Pelton and Nichols 1972). The Florida black bear was placed on the state's Threatened Species List in 1974 (Brady and Maehr 1985) to prevent extinction of the subspecies. Despite multiple petitions to obtain a federal listing under the Endangered Species Act, the U.S. Fish and Wildlife Service concluded that listing the Florida black bear as endangered or threatened species was not warranted (Wesley 1991, Bentzien 1998, Kasbohm 2004).

Continued efforts to maintain bear habitat, to enforce harvest bans, and to minimize bear-human conflict (Florida Fish and Wildlife Conservation Commission [FWC] 2013) have allowed

for a marked increase in subpopulation numbers (Simek et al. 2005). Today, 5 major subpopulations remain in the state of Florida, though some other bears exist in small pockets of habitat scattered across the state (e.g., Chassahowitzka, Glades-Highlands. Every subpopulation is impacted by habitat fragmentation, which restricts movements and genetic interchange (Dixon et al. 2006, Dixon et al. 2007). A large number of bears are killed on Florida highways each year (FWC 2016), the demographic effects of which are not known.

The Florida black bear was delisted (Telesco 2012) in 2012 following re-evaluation of its risk of extinction and the formulation of a comprehensive management plan (FWC 2012). The main components of the management plan's population objective included "…managing one bear subpopulation to be at least 1,000 individuals" and "ensuring that the smaller subpopulations are increased to a minimum of 200 bears each" (FWC 2012). Current data regarding population abundance and density are needed to determine what actions will be taken to achieve prescribed management goals.

The most recent assessment of statewide black bear population demographics was conducted from 2001 to 2003 by Simek, et al. (2005). Simek et al. (2005) estimated the size of the Apalachicola, Big Cypress, Eglin, Osceola, Ocala, and St. Johns bear subpopulations from 2001 to 2003 using mark-recapture techniques based on DNA extracted from bear hair (Paetkau et al. 1995). Hair samples were collected from barbed wire sampling sites and genotyped to individual animals; these genetic data were treated as marks. The advantages of this technique compared with traditional live-capture are that it can reduce capture biases and is relatively cost effective. Simek et al. (2005) placed baited hair-sampling sites (hair traps) within a smaller portion of occupied bear range in each of the major subpopulations in Florida so that about 4 hair traps would be present within the estimated summer home range of each female (Otis et al.

1978). Sites were constructed by enclosing 4–6 trees with 2 strands of barbed wire, 25 cm and 50 cm high. Baits consisting of corn and pastries were hung within each enclosure. Hair snares were set for 8 sampling sessions. Capture probabilities were high ($p = 0.28$) during each 12- to 16-day session, even after considerable subsampling of the hair collected. Because only a portion of the area occupied by each subpopulation was sampled, abundance and density estimates were extrapolated to the entire occupied range of that subpopulation, assuming homogeneous and equivalent densities across the broader area. Abundances ranged from 63–101 bears at Eglin to 729–1,056 bears at Ocala.

Simek et al. (2005) used Program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991) to estimate within-year population parameters. Program CAPTURE may not always properly select among competing models or detect capture heterogeneity when it is present (Menkens and Anderson 1988, Stanley and Burnham 1998, Boulanger et al. 2002), and options for modeling heterogeneous capture probabilities are limited to non-parametric estimators (i.e., Jackknife [Otis et al. 1978] and Chao methods [Chao 1989]). Likelihood-based estimators have since been developed to estimate capture heterogeneity (Huggins 1989, 1991; Pledger 2000), thus permitting comparisons among all models using information-theoretic methods (Burnham and Anderson 2002). Information-theoretic procedures are considered superior to the model selection method in Program CAPTURE (Stanley and Burnham 1998) and also allow model averaging of parameter estimates, which helps account for model selection error and improves inference (Luikart et al. 2010).

Lastly, recent research has led to the development of population estimation methods that make use of not only individual capture histories, but also the locations of the captures on the landscape (Efford 2004, Borchers and Efford 2008, Efford and Fewster 2013, Royle et al. 2014,

Efford 2016). Such spatially explicit capture recapture estimators have advantages over non-spatial methods, e.g., the ability to explicitly estimate the area sampled by the traps and a reduction in capture heterogeneity due to an animal's location on the trapping grid.

Objectives and Hypotheses

My study objectives were to use spatially explicit capture-recapture to:

1. estimate bear population abundance and density for each of the subpopulations surveyed by Simek et al. (2005), and
2. evaluate spatial covariates of density to estimate bear numbers in areas not surveyed.

Chapter 2: Study Areas

My thesis research focused on 5 subpopulations of the Florida black bear, the locations of which ranged from the Florida panhandle region to the southern tip of the peninsula (Fig. 1). Because the Ocala and St. Johns study areas listed by Simek et al. (2005) included contiguous bear subpopulations that are genetically indistinguishable (Dixon et al. 2007) and now managed as one (FWC 2012), I combined them to create a single Ocala/St. Johns study area. Habitat conditions among these 5 subpopulations vary tremendously because of their wide geographic distribution and the varying influences of human development across the landscape. Habitat ranged from upland hardwoods in Apalachicola to tropical prairie and pine islands in Big Cypress. The combined total area sampled for all 5 study areas was 38,960 km^2. Thus, about 28% of the total land area of the State of Florida (138,887 km^2, U.S. Census Bureau 2010) was included in this study.

The Eglin study area was located in the western panhandle and was comprised of areas in and around Eglin Air Force Base. Eglin was the smallest study area at 4,795 km^2. This area was characterized by high pine and scrub communities and freshwater forested wetlands. The predominant habitat type was high pine and scrub, which is described by the Florida Natural Areas Inventory (FNAI 2010) as mesic or xeric woodlands or shrublands with open canopy consisting mainly of pine. Freshwater forested wetlands, namely seepage slope and dome swamp communities, were scattered among lowland areas of the region. Small alluvial forests and bottomland forests occupied the floodplains of major waterways such as the Choctawhatchee River in the east and the Yellow River in the west. About 33% of the combined area for the Eglin study area was designated as some form of agriculture or human development (FWC and FNAI 2015), which includes military training grounds on Eglin Air Force Base.

The Apalachicola study area was located in the eastern panhandle region and was comprised of habitat in and around Apalachicola National Forest. At 12,953 km^2, Apalachicola was the largest of the 5 study areas. Apalachicola National Forest encompassed roughly 2,570 km^2 (USDA Forest Service 2015), or about 20% of the total area analyzed for the Apalachicola subpopulation. More than 40% of this study area was interspersed with some form of agricultural land or human development; a large portion of the agricultural land consisted of tree plantations (FWC and FNAI 2015). The predominant habitat type was freshwater forested wetlands (~30%, FWC and FNAI 2015) which was mainly comprised of floodplain swamp and hydric hammock communities. Hardwood forested uplands, pine flatwoods and dry prairie, and high pine and scrub habitats constituted much of the remaining land cover (FWC and FNAI 2015).

The Osceola study area was on the northern border of the Florida peninsula and was comprised of habitat in and around Osceola National Forest. This study area included John M. Bethea State Forest in Florida and the southern border of the Okefenokee National Wildlife Refuge in Georgia. This area was heavily influenced by agricultural development; roughly 40% of the total land cover was designated agricultural, most of which was tree plantations (FWC and FNAI 2015). The predominant habitat type was freshwater forested wetlands (FNAI 2010), which was comprised of communities such as bay gall, hydric hammock, and basin swamp. These forested wetlands were concentrated in the central portion of the study area with interspersed pine flatwoods. The northern portion of the study area was more frequently associated with the outer edges of freshwater non-forested wetlands including prairie and bog communities.

The Ocala/St. Johns study area was located mainly in central Florida and was comprised of habitat in and around Ocala National Forest as well as Flagler and Volusia counties east of the St. Johns River. Ocala/St. Johns varied considerably by geographic region; the northern end and the eastern half of the study area were comprised mainly of pine plantations, with small pockets of high pine and scrub and suburban developments towards the outer edges of those regions (FWC and FNAI 2015). Ocala National Forest comprised most of the western half of the study area; this region was dominated by high pine and scrub habitat, which was mainly scrub and sandhill communities. The predominant habitat type for the extent of the study area was freshwater forested wetlands (FNAI 2010, FWC and FNAI 2015), due to the extensive network of watercourses that comprises the St. Johns River watershed.

Finally, the Big Cypress study area was in the southern portion of the Florida peninsula and was comprised of habitat in and around Big Cypress National Preserve (BICY). This unique tropical region was dominated by forested and non-forested wetlands; more than half of the study area was comprised of wide swaths of marl prairie and glades marsh in the southeastern section where BICY borders the Everglades Wildlife Management Area to the east, with large pockets of cypress (*Taxodium* spp.) swamp and other forested freshwater wetlands interspersed (FNAI 2010, FWC and FNAI 2015). BICY was bordered to the west by a substantial strand swamp community demarcated by Picayune Strand State Forest, Fakahatchee Strand State Preserve, and the Florida Panther National Wildlife Refuge. The northern section of the study area was more urbanized, with large tracts of agricultural land used for pasture and citrus groves, as well as small towns such as Immokalee. Towards the Gulf of Mexico lay a long stretch of salt marsh and mangrove swamp that was not sampled directly due to time constraints, but which was included in my analysis.

Chapter 3: Materials and Methods

Trap Placement

Before establishing hair snares, a number of cluster configurations were evaluated to assess bias and optimize efficiency (J. Clark, U.S. Geological Survey, unpublished data). First, the Simek et al. (2005) trap and capture data for 2003 were obtained. Only 1 year of data were used because each of my population estimates were to be based on 1 year of sampling. Capture probabilities (g_0) and a home range parameter (σ) were estimated based on 2003 bear densities (D) from Simek et al. (2005) for each study area using package `secr`, which is an R-based (R Core Team 2015) SCR routine based on maximum likelihood estimation methods (Efford 2004). The package is a collection of functions to estimate the density and size of a spatially distributed animal population sampled with an array of passive detectors, such as traps, or by searching polygons or transects. Models incorporating distance-dependent detection are fitted by maximizing the likelihood (Efford 2016). Given those estimates, simulations of various trap configurations and cluster sizes in `secr` were conducted for each study area to assess bias and precision. Given estimates obtained with those data, D = 0.15 bears/km^2, σ = 1,000 m, and g_0 = 0.1 were used to conduct simulations of various trap configurations and cluster sizes in `secr` to assess bias and precision ($\geq$10 replicates of each). Traps within simulated clusters were spaced 500, 1,000, 1,500, 2,000, 2,500, 3,000, 3,500, and 4,000 m apart; spacings between clusters (center to center) of 10,000, 12,000, 14,000, 16,000, 18,000, 20,000, 25,000, and 30,000 m; 2 × 2, 3 × 3, and 4 × 4 trap clusters; and sampling periods of 4, 6, or 8 weeks were evaluated. The evaluation area was 10,000 km^2 in size. The 3 × 3 trap cluster configuration with traps 2,000 m apart, clusters spaced 16,000 m between cluster centers, and conducted over a 6-week sampling period performed well within a 10,000 km^2 sampling area, resulting in nominal relative bias (-

0.009, 95% CI = -0.107–0.090) and reasonable confidence intervals (D = 0.149, 95% CI = 0.110–0.201; J. Clark, U.S. Geological Survey, unpublished data).

Based on this trap cluster configuration, prospective trap sites were projected onto maps of each study area and field personnel were instructed to find sites with suitably spaced trees within 250 m of the assigned trap coordinates. The areas to which this cluster sampling was applied were loosely based upon a map of primary and secondary bear range in Florida developed by Scheick and McCown (2014). However, when unable to strictly adhere to site locations due to human development, impenetrable vegetation, or property access, an alternate site within 500 m was selected. If no suitable site within 500 m of the proposed location was available, I deleted that hair snare from the cluster. A study team composed of FWC employees, volunteers, and I constructed and checked hair snares on Osceola and Ocala/St. Johns during 2014 and on Eglin, Apalachicola, and Big Cypress during 2015.

Sample Collection

Hair snares for all study areas consisted of enclosures comprised of 2 strands of 15.5-gauge, high-tensile barbed wire with 4 prongs per barb and barb spacing of 12.7 cm (Gaucho®, Bekaert Corporation, Marietta, GA, USA) stretched around 3–5 trees. Crews positioned the strands 35–40 and 65–70 cm above the ground and blocked variations in the terrain (e.g., small gullies, mounds) with vegetation and woody debris to prevent bears from crossing over or under the wires per the methods of Laufenberg et al. (2016). Bait (bakery products) was hung from a line that spanned the enclosure. Commercial bear lure (Code Blue Bear Magnet Raspberry Donut Attractant, Code Blue, Calera, AL, USA, or Bait Station Bear Bait, Evolved, New Roads, LA, USA) was also used as a scent attractant. Hair samples were placed in coin envelopes and stored at room temperature prior to analysis. Lighters and propane torches were used to burn any

remaining hair off the barbs after each hair collection occasion. All hair snares were checked and rebaited weekly for 6 consecutive weeks, beginning in June of each year.

Genetic Analysis

Hair samples were genotyped at Wildlife Genetics International (WGI; Nelson, British Columbia, Canada) after subsampling (Laufenberg et al. 2013). Because Augustine et al. (2014) identified potential problems arising from subsampling in conjunction with a potential behavioral response to traps, all samples from week 1 were genotyped to evaluate the potential for introduced behavioral bias from subsequent recaptures (i.e., "trap-happy" bears) during 2014. One sample per site per week was selected for genotyping for weeks 2–6. Technicians at WGI randomized the samples within each site-week and selected the first sample encountered containing >30 underfur or 5 guard hair roots. If none of the samples at a site-week met this quality threshold, technicians chose the best available sample from the site, using a minimum quality threshold of 1 guard hair root or 5 underfur hairs. If none of the samples met this more lenient threshold, the site was left out of the analysis for that sampling event.

Analyses subsequent to Augustine et al. (2014) indicated that subsampling bias is not significant with SCR methods when a consistent percentage of the hair samples are subsampled from week to week (B. Augustine, University of Kentucky, unpublished data). Thus, in 2015 subsampling was performed for all weeks, but 2 samples were selected at random per visited hair snare per week for genotyping (ensuring the 2 samples were from different sides of the hair trap) to maximize the success rate for all sampling weeks while reducing the number of duplicate samples.

Following standard protocols (Woods et al. 1999, Paetkau 2003, Roon et al. 2005), DNA was extracted using QIAGEN DNeasy Blood and Tissue spin columns. The number of markers

required to correctly identify individuals depends on the size and genetic structure of the subpopulation. WGI had analyzed the samples collected by Simek et al. (2005) and used their knowledge of each subpopulation's genetic structure in their marker recommendations (WGI, unpublished data, 2014). The analysis of individual identity was based on 8 markers comprised of a gender marker and 7 microsatellites, except for Big Cypress where 9 markers (8 microsatellites and 1 gender marker) were used. Samples that match at all but one or two markers may be different individuals (often siblings) or they may be the same individual misidentified by genotyping errors (Paetkau 2003). To find and correct such misidentifications, all 1- or 2-mismatched markers were reanalyzed to ensure the dataset had not been affected by undetected genotyping error (Kendall et al. 2009). Allelic frequencies at each microsatellite locus for each sampling area are displayed in Tables 1 – 5.

Population Analysis

Traditional mark-recapture techniques seek to estimate population parameters under the assumption of closure, meaning that there are no births, deaths, immigration, or emigration (Otis et al. 1978). Various forms of bias arise from this assumption. For example, edge effect, or capture probability bias, can result from the movements of animals whose home ranges are only partially enclosed by the study area (Seber 1986). It is difficult to account for this bias when estimating density of a population using traditional capture-mark-recapture techniques. Density estimation through capture-mark-recapture requires a defined sampling area, across the boundaries of which it is assumed no animals move in or out. Non-parametric attempts to define sampling area, such as placing a buffer equal to the mean maximum distance moved around the convex hull of the trapping array (Parmenter et al. 2003) or placing a buffer width equal to the mean female home range radius (Bales 2005), are essentially arbitrary because bias from edge

effects cannot be statistically verified. Traps must be placed close enough together to minimize this bias between traps; thus, sampling area sizes are limited by the number of traps one can afford to build and check in a given field season.

Spatially explicit capture-recapture incorporates space-use data into the analysis by defining the relationship between capture data and the spatial locations of detectors (Borchers and Efford 2008). There are two models described in this method: a spatial detection model (observation model) to estimate animal home-range centers or "activity centers"; and a state model, which describes the distribution of those activity centers on the landscape (Efford 2016). The observation model relates the probability of detecting an individual at a particular detector to the distance of the detector from that animal's activity center. This type of model allows for individual heterogeneity in capture probability based on an animal's location in relation to the trapping grid (Borchers and Efford 2008, Efford and Fewster 2013). The state model uses the results of the observation model as well as optional data in the form of spatial covariates of density to infer the distribution of home range centers on the landscape. The state model can either be treated as a homogeneous Poisson point process, whereby density is the sole parameter of the process; or it can be treated as an inhomogeneous process, whereby the effects of habitat variables can be modelled on density (Efford 2016). By describing the distribution of animal home ranges on the landscape through the state model, the number of activity centers within the trapping grid is explicitly estimated and guessing at the effective trapping area is not necessary. This approach circumvents the bias associated with edge effects and allows for indirect estimation of areas not sampled, thus making possible a clustered sampling design whereby gaps can be incorporated into the trap layout, given appropriate trap spacing (Sollmann et al. 2012, Efford and Fewster 2013, Sun et al. 2014). This clustered design enables sampling of much

larger areas that would not otherwise be feasible under the constraints of traditional capture-mark-recapture. By defining the sampling area based on spatial distribution data, empirical estimates of density that are robust to edge effects and do not depend on the trap layout can be made (Borchers and Efford 2008, Efford and Fewster 2013).

I used ver. 2.10.2 of the R package `secr` to estimate population parameters (Efford 2004, Efford et al. 2004, Borchers and Efford 2008, Efford 2012, R Core Team 2015) within an information theoretic model selection framework based on Akaike's Information Criterion adjusted for small sample size (AICc, Anderson 2008), whereby sample size *n* was the number of animals detected at least once across all site-weeks (Efford 2016). Package `secr` estimates 3 parameters: density (*D*), detection probability if a trap's location coincided with an animal's activity center (g_0), and sigma (σ), the probability of detection as a function of the distance between an animal's home range center and a trap. The parameters g_0 and σ are used by `secr` to jointly define the model for detection probability as a function of location, which is then used to estimate the distribution of home range centers on the landscape, or *D* (Efford 2016). Package `secr` uses maximum likelihood estimation (MLE) to infer the likelihood that the model accurately explains the parameters, given the data. Model-fitting using MLE and AIC allows one to compare the efficacy of a set of candidate models by utilizing information theory. AIC is an estimator that directly links the maximized log-likelihood of a model (i.e., model fit using MLE) to Kullback-Leibler (K-L) information, which is essentially a dimensionless quantitative measure of how far a model is from the true latent process that governs a phenomenon of interest, or "full reality" (Anderson 2008). The main caveat of using K-L information is that full reality is defined as a latent process, there is no way to determine how close to full reality the model is in an absolute sense. Thus, AIC only allows one to compare the distances of candidate

models from the true underlying process relative to each other. It was therefore important to consider the ecological and biological relevance of the variables used in my analyses. I used a second-order bias correction to AIC (AIC_c) that introduces an additional term to account for sample sizes that are small relative to the number of parameters (K) used in each model.

I evaluated models whereby heterogeneity in g_0 or σ was explained by a hybrid mixture model with sex specified as the mixture (h2; Pledger 2000, Efford 2014*a*). For example, male home ranges are generally larger than those for females so the probability that a site would be found by a bear at that animal's activity center (g_0) and the distance from the activity center that a bear would likely be detected (σ) could differ by sex. I also evaluated models whereby heterogeneity in detection probabilities was explained by a site-specific behavioral response (bk) to trap encounter (i.e., "trap-happy" or "trap-shy"). I also modeled potential differences in g_0 during week 1 versus weeks 2 – 6 to reflect my subsampling scheme during 2014.

I evaluated land cover variables and other landscape metrics as covariates of bear density for each subpopulation. I used state-level land use/land cover (LULC) data at 10-m spatial resolution (i.e., cell size) from FWC and Florida Natural Areas Inventory Cooperative Land Cover Map v3.1 (FWC and Florida Natural Areas Inventory 2015). I also used TIGER/Line® roads data (U.S. Census Bureau 2015); both were processed with ArcMap (ArcGIS 10.2.2 for Desktop, c 1999 – 2013 ESRI Inc., www.esri.com).

Because the number of land cover classes in the LULC database was large, I grouped individual classes into categories that I deemed to be potentially important to bears (e.g., mast-producing cover). First, I created a "forest" layer consisting of the following classes from the Florida Land Cover Classification System (Kawula 2014): Upland Hardwood Forest (1110), Mesic Hammock (1120), Rockland Hammock (1130), Slope Forest (1140), Xeric Hammock

(1150), Sand Pine Scrub (1213), Upland Pine (1231), Sandhill (1240), Pine Flatwoods and Dry Prairie (1300), Dry Flatwoods (1310), Mesic Flatwoods (1311), Scrubby Flatwoods (1312), Mixed Hardwood-Coniferous (1400), Maritime Hammock (1650), Freshwater Forested Wetlands (2200), Cypress/Tupelo Mixed (2210), Cypress (2211), Tupelo (2213), Strand Swamp (2214), Floodplain Swamp (2215), Other Coniferous Wetlands (2220), Wet Flatwoods (2221), Other Hardwood Wetlands (2230), Baygall (2231), Hydric Hammock (2232), and Tree Plantations (18333). This layer was representative of forested habitat that may be important to bears as foraging or escape cover. I excluded forested cover types that I judged were unimportant to bears, such as mangrove. A "swamp" layer was created by grouping the above classes ranging from 2200 to 2232, to which I added Non-vegetated Wetland (2300), Cultural-Palustrine (2400), Bottomland Forest (22131), and Basin Swamp (22132). This layer was representative of perennially and annually flooded habitat dominated by forest cover and other woody vegetation. A "natural" layer was created by grouping all classes within the Hardwood Forested (1100), High Pine and Scrub (1200), Pine Flatwoods and Dry Prairie (1300), Mixed Hardwood-Coniferous (1400), Scrub and Brushland (1500), Coastal Uplands (1600), Barren and Outcrop Communities (1700), Other Palustrine (2000), Freshwater Non-Forested Wetlands (2100), Freshwater Forested Wetlands (2200), Exotic Plants (7000), and Tree Plantations (18333). This layer was representative of areas not influenced by human development (i.e., urbanization, transportation, and agriculture).

I created 3 hard and soft mast-producing layers because of the possibility that some cover types might produce mast on 1 study area but not on another. For example, Tree Plantations (18333) may be important sources of saw palmetto (*Serenoa repens*) in the Osceola study area but may not be a source of soft mast in Big Cypress. The first mast layer was created by

grouping categories Upland Hardwood Forest (1110), Mesic Hammock (1120), Slope Forest (1140), Xeric Hammock (1150), Other High Pine and Scrub (1210), Sand Pine Scrub (1213), Dry Flatwoods (1310), Mesic Flatwoods (1311), Scrubby Flatwoods (1312), Mixed Hardwood-Coniferous (1400), Maritime Hammock (1650), Freshwater Forested Wetlands (2200), Strand Swamp (2214), Other Coniferous Wetlands (2220), Wet Flatwoods (2221), Other Hardwood Wetlands (2230), Hydric Hammock (2232), Exotic Plants (7000), and Basin Swamp (22132). The second mast layer was created by adding Floodplain Swamp (2215) and Cypress/Tupelo (2210) to the first mast layer. I created a third mast layer by adding Tree Plantations (18333) to the second mast layer.

For each of the above layers, I coded each cell with the grouped cover types as 1 and all other cover types as 0 and calculated the mean value for each cell based on a circular moving window analysis with a radius of 2,372 m (σ for both sexes combined based on the 2003 data). The moving window analysis resulted in the new raster data layers that I used as density covariates: percent forest cover (f_perfor); percent swamp forest (f_perswamp); percent natural cover (f_pernatural); and percent hard and soft mast cover layers 1, 2, and 3 (f_pershmas, f_persh2, f_persh3, respectively).

Bear movement across the landscape may be hindered by the presence of major roads (Beringer et al. 1990, Cushman and Lewis 2010, Lewis et al. 2011, Coster and Kovach 2012) and bears may preferentially choose habitats located further from roads and major human development (Lewis et al. 2011, Hiller et al. 2015). I assessed the effects of anthropogenic disturbance on home range distribution by including “urban”, “high-intensity urban”, and “major roads” distance-to-feature covariates in my analysis. I created an “urban” category by grouping High Intensity Urban (1822) with Low Intensity Urban (1821) from the FWC-FNAI (2015)

dataset, as well as a "high intensity urban" category that only included 1822. From the TIGER/line (2015) dataset I created a "major roads" layer by keeping feature classes S1100, S1200, S1630, S1640, S1780, and S2000. This layer was representative of arterial highways and their connectors, medians, and access points.

Finally, I created a "fresh water" category by grouping Non-vegetated Wetland (2300), Cultural-Palustrine (2400), Lacustrine (3000), Natural Lakes and Ponds (3100), Cultural-Lacustrine (3200), Riverine (4000), Natural Rivers and Streams (4100), Cultural-Riverine (4200), and Open Water (8000) from the FWC-FNAI (2015) data set. I created distance covariates of density from the high-intensity urban layer (f_dishiur), the urban layer (f_disurb), the major roads layer (T_no14_dis), and the water layer (f_dish2o) using Euclidean distance operations in ArcMap for each feature. I included negative distances to water, high-intensity urban development, and general urban development for the spatial representations of those features; e.g., f_disurb raster cells that were located towards the interior of an urban area would have increasingly large negative values. I did not include >1 forest (i.e., f_perfor, f_perswamp, f_pernatural, f_pershmas, f_persh2, and f_persh3) or urban (f_dishiur, f_disurb) variables in the same model. Exclusive of those, I ran all 2-covariate model combinations including additive and interaction effects.

Combining spatially correlated covariates may lead to the inclusion of spurious models. I used the Coefficients of Determination (R^2) to assess potential correlation among all 2-covariate combinations that I used in additive and interaction models (e.g., D ~ f_perswamp + f_dish2o). R^2 is interpreted as the proportion of the variance in the dependent variable that is predictable from the independent variable. It is commonly used in linear regression to assess correlation between those variables. I assessed the degree of correlation between 2-covariate pairings by

calculating R^2 between data paired by common spatial coordinates. No significant correlations ($R^2 \leq 0.393$) were observed for any 2-covariate pairings (Tables 13 – 17).

Although all Osceola hair snares were located in Florida, my estimation process had to account for bears that may have visited Osceola hair snares but whose activity centers were in Georgia. Excluding the Georgia portion from the estimation area would have forced the activity centers of Georgia bears to be placed in Florida, which would have inflated estimates for the Florida portion of the Osceola sampling area. However, the FWC-FNAI categorical raster only had LULC data for the state of Florida. I explored the option of performing a cross-walk between Southeastern Gap Project LULC classes (Southeastern Gap Analysis Project 2009) and FWC-FNAI data; however, the most recent update to the Southeastern Gap Project data set was published in 2008. Because I did not have current, in-depth LULC data for the Georgia portion, I used the mean percent cover values of each habitat covariate from the Florida portion of the sampling area and assigned those values to the Georgia portion. Once density was estimated for the 2-state area, I excluded Georgia from the abundance and mean density estimates.

I estimated density and abundance within a 16-km buffer area around the trap sites (the average distance between cluster centers, excluding water bodies, cities, etc.). I used a half-normal detection function to model covariates of spatial capture probability (i.e., g_0 and σ). For each sampling area, I used the `secr` function 'region.N' to derive estimates of N for top models with ΔAICc $\leq$4, then I averaged the parameter estimates for those models based on their respective model weights (Anderson 2008). I kept top models with ΔAICc $\leq$4 for model-averaging of parameter estimates to account for the bulk of the total relative weight of models on estimates while minimizing the chances that spurious estimates might influence model averages. Unconditional standard errors were calculated according to methods outlined in Anderson (2008)

to account for model selection uncertainty. I calculated asymmetrical confidence intervals using the number of uniquely identified captured bears as a lower bound (Rexstad and Burnham 1991). Mean density was defined as *N* divided by study area size. Confidence intervals for mean density were also calculated by dividing the upper and lower bounds of *N* by study area size. I plotted model-averaged density surface maps based on the relationships between habitat covariates and density with the function "predictDsurface" in `secr` (Efford 2014*b*).

Chapter 4: Results

Apalachicola

The study team, which consisted of FWC employees, volunteers, and myself, checked 324 hair snares on Apalachicola from 15 June to 26 July 2015 (Fig. 2). Based on the subsampling protocol, WGI selected 683 of 4,027 hair samples for genotyping from Apalachicola. Genotyping indicated that 217 (124M:92F) bears visited hair snares 519 times during the 6-week sampling period (Fig. 2).

Top models for Apalachicola tended to support negative associations between density and percent mast-producing cover, floodplain forest, and tree plantations (f_persh3; top model β = -1.682, 95% CI = -3.061 – 0.303), when coupled with an interaction effect (top model β = 4.261, 95% CI = 0.962 – 7.560; Table 6) with distance to urban development (f_disurb; top model β = -2.954, 95% CI = -5.673 – 0.234). Sex (h2) and site-specific behavioral effects (bk) were supported for Apalachicola both as interaction and additive terms for g_0, and sex (h2) was supported as an effect on σ. Model-averaged mean density at Apalachicola was 0.082 bears/km^2 (95% CI = 0.064 – 0.107, Table 7). When applied to the 12,953-km^2 study area, model-averaged mean abundance (expected N) was 1,060.3 bears (95% CI = 825.4 – 1,385.9). Model-averaged bear densities tended to be higher in areas of heavy mast-producing and floodplain forest cover if far from urban areas, but were also higher in sparse forest cover near urban areas due to the interaction effect (Fig. 3).

Big Cypress

We checked 134 hair snares on Big Cypress from 15 June to 26 July 2015 (Fig. 4). WGI selected 316 of 2,038 hair samples for genotyping, which represented 128 (81M:47F) different bears visiting hair snares 258 times (Fig. 4). One female bear travelled >27 km over the 6-week

study period. The first sample from this animal was recorded during week 2 at a hair sampling site in the southwest corner of Big Cypress National Preserve whereas all subsequent samples identified from that animal were collected within a cluster in the southeastern corner of the Preserve. The distance between the first and second detections (~27 km) was exceptionally large for a female black bear so I assumed these data represented a dispersal or other unusual movement. As such, I did not use the first sample from that bear in my analysis because it would have overly inflated σ. The top models for Big Cypress tended to support a positive association of density with percent soft and hard mast-producing cover, floodplain forest, and tree plantations (top model β = 1.293, 95% CI = 0.228 – 2.358) though other forest variables were also supported. I found a negative association between density and distance to roads (top model β = -0.745, 95% CI = -1.177 – 0.313; Table 8). Sex (h2) and site-specific behavioral effects (bk) were supported for Big Cypress both as interaction and additive terms for g_0, and sex (h2) was supported as an effect on σ. Model-averaged mean density was 0.132 bears/km^2 (95% CI = 0.096 – 0.184, Table 7). When applied to the 7,902-km^2 study area, the abundance estimate was 1,043.5 bears (95% CI = 761.1 – 1,451.8). The top model revealed higher bear densities in areas with greater percent swamp forest cover and nearer roads, as was shown in the model-averaged density surface plot (Fig. 5).

Eglin

We checked 93 hair snares on Eglin from 16 June to 24 July 2014 (Fig. 6). WGI selected 75 of 615 hair samples collected for genotyping from Eglin, indicating that 22 (13M:9F) bears visited hair snares 49 times during the 6-week sampling period. The top model did not include covariates of density (D ~ 1, Table 9), though some covariates were present in lower-ranked supported models. Sex (h2) and site-specific behavioral effects (bk) were supported for Eglin

both as interaction and additive terms for g_0, and sex (h2) was supported as an effect on σ. Model-averaged mean density was 0.025 bears/km^2 (95% CI = 0.011 – 0.058, Table 7). When applied to the 4,795-km^2 study area, the abundance estimate was 119.6 bears (95% CI = 59.4 – 276.2). The model-averaged density surface map identified a few small areas with swamp forest as having relatively higher bear densities but densities were low in the majority of the study area (Fig. 7).

Ocala/St. Johns

We checked 190 hair snares on Ocala/St. Johns from 16 June to 24 July 2014 (Fig. 8). WGI selected 925 of 6,010 hair samples for genotyping from Ocala/St. Johns indicating that 264 (150M:114F) bears had visited hair snares 590 times during the 6-week sampling period. Top models tended to support a positive association between bear density and percent soft and hard mast-producing cover (top model β = 3.336, 95% CI = 2.275 – 4.397), distance to water (top model β = 3.732, 95% CI = 1.115 – 6.350), and a negative association between bear density and their interaction (top model β = - 5.731, 95% CI = - 9.436 – 2.026; Table 10) though percent mast-producing cover and floodplain forest was also supported as a covariate of density. Sex (h2) and site-specific behavioral effects (bk) were supported for Ocala/St. Johns both as interaction and additive terms for g_0, and sex (h2) was supported as an effect on σ. Model-averaged mean density for the Ocala St./Johns subpopulation was 0.127 bears/km^2 (95% CI = 0.101 – 0.161, Table 7). When applied to the 9,416-km^2 study area, the abundance estimate was 1,192.6 bears (95% CI = 950.8 – 1,519.5). The density surface map revealed increasing densities with increasing mast-producing forest cover and increasing distance to water, with the effect of distance to water being slightly greater when forest cover was sparse (Fig. 9).

Osceola

We checked 83 hair snares on Osceola from 16 June to 24 July 2014 and WGI genotyped 258 of 2,265 hair samples (Fig. 10). Genotyping indicated that 81 (52M:29F) bears visited hair snares 166 times at Osceola. The top models tended to support a positive association between bear density and percent soft and hard mast-producing cover (f_pershmas; top model β = 2.188, 95% CI = 0.934 – 3.443) and distance to major roads (T_no14_dis; top model β = 1.321, 95% CI = 0.686 – 1.955, Table 11), though other forest cover variables and the distance-to-roads variable were also supported. Sex (h2) and site-specific behavioral effects (bk) were supported for Osceola both as interaction and additive terms for g_0, and sex (h2) was supported as an effect on σ. Model-averaged mean density on the Florida portion of the study area was 0.127 bears/km^2 (95% CI = 0.082 – 0.203, Table 7). When applied to the 3,894-km^2 study area, the abundance estimate was 492.9 bears (95% CI = 319.5 – 792.4). Bear densities were higher in the center of the study area where percent mast-producing cover was high and the distance from major roads was greatest (Fig. 11). Across all study areas combined, the total bear abundance was 3,908.8 (95% CI = 2,916.2 – 5,425.8, CIs estimated by summation across all study areas).

Chapter 5: Discussion

Comparisons with Other Studies

My density estimates were low compared with estimates from other bear subpopulations in the Southeast (Table 12). However, densities reported in the literature are typically for small study areas that were selected because of established bear subpopulations and relatively high population densities. My study areas were intentionally extensive and included areas where bear abundance and even occupancy was expected to vary; thus, it is not surprising that my estimates were lower. Additionally, non-spatial methods tend to overestimate density to varied degrees depending on choice of study area buffer (Gerber et al. 2012). My estimates do not include cubs of the year, which I presume were too small to be sampled by the lowest barbed wire. This presumption is supported by Laufenberg et al. (2016), who employed long-term live-capture and hair-sampling data to conclude that cubs are not captured using the same wire configuration.

Simek et al. (2005) estimated 63.4 bears (95% CI = 49 – 77) on their 1,061-km^2 Apalachicola study area in 2002. When I used my top models to estimate *N* within the same boundaries described by Simek et al. (2005), my estimate was 80.9 bears (95% CI = 61.2 – 112.6) during 2015. Similarly, Simek et al.'s (2005) estimates on Big Cypress, Eglin, Ocala, Osceola, and St. Johns were 104.0 (95% CI = 77 – 131), 60.9 (95% CI = 47 – 75), 134.6 (95% CI = 110 – 159), 132.0 (95% CI = 103 – 161), and 69.6 (95% CI = 50 – 89), respectively, compared with my estimates on those same sites of 141.8 (95% CI = 106.0 – 198.4), 27.3 (95% CI = 21.0 – 75.6), 157.9 (95% CI = 124.5 – 210.1), 207.0 (95% CI = 136.8 – 338.1), and 107.9 (95% CI = 83.8 – 142.7), respectively. Thus, the 2014-2015 estimates were higher than those in 2002 for all but the Eglin study area, though all 95% CIs overlapped. I note that direct comparisons of density and abundance estimates between studies should be made cautiously

because methodologies differed. My spatially explicit estimates have the advantage of estimating density directly and incorporating the effects of spatial heterogeneity into the estimate (Royle et al. 2014), techniques that were not available to Simek et al. (2005).

Density Surface Trends

The top models generally reflected a positive relationship between percent forest cover, in one form or another, on bear densities. This trend is in agreement with the findings of Maehr et al. (2001). The one exception was in the Apalachicola study area; models indicated higher densities where forest cover was high and closer to urban development, or if forest cover was sparse and closer to urban development, due to an interaction effect between the two variables. This relationship between forest cover and urban development may have been due to the presence of garbage, corn feeders for white-tailed deer (*Odocoileus virganianus*), crops, or other anthropogenic factors. Heavier forest cover was associated with higher bear densities if far from urban areas, which is similar to the other study areas. Additionally, I found a generally negative relationship between bear densities and open water on many of the study areas. This may be because housing and other human developments are often associated with water bodies in Florida.

The model-averaged density surface for the Eglin subpopulation (Fig. 7) and the second-ranked top model (D ~f_perswamp, β = 4.231, 95% CI = 1.705 – 6.757) suggested a positive relationship between population density and my percent swamp cover covariate. This relationship is consistent with the findings of Stratman et al. (2001) who reported that primary annual habitat used by Eglin bears was riparian zones, followed by swamps. However, the Eglin subpopulation's top model had no habitat covariates of density (D ~ 1). The low sample size of this study area may have limited my ability to detect a relationship between home range

distribution and habitat characteristics. More intensive sampling may be needed to make any solid inferences regarding spatial trend in density for the Eglin subpopulation.

The density surface maps are a reflection of the covariates I used in the modeling process, and those covariates were an oversimplification of a subset of the myriad factors influencing bear population density. I constructed them to improve my ability to estimate bear abundance and density in areas between trap clusters that were not sampled. No single covariate or combination of covariates was successful in predicting bear densities across all study areas. This was not unexpected due to the high variation in ecological pattern and human influence across the geographic extent of Florida. Topology, hydrology, plant communities, weather patterns, anthropogenic influences, and other natural and non-natural factors influence population dynamics of the Florida black bear and that is reflected by the different habitat relationships I found across study areas.

Study Design

While it is not prudent to test every conceivable variable and model structure possible to achieve results, I suggest further consideration of the criteria by which I created the habitat covariates. For example, coding raster data to their corresponding community-types as outlined by the FNAI Guide to the Natural Communities of Florida (2010) could give a sharper picture of the spatial relationships between certain habitat types and bear population density.

Many kilometers of Florida panther (*Puma concolor coryi*) fencing borders Interstate Highway 70 and State Road 29 within the Big Cypress study area; bordering those fences on either side of the highways are water control structures. The fences were built to minimize road crossing mortality associated with the Florida panther (U.S. Fish and Wildlife Service 1999), but they also serve as a barrier to bear movement except in a few locations where underpasses have

been installed. The Fakahatchee Strand is oriented northeast to southwest adjacent to and through this fenced area; its spatial coincidence may have caused a misleading inflation of the importance of the water structures and the highways in my models. I would also recommend further study of the spatial relationship between trap placement and spatial covariates to help eliminate potential sources of bias associated with consistently placing more traps nearer to some features over others. Biases can occur if the decision to reject sites is associated with some habitat covariate that I modelled (e.g., non-forest cover type) or if placement of trap sites is limited to a certain feature of interest such as major roadways. In selecting sites for hair snare placement, I strove to avoid that bias or else excluded the area from the density calculations (e.g., large urban areas, water bodies).

I used the mean of each percent cover covariate on the Florida portion of the Osceola study area and applied that to the Georgia portion of the study area because I did not have current landscape variable data from Georgia. However, if habitat conditions in Georgia are substantially different than in Florida, the abundance estimates in Florida could be affected. To evaluate this potential bias, I reanalyzed the Osceola mark-recapture data based on GAP land cover data (Southeastern Gap Analysis Project 2009), which was available for both Florida and Georgia, using similar land cover classifications. My estimate of abundance for the Florida portion of the study area with GAP land cover was lower (N = 415.7, 95% CI = 289.7 – 758.9) than my results based on the FWC-FNAI land cover data (N = 492.9, 95% CI = 319.5 – 792.4) but confidence intervals overlapped significantly.

Similarly, I re-ran my top models for the Big Cypress study area inclusive of the initial capture from the female that was subsequently detected 27 km away. The inclusion of that data point resulted in a lower model-averaged estimate of density (D = 0.091, 95% CI = 0.064 –

0.135) and *N* (722.8, 95%CI = 505.4 – 1,065.5) compared with my estimates without that datum (*D* = 0.132, 95% CI = 0.096 – 0.184; *N* = 1,043.5, 95% CI = 761.1 – 1,451.8). The differences were caused by an inflated estimate of the female home range parameter (σ = 5,091 m), which would result in a dramatic inflation of the spatial distribution of female home range centers in the state model and a corresponding decrease in density. That estimate was several times higher than the original estimate for females on Big Cypress and any of the other study areas so I conclude that the exclusion of that data point was reasonable.

I estimated density and abundance within a 16-km buffer area based on the average distance between cluster centers around the trap sites. This buffer was somewhat arbitrary but I judged that the extent was sufficient to include the full extent of home ranges potentially occupied by bears on the periphery of my trapping grids. Although density estimates are unaffected by this buffer choice, estimates of *N* can be affected if the buffer is too large or too small. By incorporating habitat covariates, however, this bias was minimized. In most cases, densities were predicted to be low in areas peripheral to my trapping grids, so inclusion or exclusion of those areas would have had only a minor effect on *N*. Additionally, I ran a post-hoc buffer calculation using the `secr` function suggest.buffer for each study area with estimated male σ and g_0 values; the only study for which the post-analysis buffer was greater than 16 km was the Eglin study area. I re-ran all models using a 19-km buffer around the trapping grid and found that the density estimate (0.026 bears/km^2, 95% CI = 0.013 – 0.060) for the 19-km buffer was nearly identical to density for the 16-km buffer (0.025 bears/km^2, 95% CI = 0.012 – 0.058).

Some of the prospective sites on the Big Cypress study area were burning or had recently been burned by wildfires when crews were building snares and were not accessible for sampling. Bears may have left the burned areas and been susceptible to capture in adjacent hair trapping

clusters. That would not result in a bias unless the bears vacated the sampling area. However, egress of bears from burned areas may have artificially increased the density of bears in adjacent areas thereby skewing the relationships between density and the habitat covariates. In the burned areas where I did sample, I ran a post hoc model with fire as a covariate for individual traps as an effect on g_0 but the 95% CI of the effect included zero (β = 0.451, 95% CI = - 0.459 – 1.361) indicating that the fire was not significant. I then ran a series of post-hoc variations of the top model (D ~ f_persh3 + T_no14_dis, g_0 ~ bk × h2, σ ~ h2) that included a distance-to-fire covariate of density, a percent area burned covariate of density, and the trap-level fire covariate to determine whether the addition of these covariates together would affect my estimates. Although the AICc for the top post-hoc model (D ~ f_persh3 + T_no14_dis, × f_perburn) was 0.715 units lower than the previous top model D, abundance estimates (top model, N =1,021.9, 95% CI = 737.1 – 1,416.8; top post-hoc model, N = 1,026.2, 95% CI = 740.7 – 1,421.8), were similar suggesting that any effects of fire on the density-habitat relationship did not appreciably bias my estimates.

One of the major disadvantages of the modelling of σ is the uniformity, from a radial standpoint, of its probability distribution function (PDF) in relation to trap location. This means the estimated detection area around a trap as defined by σ will always be a circle; using a half normal detection function or other function of similar shape will produce a roughly bell-shaped 3-dimensional PDF with the center (the trap) representing the area of highest detection probability and the outer edge representing the area of lowest detection probability as it approaches zero. Further research needs to be conducted to determine the efficacy of using spatial covariates to alter the shape of the probability distribution function in order to better reflect the probability of detecting an animal at the same Euclidean distance from a trap but in

differing habitat types, and ultimately, to gain a better-informed estimate of the distribution of home range centers on the landscape.

Finally, I believe it would be wise to delve further into the relationship between model predictions and the moving window size at which continuous spatial covariates are created. Home range size (and by proxy the spatial distribution of home range centers on the landscape) is inextricably linked to resource selection and the influence of human development on the landscape (Lyons et al. 2002, Koehler and Pierce 2003, Maehr et al. 2003, Benson and Chamberlain 2007, Moyer et al. 2007, Brodeur et al. 2008, Karelus et al. 2016). The scale, or spatial extent, at which the most meaningful species-landscape relationships from those spatial data can be drawn is an important yet often overlooked aspect of landscape ecology (Jackson and Fahrig 2014, McGarigal et al. 2016). I used the combined male and female σ estimate from Simek et al. (2005) for their Ocala study area as the radius of the moving window analysis that defined my percent cover covariates, but it is unknown if that was the optimum scale at which my covariates should be calculated. Furthermore, Laforge et al. (2016) conducted a study on the relationships between habitat type, grain size (size of resource unit), and functional response in female white-tailed deer. They concluded that animals make decisions on resource selection at multiple grains, depending on habitat. I believe this concept could be applied to the focal-statistics-based approach I used to calculate my habitat covariates. I recommend a comparative study of habitat covariates created at multiple scales to test the hypotheses of an optimal window size (effect size) at which habitat covariates of density most accurately describe the distribution of bears on the landscape.

Chapter 6: Conclusions and Management Implications

My estimate of population abundance provides a baseline upon which the current bear management program in Florida can be centered. My results suggest positive population growth since the study by Simek et al. (2005) for all subpopulations except Eglin. However, a population estimate is not, in itself, indicative of population health, and I suggest continued demographic research to monitor abundance over time, especially for smaller subpopulations such as Eglin. SCR methods based on DNA samples can also be used to estimate parameters that are more indicative of population growth and sustainability, such as survival and fecundity, by sampling across years or integrating data types (Royle et al. 2014, Chandler and Clark 2014). Finally, hair sampling methods provide ready access to DNA for assessing genetic health, which may be important for some of the smaller and more isolated bear subpopulations in Florida. My use of 3 × 3 trap clusters and spatially explicit methods enabled me to efficiently estimate bear abundance and density across a large area that would not have been possible otherwise. The landscape covariates were valuable in predicting bear densities in areas that I did not sample and allowed me to relax the assumption of spatial homogeneity. I did not estimate shared parameters across subpopulations (e.g., g_0 or σ) because habitat conditions were so varied. In some situations, however, such pooling can be advantageous because it can result in increased efficiencies over broad landscapes. Thus, cross-jurisdictional studies may result in significant economies of scale. I urge resource managers to consider spatially explicit cluster sampling designs for surveying wildlife populations across extensive areas.

I estimated population demographics for 5 of the 7 subpopulations of the Florida black bear listed in the FWC's Florida Black Bear Management Plan (2012). Of the remaining 2, the most recent Glades-Highlands subpopulation estimate was published in 2009 at (175 bears, FWC

2012), and the most recent Chassahowitzka subpopulation estimate was conducted in 2003 (20 bears, FWC 2012). Both subpopulations could benefit from a multi-year spatially explicit capture-recapture study to assess population numbers, growth rate, and habitat selection over time.

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Appendices

Appendix A: Tables

Table 1. Observed alleles and frequencies for 217 bears identified from hair samples for the Apalachicola sampling area, Florida, 2015.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1A	202.202	7	0.032	G10L	153.155	11	0.051
	200.202	20	0.092		155.155	6	0.028
	196.200	9	0.041		153.157	30	0.138
	196.202	12	0.055		157.157	17	0.078
	190.198	12	0.055		151.155	2	0.009
	192.202	2	0.009		155.157	19	0.088
	190.200	12	0.055		135.157	22	0.101
	192.192	1	0.005		135.153	15	0.069
	192.198	7	0.032		153.153	7	0.032
	190.202	19	0.088		143.153	6	0.028
	196.196	2	0.009		135.155	9	0.041
	192.196	5	0.023		143.157	19	0.088
	200.200	11	0.051		135.143	8	0.037
	190.194	2	0.009		151.157	5	0.023
	194.200	10	0.046		151.153	7	0.032
	190.190	7	0.032		139.157	5	0.023
	194.198	13	0.060		139.151	2	0.009
	190.196	5	0.023		143.151	3	0.014
	196.198	5	0.023		151.151	1	0.005
	198.202	7	0.032		141.143	1	0.005
	194.202	4	0.018		135.151	2	0.009
	198.200	23	0.106		143.143	2	0.009
	194.194	3	0.014		135.135	6	0.028
	194.196	5	0.023		139.153	1	0.005
	198.198	5	0.023		141.153	2	0.009
	192.194	3	0.014		135.141	3	0.014
	192.200	5	0.023		143.155	3	0.014
	190.192	1	0.005		139.143	1	0.005
					139.141	1	0.005
G1D	178.186	5	0.023		141.157	1	0.005
	186.190	11	0.051				
	186.186	11	0.051	G10M	206.214	21	0.097
	176.176	39	0.180		214.214	48	0.221
	176.186	32	0.147		206.216	6	0.028
	188.190	7	0.032		206.212	10	0.046
	182.182	5	0.023		212.214	49	0.226
	176.182	19	0.088		214.216	14	0.065

Table 1 Continued.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1D	176.178	3	0.014	G10M	214.218	18	0.083
	176.180	3	0.014		212.212	15	0.069
	172.176	4	0.018		206.206	3	0.014
	176.190	16	0.074		212.216	11	0.051
	172.172	2	0.009		216.216	3	0.014
	172.180	3	0.014		214.220	1	0.005
	172.186	2	0.009		216.218	8	0.037
	172.190	2	0.009		210.212	2	0.009
	182.184	2	0.009		212.218	3	0.014
	176.188	10	0.046		210.214	2	0.009
	182.186	9	0.041		218.218	2	0.009
	180.190	2	0.009		210.216	1	0.005
	180.180	1	0.005				
	188.188	1	0.005	MU23	195.205	40	0.184
	190.190	3	0.014		195.195	23	0.106
	186.188	6	0.028		201.205	17	0.078
	176.184	3	0.014		187.195	18	0.083
	184.188	2	0.009		187.205	17	0.078
	180.186	1	0.005		187.201	7	0.032
	182.188	2	0.009		205.205	13	0.060
	182.190	5	0.023		197.205	7	0.032
	184.186	2	0.009		201.201	6	0.028
	184.190	2	0.009		195.201	20	0.092
	172.182	1	0.005		191.195	7	0.032
	172.188	1	0.005		191.191	2	0.009
					187.191	7	0.032
G10X	141.155	9	0.041		187.187	7	0.032
	139.139	1	0.005		187.197	2	0.009
	147.149	21	0.097		205.207	4	0.018
	141.141	15	0.069		195.207	6	0.028
	137.141	15	0.069		191.207	1	0.005
	141.147	25	0.115		191.205	5	0.023
	137.155	7	0.032		197.201	3	0.014
	149.149	5	0.023		191.201	1	0.005
	137.147	11	0.051		195.197	2	0.009
	147.155	33	0.152		187.207	2	0.009
	139.141	1	0.005				

Table 1 Continued.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10X	137.137	4	0.018	G10B	156.160	52	0.240
	139.147	5	0.023		156.156	50	0.230
	141.149	20	0.092		158.160	5	0.023
	149.155	13	0.060		156.158	13	0.060
	155.155	5	0.023		162.164	6	0.028
	147.147	14	0.065		156.162	31	0.143
	137.149	7	0.032		160.160	17	0.078
	139.149	1	0.005		156.164	7	0.032
	147.151	1	0.005		158.158	3	0.014
	151.155	1	0.005		158.162	4	0.018
	137.139	2	0.009		162.162	5	0.023
	147.153	1	0.005		160.162	15	0.069
					160.164	4	0.018
					152.158	1	0.005
					154.156	2	0.009
					152.156	1	0.005
					152.160	1	0.005

Table 2. Observed alleles and frequencies for 128 bears identified from hair samples for the Big Cypress sampling area, Florida, 2015.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10B	154.160	16	0.125	G10L	135.153	4	0.031
	152.156	11	0.086		139.155	14	0.109
	154.156	21	0.164		139.141	3	0.023
	154.164	11	0.086		139.157	14	0.109
	156.156	7	0.055		139.153	10	0.078
	156.160	12	0.094		139.139	23	0.180
	152.160	5	0.039		153.157	3	0.023
	164.164	1	0.008		139.161	12	0.094
	160.160	4	0.031		135.141	1	0.008
	152.164	1	0.008		135.139	8	0.063
	152.154	15	0.117		155.157	2	0.016
	158.160	1	0.008		153.155	5	0.039
	152.152	2	0.016		153.153	6	0.047
	156.164	7	0.055		135.155	2	0.016
	160.164	7	0.055		157.161	4	0.031
	154.154	7	0.055		135.157	2	0.016
					155.155	3	0.023
G1D	172.176	14	0.109		135.135	1	0.008
	176.186	26	0.203		141.155	1	0.008
	178.184	4	0.031		153.161	1	0.008
	172.184	2	0.016		135.161	3	0.023
	184.184	6	0.047		141.157	1	0.008
	172.186	8	0.063		155.161	1	0.008
	176.176	19	0.148		157.157	2	0.016
	186.186	13	0.102		161.161	1	0.008
	184.186	11	0.086		141.153	1	0.008
	176.178	3	0.023				
	172.172	3	0.023				
	176.184	14	0.109				
	172.188	2	0.016				
	176.188	1	0.008				
	178.186	1	0.008				
	176.192	1	0.008				

Table 2 Continued.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10H	241.241	12	0.094	G10P	159.163	27	0.211
	241.253	50	0.391		159.159	11	0.086
	241.249	3	0.023		147.161	4	0.031
	241.261	3	0.023		147.159	12	0.094
	253.253	28	0.219		163.163	28	0.219
	235.253	16	0.125		147.163	29	0.227
	249.253	4	0.031		147.147	5	0.039
	235.241	5	0.039		161.163	7	0.055
	241.252	1	0.008		159.161	3	0.023
	252.252	1	0.008		161.161	1	0.008
	235.249	1	0.008		147.157	1	0.008
	251.253	1	0.008				
	249.249	1	0.008	CPH9	141.143	17	0.133
	241.251	1	0.008		143.143	13	0.102
	253.261	1	0.008		143.149	20	0.156
					143.147	8	0.063
G10J	185.187	29	0.227		139.143	10	0.078
	199.199	14	0.109		141.141	8	0.063
	185.199	21	0.164		139.149	10	0.078
	187.187	26	0.203		141.149	11	0.086
	187.199	28	0.219		147.149	3	0.023
	185.195	1	0.008		143.151	1	0.008
	185.185	5	0.039		141.147	4	0.031
	185.203	1	0.008		147.147	4	0.031
	187.195	1	0.008		139.141	8	0.063
	187.203	1	0.008		139.147	4	0.031
	195.199	1	0.008		149.149	5	0.039
					149.151	1	0.008
G10M	212.218	2	0.016		147.151	1	0.008
	210.216	1	0.008				
	212.214	43	0.336				
	212.212	24	0.188				
	210.212	13	0.102				
	210.214	20	0.156				
	214.214	16	0.125				
	210.210	2	0.016				
	212.216	5	0.039				
	214.218	2	0.016				

Table 3. Observed alleles and frequencies for 22 bears identified from hair samples for the Eglin sampling area, Florida, 2015.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1A	196.200	7	0.318	G10M	214.214	5	0.227
	200.202	1	0.045		214.218	5	0.227
	200.200	5	0.227		206.218	2	0.091
	196.196	4	0.182		210.212	1	0.045
	190.194	1	0.045		210.210	1	0.045
	190.200	1	0.045		206.214	2	0.091
	190.202	1	0.045		216.218	1	0.045
	194.196	1	0.045		210.214	1	0.045
	196.202	1	0.045		206.206	1	0.045
					206.210	1	0.045
G10B	156.164	9	0.409		212.218	2	0.091
	156.160	5	0.227				
	160.160	2	0.091	G10X	139.141	5	0.227
	164.164	2	0.091		139.149	4	0.182
	160.164	1	0.045		141.141	1	0.045
	156.156	3	0.136		149.149	1	0.045
					139.139	2	0.091
G1D	176.190	3	0.136		137.149	1	0.045
	176.178	5	0.227		139.143	1	0.045
	176.176	3	0.136		137.137	2	0.091
	176.186	3	0.136		141.149	1	0.045
	178.186	2	0.091		137.143	1	0.045
	178.190	3	0.136		137.141	1	0.045
	178.178	1	0.045		137.139	2	0.091
	186.186	2	0.091				
				MU23	195.205	3	0.136
G10L	151.153	3	0.136		201.205	5	0.227
	149.155	1	0.045		205.205	2	0.091
	153.153	3	0.136		195.195	4	0.182
	135.153	2	0.091		201.201	1	0.045
	151.155	4	0.182		195.201	2	0.091
	153.155	2	0.091		199.205	2	0.091
	155.155	5	0.227		187.201	1	0.045
	149.153	1	0.045		199.201	1	0.045
	153.157	1	0.045		203.205	1	0.045

Table 4. Observed alleles and frequencies for 264 bears identified from hair samples for the Ocala/St. Johns sampling area, Florida, 2014.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1A	194.196	2	0.008	MU50	122.134	95	0.367
	198.198	15	0.058		134.134	50	0.193
	190.194	30	0.116		122.128	12	0.046
	190.190	12	0.046		122.122	51	0.197
	192.196	3	0.012		134.138	15	0.058
	192.194	26	0.100		122.138	9	0.035
	194.194	23	0.089		128.134	13	0.050
	190.198	24	0.093		122.124	1	0.004
	192.198	24	0.093		128.144	1	0.004
	192.192	16	0.062		134.144	4	0.015
	190.196	3	0.012		128.128	1	0.004
	190.192	25	0.097		124.134	1	0.004
	194.198	32	0.124		134.140	2	0.008
	190.200	6	0.023		122.144	1	0.004
	196.198	2	0.008		138.138	1	0.004
	192.200	3	0.012		138.140	1	0.004
	198.200	5	0.019		122.140	1	0.004
	194.200	5	0.019		122.126	1	0.004
	186.194	2	0.008				
	186.198	1	0.004	G10H	241.249	41	0.158
					249.249	19	0.073
G10B	154.164	2	0.008		241.259	43	0.166
	156.156	76	0.293		241.253	23	0.089
	154.156	38	0.147		249.259	27	0.104
	160.164	2	0.008		241.241	44	0.170
	156.164	10	0.039		243.243	2	0.008
	154.160	8	0.031		253.253	4	0.015
	152.156	47	0.181		249.253	18	0.069
	156.160	35	0.135		259.259	6	0.023
	152.160	10	0.039		241.243	7	0.027
	152.152	7	0.027		253.259	9	0.035
	154.154	4	0.015		243.249	4	0.015
	152.154	7	0.027		243.259	6	0.023
	152.164	5	0.019		243.253	2	0.008
	160.160	4	0.015		255.259	2	0.008
	154.158	2	0.008		249.255	1	0.004
	158.160	1	0.004		253.255	1	0.004
	156.158	1	0.004		241.255	1	0.004

Table 4 Continued.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1D	176.184	37	0.143	MU59	243.245	9	0.035
	172.186	7	0.027		239.239	31	0.120
	176.188	7	0.027		231.247	4	0.015
	184.188	12	0.046		231.241	7	0.027
	172.184	49	0.189		231.245	26	0.100
	172.190	10	0.039		243.243	3	0.012
	172.172	16	0.062		231.239	53	0.205
	184.184	39	0.151		237.245	2	0.008
	172.176	19	0.073		231.231	31	0.120
	184.190	15	0.058		239.245	12	0.046
	184.186	14	0.054		231.243	8	0.031
	176.176	7	0.027		239.243	21	0.081
	190.190	3	0.012		237.239	6	0.023
	188.190	7	0.027		239.247	2	0.008
	172.188	6	0.023		241.241	2	0.008
	188.188	2	0.008		231.237	4	0.015
	186.186	1	0.004		245.245	5	0.019
	180.184	1	0.004		237.243	1	0.004
	176.190	3	0.012		235.245	3	0.012
	176.180	1	0.004		241.247	1	0.004
	176.186	3	0.012		237.237	1	0.004
	186.190	1	0.004		241.245	4	0.015
					235.239	9	0.035
MU23	191.205	58	0.224		231.235	1	0.004
	187.205	45	0.174		241.243	5	0.019
	205.205	35	0.135		235.243	4	0.015
	191.191	49	0.189		239.241	1	0.004
	187.191	41	0.158		243.247	3	0.012
	187.187	17	0.066		245.247	1	0.004
	195.205	7	0.027				
	191.195	4	0.015				
	195.201	1	0.004				
	187.195	2	0.008				
	195.195	1	0.004				

Table 5. Observed alleles and frequencies for 81 bears identified from hair samples for the Osceola sampling area, Florida, 2014.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10B	160.160	11	0.129	G10H	243.251	2	0.024
	156.160	22	0.259		241.255	3	0.035
	152.160	4	0.047		235.243	7	0.082
	166.166	1	0.012		241.243	15	0.176
	160.166	6	0.071		243.243	12	0.141
	156.156	6	0.071		235.241	7	0.082
	154.156	6	0.071		249.259	1	0.012
	154.164	1	0.012		235.255	5	0.059
	156.164	3	0.035		243.255	3	0.035
	156.166	3	0.035		241.253	3	0.035
	152.156	2	0.024		251.255	2	0.024
	152.154	1	0.012		243.249	2	0.024
	158.164	1	0.012		243.245	3	0.035
	156.158	3	0.035		235.253	2	0.024
	154.160	4	0.047		241.241	8	0.094
	160.164	5	0.059		255.259	1	0.012
	158.160	4	0.047		245.255	1	0.012
	152.166	1	0.012		243.253	4	0.047
	152.158	1	0.012		255.255	1	0.012
					249.255	1	0.012
G1D	176.186	8	0.094		253.253	1	0.012
	176.188	18	0.212		249.253	1	0.012
	176.176	12	0.141				
	176.190	4	0.047	MU23	191.205	6	0.071
	176.184	7	0.082		187.207	2	0.024
	184.188	6	0.071		187.195	4	0.047
	184.186	5	0.059		191.191	1	0.012
	176.180	2	0.024		199.205	4	0.047
	186.188	1	0.012		195.195	1	0.012
	186.190	1	0.012		187.199	7	0.082
	178.186	2	0.024		187.191	4	0.047
	176.178	3	0.035		187.187	5	0.059
	172.184	2	0.024		203.205	4	0.047
	172.188	1	0.012		199.203	1	0.012
	172.176	3	0.035		201.207	2	0.024
	184.184	3	0.035		187.205	5	0.059
	188.188	2	0.024		191.203	2	0.024

Table 5 Continued.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1D	186.186	1	0.012	MU23	205.205	4	0.047
	172.178	1	0.012		187.201	4	0.047
	178.188	2	0.024		195.199	6	0.071
	178.184	1	0.012		205.207	1	0.012
					201.201	2	0.024
MU50	134.134	26	0.306		195.205	3	0.035
	134.144	4	0.047		195.203	1	0.012
	122.134	27	0.318		191.195	3	0.035
	126.126	2	0.024		201.205	4	0.047
	124.134	4	0.047		203.207	1	0.012
	122.126	5	0.059		201.203	2	0.024
	124.126	2	0.024		195.201	3	0.035
	126.134	6	0.071		199.199	2	0.024
	144.144	1	0.012		199.207	1	0.012
	122.144	1	0.012				
	122.122	2	0.024	G1A	194.196	9	0.106
	124.144	1	0.012		198.200	9	0.106
	134.140	1	0.012		194.194	23	0.271
	126.144	1	0.012		194.198	4	0.047
	122.138	2	0.024		196.200	7	0.082
					196.198	4	0.047
MU59	231.239	19	0.224		192.198	2	0.024
	239.239	23	0.271		190.192	3	0.035
	239.241	4	0.047		194.200	12	0.141
	239.249	2	0.024		192.194	2	0.024
	231.241	4	0.047		192.200	2	0.024
	231.231	8	0.094		200.200	2	0.024
	239.243	14	0.165		198.198	1	0.012
	241.243	1	0.012		190.194	1	0.012
	243.243	2	0.024		190.200	2	0.024
	231.243	5	0.059		190.196	1	0.012
	231.249	2	0.024		190.190	1	0.012
	237.247	1	0.012				

Table 6. Model selection results for the Apalachicola study area, Florida, 2015, for models with a difference in bias-corrected Akaike information criterion (ΔAICc) ≤4 that were averaged. *D* represents density; f_pershmas represents percent mast-producing forest cover; f_persh2 represents percent mast-producing and floodplain forest cover; f_persh3 represents percent mast-producing, floodplain, and tree plantation cover; f_perswamp represents percent swamp forest; f_perfor represents percent forested cover; f_dish2o represents distance to water; T_no14_dis, represents distance to major roads; f_dishiur represents distance to high-intensity urban development; f_disurb represents distance to urban development; g_0 is detection rate; σ is a home range parameter; pmix is the ratio of males to females; h2 is a heterogeneous sex effect; and bk is a site-specific behavioral effect.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~f_persh3 × f_disurb, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1750.613	3522.293	0.000	0.080
D~f_perfor × f_disurb, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1750.691	3522.450	0.157	0.074
D~f_perswamp + f_disurb, g_0~h2+ bk, σ ~h2, pmix~h2	9	-1752.101	3523.071	0.778	0.054
D~f_perswamp + T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	9	-1752.115	3523.099	0.806	0.053
D~f_persh2 + T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	9	-1752.259	3523.387	1.094	0.046
D~f_perswamp × f_disurb, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1751.163	3523.394	1.101	0.046
D~f_persh2 + f_disurb, g_0~h2 + bk σ ~h2, pmix~h2	9	-1752.439	3523.748	1.455	0.039
D~f_persh3 × f_disurb, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1750.410	3524.108	1.815	0.032
D~f_persh2 × f_dish2o, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1751.522	3524.112	1.819	0.032
D~f_persh2, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1753.786	3524.264	1.971	0.030
D~f_perswamp + f_dishiur, g_0~bk + h2, σ ~h2, pmix~h2	9	1752.701	3524.273	1.980	0.030
D~f_perfor × f_disurb, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1750.500	3524.288	1.995	0.030
D~f_perswamp, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1753.817	3524.327	2.034	0.029
D~f_persh2 × f_disurb, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1751.661	3524.391	2.098	0.028
D~T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1753.851	3524.394	2.101	0.028
D~f_persh2 + f_dishiur, g_0~h2 + bk, σ ~h2, pmix~h2	9	-1752.935	3524.74	2.447	0.024
D~1, g_0~h2 + bk, σ ~h2, pmix~h2	7	-1755.117	3524.771	2.478	0.023
D~f_disurb, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1754.106	3524.904	2.611	0.022

Table 6 Continued.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1753.851	3524.394	2.101	0.028
D~f_perswamp + T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	10	-1751.954	3524.975	2.682	0.021
D~f_perswamp + f_disurb, g_0~h2 × bk, σ ~h2, pmix~h2	10	-1751.973	3525.015	2.722	0.021
D~f_perswamp × f_dishiur, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.027	3525.123	2.830	0.019
D~f_perswamp × T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.089	3525.247	2.954	0.018
D~f_persh2 + T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	10	-1752.090	3525.248	2.955	0.018
D~f_perswamp × f_disurb, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1751.025	3525.337	3.044	0.017
D~f_persh2 × T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.225	3525.519	3.226	0.016
D~f_persh2 + f_disurb, g_0~h2 × bk, σ ~h2, pmix~h2	10	-1752.303	3525.673	3.380	0.015
D~f_pershmas + T_no14_dis, g_0~ h2 + bk, σ ~h2, pmix~h2	9	-1753.412	3525.693	3.400	0.015
D~f_pershmas + f_disurb, g_0~ h2 + bk, σ ~h2, pmix~h2	9	-1753.520	3525.91	3.617	0.013
D~f_persh2 × f_dishiur, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.438	3525.945	3.652	0.013
D~f_persh2 × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1751.366	3526.021	3.728	0.012
D~f_dishiur, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1754.682	3526.057	3.764	0.012
D~f_perswamp × f_dish2o, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.520	3526.109	3.816	0.012
D~f_persh2, g_0~h2 × bk, σ ~h2, pmix~h2	9	-1753.637	3526.144	3.851	0.012
D~f_pernat × f_dish2o, g_0~h2 + bk, σ ~h2, pmix~h2	10	-1752.538	3526.144	3.851	0.012
D~f_pernat, g_0~h2 + bk, σ ~h2, pmix~h2	8	-1754.744	3526.179	3.886	0.011
D~f_perswamp + f_dishiur, g_0~h2 × bk, σ ~h2, pmix~h2	10	-1752.572	3526.212	3.919	0.011
D~f_perswamp, g_0~h2 × bk, σ ~h2, pmix~h2	9	-1753.675	3526.22	3.927	0.011
D~T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	9	-1753.688	3526.245	3.952	0.011
D~f_persh2 + f_dish2o, g_0~bk + h2, σ ~h2, pmix~h2	9	-1753.692	3526.254	3.961	0.011

Table 7. Model-averaged parameter estimates of bears at Apalachicola, Big Cypress, and Eglin, Ocala/St. Johns, and Osceola study areas, Florida, whereby *D* is mean density (bears/km^2), *N* is expected abundance, g_0 is the detection rate, σ is a home range parameter expressed in meters, and mixture is the sex ratio.

Parameter	Estimate	SE[1]	LCL[2]	UCL[3]
Apalachicola				
D	0.082	0.011	0.064	0.107
N	1,060.3	141.5	825.4	1,385.9
Female				
g_0 (mixture = 68.0%)	0.079	0.018	0.051	0.121
σ	1,638.0	189.4	1,306.7	2,053.1
Male				
g_0 (mixture = 32.0%)	0.044	0.007	0.032	0.059
σ	3,896.7	259.1	3,421.0	4,438.6
Big Cypress				
D	0.132	0.022	0.096	0.184
N	1,043.5	173.8	761.1	1,451.8
Female				
g_0 (mixture = 43.0%	0.166	0.049	0.090	0.286
σ	1,233.6	157.2	962.0	1,581.8
Male				
g_0 (mixture = 57.0%	0.057	0.017	0.032	0.100
σ	2,197.4	313.4	1,663.9	2,902.0
Eglin				
D	0.025	0.008	0.011	0.058
N	119.6	37.1	59.4	276.2
Female				
g_0 (mixture = 70.9%)	0.144	0.122	0.024	0.541
σ	1,385.1	603.0	612.1	3,134.1
Male				
g_0 (mixture = 29.1%)	0.032	0.015	0.012	0.079
σ	5,223.1	1,036.1	3,553.9	7,676.2

[1] Standard error
[2] Lower confidence limit
[3] Upper confidence limit

Table 7 Continued.

Parameter	Estimate	SE[1]	LCL[2]	UCL[3]
Ocala/St. Johns				
D	0.127	0.015	0.101	0.161
N	1,192.6	143.8	950.8	1,519.5
Female				
g_0 (mixture = 59.6%)	0.088	0.021	0.055	0.139
σ	1,735.0	210.1	1,369.7	2,197.7
Male				
g_0 (mixture = 40.4%)	0.071	0.011	0.053	0.094
σ	2,883.3	230.3	2,466.2	3,371.0
Osceola				
D	0.127	0.030	0.082	0.203
N	492.9	117.1	319.5	792.4
Female				
g_0 (mixture = 61.5%)	0.100	0.052	0.035	0.256
σ	1,106.7	260.8	701.7	1,745.5
Male				
g_0 (mixture = 38.5%)	0.094	0.023	0.057	0.150
σ	2,197.1	390.6	1,554.8	3,104.6

[1] Standard Error
[2] Lower confidence limit
[3] Upper confidence limit

Table 8. Model selection results for the Big Cypress study area, Florida, 2015, for models with a difference in bias-corrected Akaike information criterion (ΔAICc) ≤4 that were averaged. *D* represents density; f_pershmas represents percent mast-producing forest cover; f_persh2 represents percent mast-producing and floodplain forest cover; f_persh3 represents percent mast-producing, floodplain, and tree plantation cover; f_perswamp represents percent swamp forest; f_perfor represents percent forested cover; f_pernat represents percent natural cover; f_dish2o represents distance to water; T_no14_dis, represents distance to major roads; g_0 is detection rate; σ is a home range parameter; pmix is the ratio of males to females; h2 is a heterogeneous sex effect; and bk is a site-specific behavioral effect.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~f_persh3 + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-838.685	1699.250	0	0.138
D~f_persh2 + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-838.687	1699.254	0.004	0.138
D~f_perfor + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.426	1700.732	1.482	0.066
D~f_perswamp + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.559	1700.999	1.749	0.058
D~f_pernat + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.581	1701.042	1.792	0.056
D~f_pernat + f_dish2o, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.667	1701.215	1.965	0.052
D~f_perfor + f_dish2o, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.709	1701.298	2.048	0.050
D~f_perswamp + f_dish2o, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.764	1701.409	2.159	0.047
D~f_persh3 × T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	11	-838.577	1701.431	2.181	0.046
D~f_persh2 × T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	11	-838.579	1701.434	2.184	0.046
D~f_persh3 + f_dish2o, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.835	1701.550	2.3	0.044
D~f_persh2 + f_dish2o, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.837	1701.554	2.304	0.044
D~f_pershmas + T_no14_dis, g_0~h2 × bk sigma~h2, pmix~h2	10	-839.863	1701.606	2.356	0.043

Table 8 Continued.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	9	-841.343	1702.211	2.961	0.031
D~f_perfor × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.132	1702.539	3.289	0.027
D~f_perswamp × T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.154	1702.584	3.334	0.026
D~f_persh3 × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.274	1702.824	3.574	0.023
D~f_persh2 × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.276	1702.827	3.577	0.023
D~f_pershmas × T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.302	1702.880	3.630	0.023
D~f_perfor × T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	11	-839.361	1702.998	3.748	0.021

Table 9. Model selection results for the Eglin study area, Florida, 2015, for models with a difference in bias-corrected Akaike information criterion (ΔAICc) ≤4 that were averaged. *D* represents density; f_persh2 represents percent mast-producing and floodplain forest cover; f_persh3 represents percent mast-producing, floodplain, and tree plantation cover; f_perswamp represents percent swamp forest; T_no14_dis, represents distance to major roads; g_0 is detection rate; σ is a home range parameter; pmix is the ratio of males to females; h2 is a heterogeneous sex effect; and bk is a site-specific behavioral effect.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~1, g_0~ h2 + bk, σ ~h2, pmix~h2	7	-195.837	413.674	0.000	0.419
D~f_perswamp, g_0~h2 + bk, σ ~h2, pmix~h2	8	-193.714	414.505	0.831	0.277
D~f_persh2 g0, g_0+ bk, σ ~h2, pmix~h2	8	-194.675	416.426	2.752	0.106
D~T_no14_dis, g_0~h2 + bk, σ ~h2, pmix~h2	8	-195.085	417.247	3.573	0.070
D~f_persh3, g_0~h2 + bk, σ ~h2, pmix~h2	8	-195.119	417.315	3.641	0.068
D~1, g_0~h2 × bk, σ ~h2, pmix~h2	8	-195.237	417.551	3.877	0.060

Table 10. Model selection results for the Ocala/St. Johns study area, Florida, 2014, for models with a difference in bias-corrected Akaike information criterion (ΔAICc) ≤4 that were averaged. *D* represents density; f_pershmas represents percent mast-producing forest cover; f_persh2 represents percent mast-producing and floodplain forest cover; f_dish2o represents distance to water; T_no14_dis, represents distance to major roads; g_0 is detection rate; σ is a home range parameter; pmix is the ratio of males to females; h2 is a heterogeneous sex effect; and bk is a site-specific behavioral effect.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~f_pershmas × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1882.997	3789.041	0.000	0.603
D~f_persh2 × f_dish2o, g_0~h2 × bk, σ ~h2, pmix~h2	11	-1883.756	3790.560	1.519	0.282
D~f_pershmas × (f_dish2o + T_no14_dis), g_0~h2 × bk, σ ~h2, pmix~h2	13	-1882.446	3792.349	3.308	0.115

Table 11. Model selection results for the Osceola study area, Florida, 2014, for models with a difference in bias-corrected Akaike information criterion (ΔAICc) ≤4 that were averaged. *D* represents density, f_pershmas represents percent mast-producing forest cover, f_persh2 represents percent mast-producing and floodplain forest cover, T_no14_dis, represents distance to major roads, g_0 is detection rate, σ is a home range parameter, pmix is the ratio of males to females, h2 is a heterogeneous sex effect, and bk is a site-specific behavioral effect.

Model	No. parameters	Log likelihood	AICc	ΔAICc	Model wt
D~f_pershmas + T_no14_dis, g_0~ h2 + bk, σ ~h2, pmix~h2	9	-564.926	1150.386	0.000	0.318
D~f_persh2 + T_no14_dis, g_0~ h2 + bk, σ ~h2, pmix~h2	9	-565.066	1150.666	0.280	0.277
D~f_pershmas × T_no14_dis, g_0~ h2 + bk, σ ~h2, pmix~h2	10	-564.663	1152.468	2.082	0.112
D~f_pershmas + T_no14_dis, g_0~h2 × bk σ ~h2, pmix~h2	10	-564.730	1152.603	2.217	0.105
D~f_persh2 × T_no14_dis, g_0~ h2 + bk, σ ~h2, pmix~h2	10	-564.810	1152.765	2.379	0.097
D~f_persh2 + T_no14_dis, g_0~h2 × bk, σ ~h2, pmix~h2	10	-564.870	1152.883	2.497	0.091

Table 12. Reported densities (bear/km^2) of select black bear subpopulations in the southeastern United States.

Location	Bears/km^2	Reference
Eglin, FL	0.025	This study
Carvers Bay, SC	0.04	Drewry (2010)
Eglin, FL	0.041	Simek et al. (2005)
Apalachicola, FL	0.06	Simek et al. (2005)
St. Johns, FL	0.067	Simek et al. (2005)
Apalachicola, FL	0.082	This study
Osceola, FL	0.127	This study
Ocala/St. Johns, FL	0.127	This study
Big Cypress, FL	0.132	This study
Big Cypress, FL	0.131	Simek et al. (2005)
Osceola, FL	0.14	Simek et al. (2005)
Upper Atchafalaya River Basin, LA	0.15–0.18	Lowe (2011)
White River National Wildlife Refuge, AR	0.22–0.25	Clark et al. (2010)
Ocala, FL	0.24	Simek et al. (2005)
Lewis Ocean Bay, SC	0.31	Drewry (2010)
Tensas River Basin, LA	0.66	Hooker (2010)

Table 13. Coefficients of Determination (R^2) values of all 2-covariate pairings for the Apalachicola study area, Florida, 2015.

Spatial Covariates	R^2
percent natural and distance to high urban	0.257
percent natural and distance to urban	0.248
percent natural and distance to roads	0.158
percent natural and distance to water	0.129
percent swamp and distance to high urban	0.103
percent hard/soft mast 3 and distance to urban	0.081
percent hard/soft mast 3 and distance to high urban	0.081
percent swamp and distance to roads	0.077
percent hard/soft mast 3 and distance to water	0.071
percent swamp and distance to urban	0.066
percent forest and distance to high urban	0.064
percent forest and distance to urban	0.057
percent hard/soft mast 1 and distance to high urban	0.041
percent hard/soft mast 2 and distance to high urban	0.030
percent hard/soft mast 2 and distance to roads	0.029
percent forest and distance to roads	0.028
percent hard/soft mast 3 and distance to roads	0.023
percent forest and distance to distance to water	0.015
percent hard/soft mast 1 and distance to urban	0.012
percent hard/soft mast 2 and distance to urban	0.008
percent hard/soft mast 1 and distance to roads	0.008
percent hard/soft mast 1 and distance to water	0.006
percent swamp and distance to water	0.005
percent hard/soft mast 2 and distance to water	0.004

Table 14. Coefficients of Determination (R^2) values of all 2-covariate pairings for the Big Cypress study area, Florida, 2015.

Spatial Covariates	R^2
percent natural and distance to high urban	0.228
percent natural and distance to urban	0.213
percent natural and distance to water	0.160
percent forest and distance to urban	0.068
percent swamp and distance to water	0.067
percent forest and distance to distance to water	0.065
percent swamp and distance to urban	0.064
percent swamp and distance to high urban	0.036
percent forest and distance to high urban	0.034
percent natural and distance to roads	0.019
percent hard/soft mast 1 and distance to water	0.009
percent hard/soft mast 2 and distance to urban	0.006
percent hard/soft mast 3 and distance to urban	0.006
percent hard/soft mast 2 and distance to water	0.006
percent hard/soft mast 3 and distance to water	0.006
percent hard/soft mast 1 and distance to urban	0.006
percent hard/soft mast 1 and distance to roads	0.002
percent swamp and distance to roads	0.001
percent hard/soft mast 1 and distance to high urban	0.000
percent forest and distance to roads	0.000
percent hard/soft mast 2 and distance to roads	0.000
percent hard/soft mast 3 and distance to roads	0.000
percent hard/soft mast 2 and distance to high urban	0.000
percent hard/soft mast 3 and distance to high urban	0.000

Table 15. Coefficients of Determination (R^2) values of all 2-covariate pairings for the Eglin study area, Florida, 2015.

Spatial Covariates	R^2
percent natural and distance to urban	0.254
percent natural and distance to high urban	0.250
percent forest and distance to urban	0.234
percent forest and distance to high urban	0.231
percent natural and distance to roads	0.209
percent natural and distance to water	0.137
percent hard/soft mast 2 and distance to water	0.133
percent swamp and distance to water	0.111
percent hard/soft mast 1 and distance to water	0.108
percent hard/soft mast 1 and distance to roads	0.106
percent hard/soft mast 3 and distance to roads	0.091
percent hard/soft mast 2 and distance to roads	0.079
percent forest and distance to distance to water	0.077
percent hard/soft mast 3 and distance to water	0.073
percent forest and distance to roads	0.047
percent swamp and distance to roads	0.046
percent hard/soft mast 1 and distance to urban	0.031
percent hard/soft mast 2 and distance to urban	0.022
percent hard/soft mast 1 and distance to high urban	0.021
percent hard/soft mast 3 and distance to urban	0.020
percent hard/soft mast 3 and distance to high urban	0.018
percent hard/soft mast 2 and distance to high urban	0.018
percent swamp and distance to high urban	0.000
percent swamp and distance to urban	0.000

Table 16. Coefficients of Determination (R^2) values of all 2-covariate pairings for the Ocala/St. Johns study area, Florida, 2014.

Spatial Covariates	R^2
percent natural and distance to urban	0.353
percent hard/soft mast 3 and distance to urban	0.280
percent forest and distance to urban	0.273
percent hard/soft mast 3 and distance to water	0.245
percent forest and distance to distance to water	0.244
percent natural and distance to high urban	0.242
percent hard/soft mast 3 and distance to high urban	0.204
percent forest and distance to high urban	0.204
percent natural and distance to water	0.197
percent hard/soft mast 1 and distance to water	0.140
percent hard/soft mast 1 and distance to urban	0.138
percent hard/soft mast 2 and distance to urban	0.129
percent hard/soft mast 2 and distance to water	0.107
percent natural and distance to roads	0.080
percent forest and distance to roads	0.039
percent hard/soft mast 1 and distance to high urban	0.036
percent hard/soft mast 2 and distance to high urban	0.033
percent hard/soft mast 3 and distance to roads	0.030
percent swamp and distance to urban	0.020
percent swamp and distance to roads	0.018
percent swamp and distance to water	0.017
percent swamp and distance to high urban	0.010
percent hard/soft mast 2 and distance to roads	0.001
percent hard/soft mast 1 and distance to roads	0.000

Table 17. Coefficients of Determination (R^2) values of all 2-covariate pairings for the Osceola study area, Florida, 2014.

Spatial Covariates	R^2
percent forest and distance to distance to water	0.393
percent forest and distance to high urban	0.267
percent forest and distance to urban	0.254
percent natural and distance to roads	0.167
percent natural and distance to high urban	0.113
percent swamp and distance to roads	0.102
percent natural and distance to urban	0.101
percent swamp and distance to high urban	0.062
percent swamp and distance to urban	0.059
percent natural and distance to water	0.037
percent hard/soft mast 1 and distance to roads	0.035
percent hard/soft mast 2 and distance to roads	0.034
percent swamp and distance to water	0.019
percent hard/soft mast 3 and distance to roads	0.016
percent hard/soft mast 3 and distance to water	0.007
percent hard/soft mast 2 and distance to urban	0.006
percent hard/soft mast 1 and distance to urban	0.005
percent hard/soft mast 2 and distance to high urban	0.005
percent hard/soft mast 1 and distance to high urban	0.005
percent hard/soft mast 3 and distance to high urban	0.001
percent forest and distance to roads	0.001
percent hard/soft mast 1 and distance to water	0.001
percent hard/soft mast 2 and distance to water	0.000
percent hard/soft mast 3 and distance to urban	0.000

Appendix B: Figures

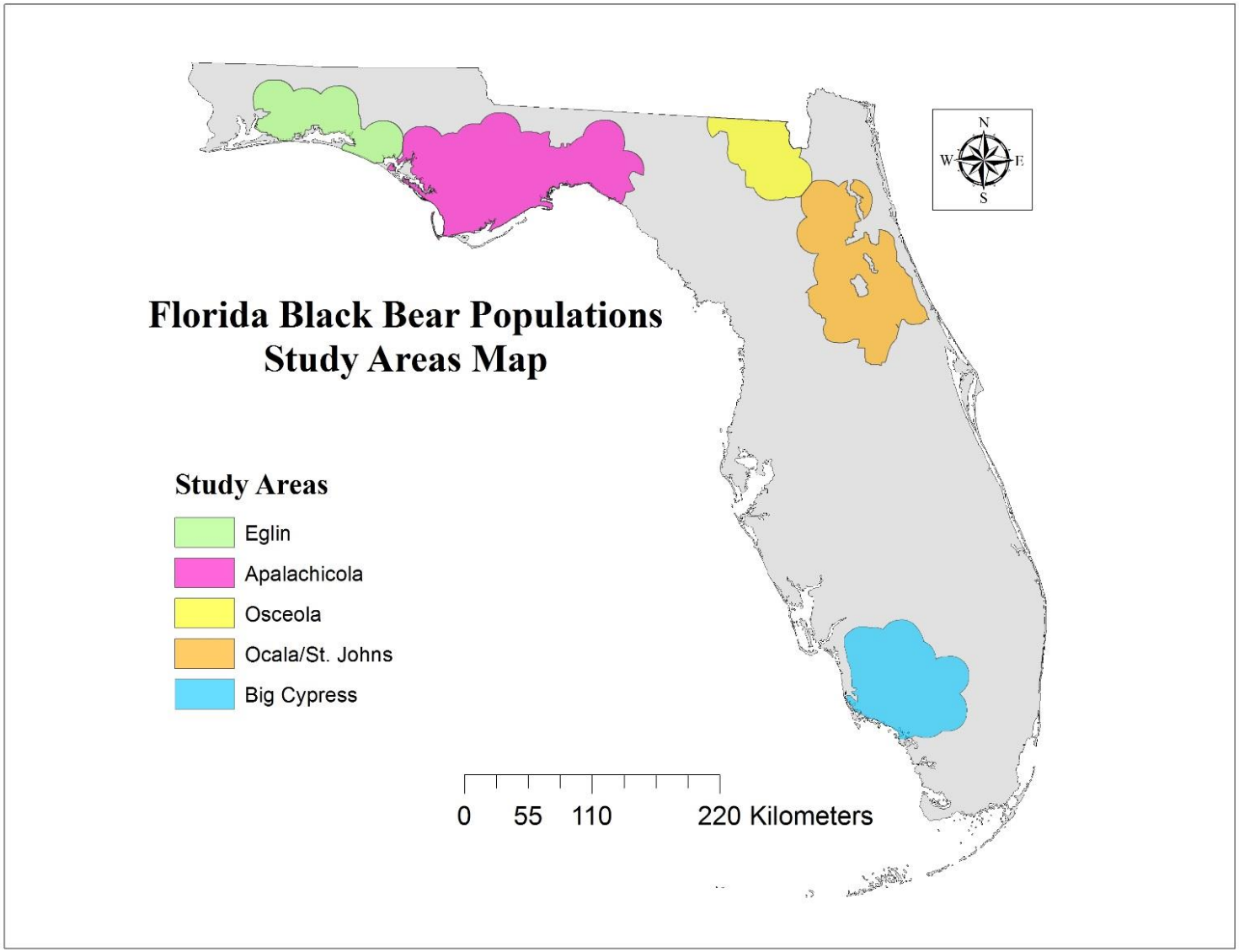

Figure 1. Study areas map. Study areas from the west end of the panhandle to the southern tip of Florida are as follows: Eglin, Apalachicola, Osceola, Ocala/St. Johns, Big Cypress.

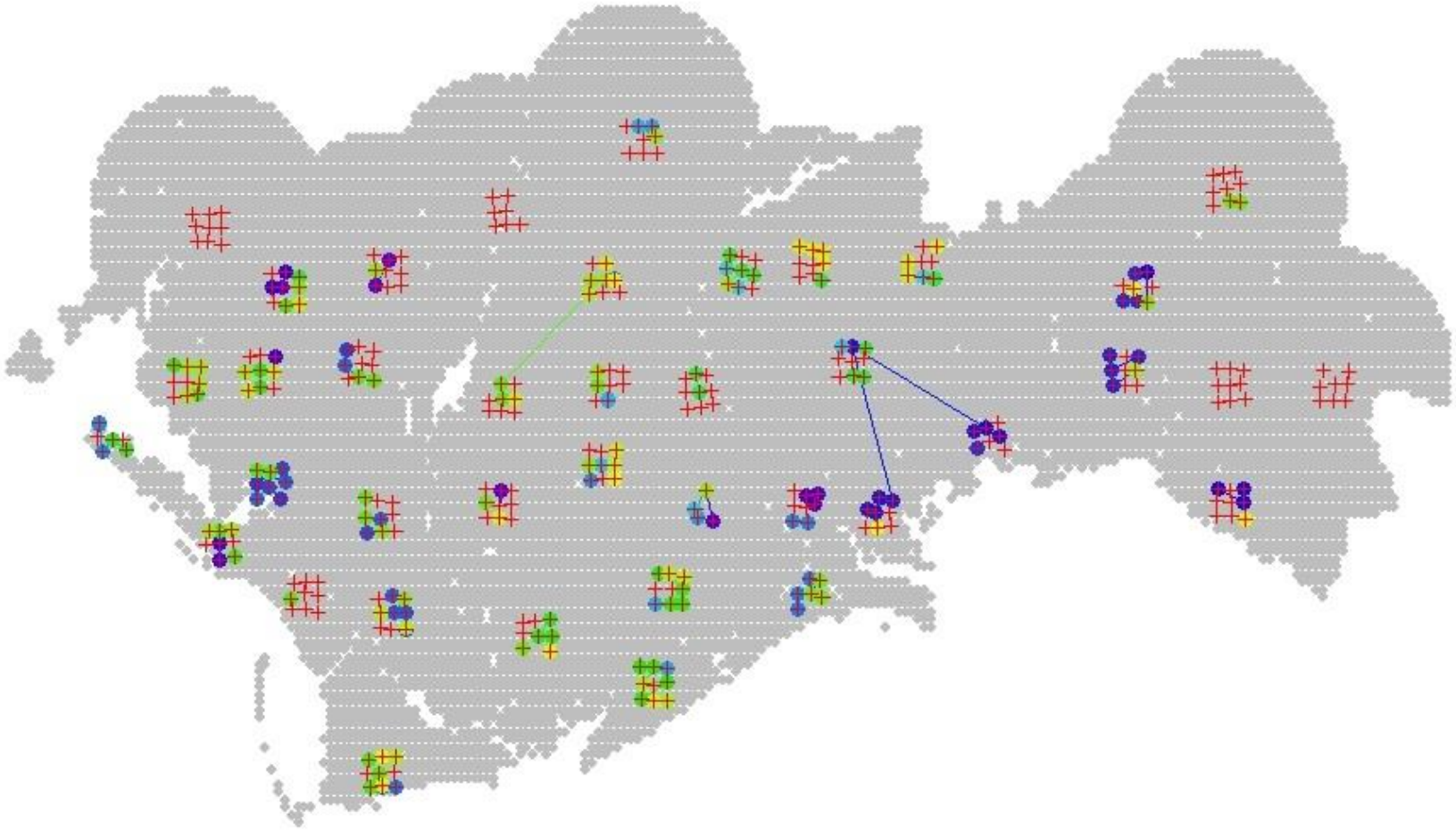

Figure 2. Trap sites and bear detections in the Apalachicola study area, Florida, 2015. The crosses represent hair traps and the colored dots within each trap cluster represent a different bear. Dots of the same color within a cluster represent the same animal. Lines between dots represent consecutive detections of the same animal.

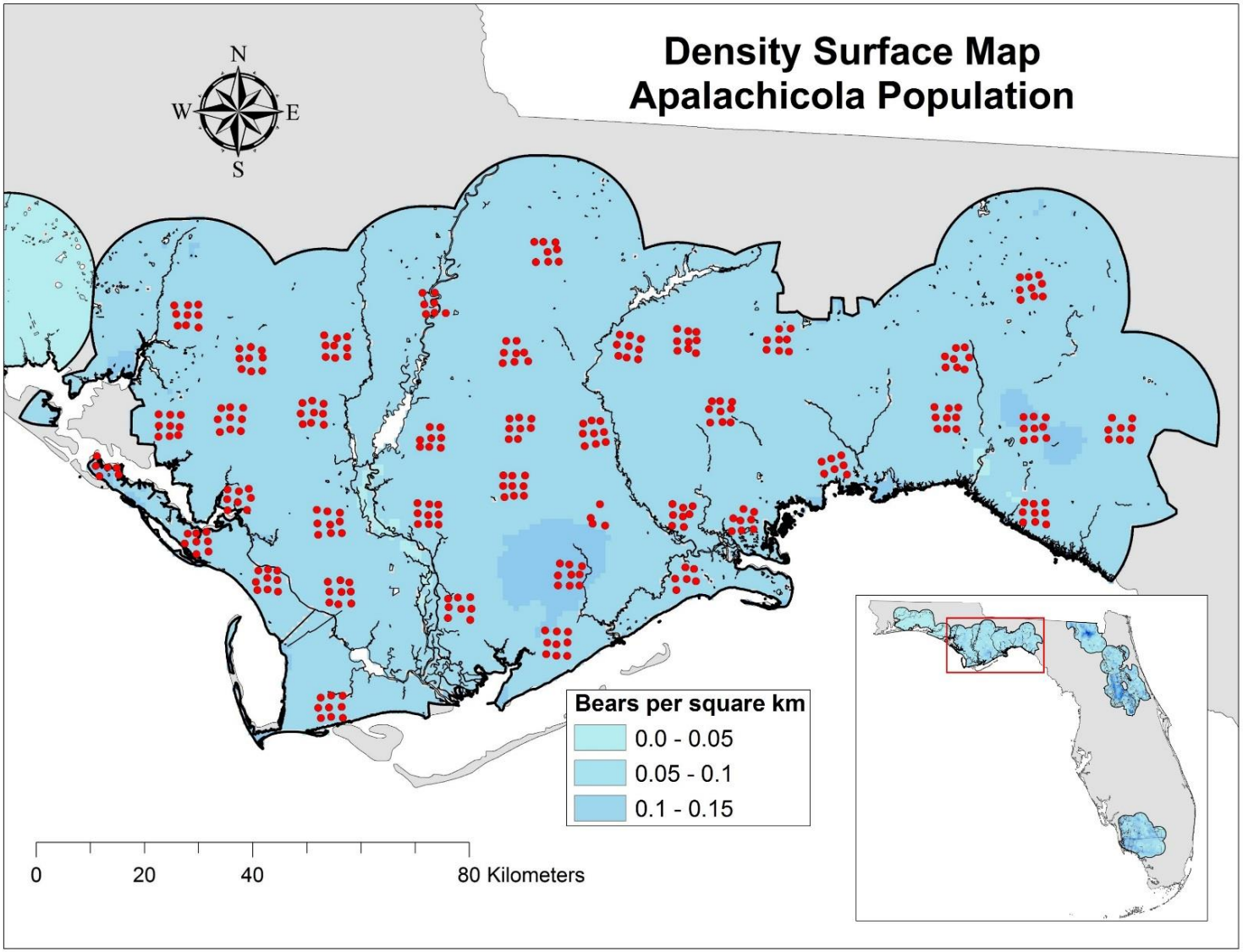

Figure 3. Model-averaged density surface map of the Apalachicola subpopulation, Florida, 2015. The red dots represent hair snare locations.

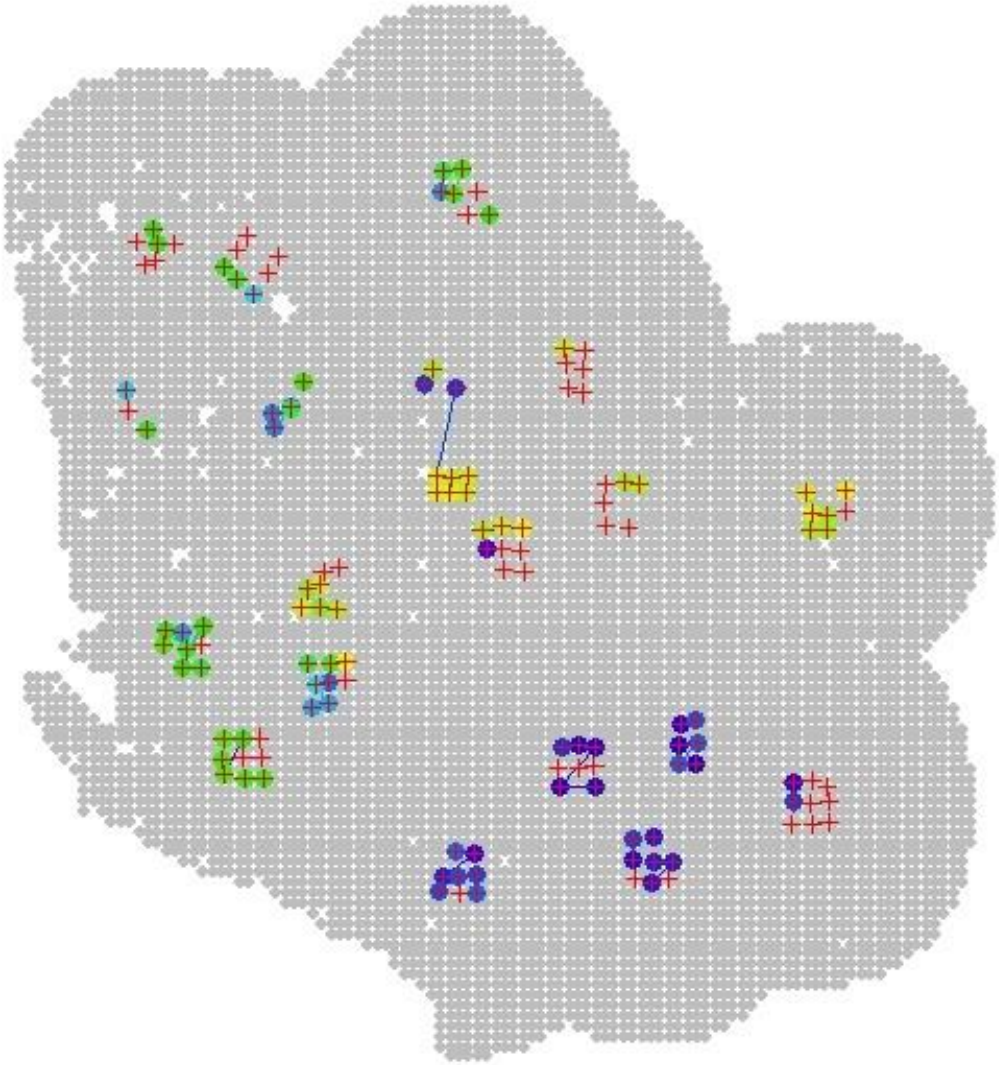

Figure 4. Trap sites and bear detections in the Big Cypress study area, Florida, 2015. The crosses represent hair traps and the colored dots within each trap cluster represent a different bear. Dots of the same color within a cluster represent the same animal. Lines between dots represent consecutive detections of the same animal.

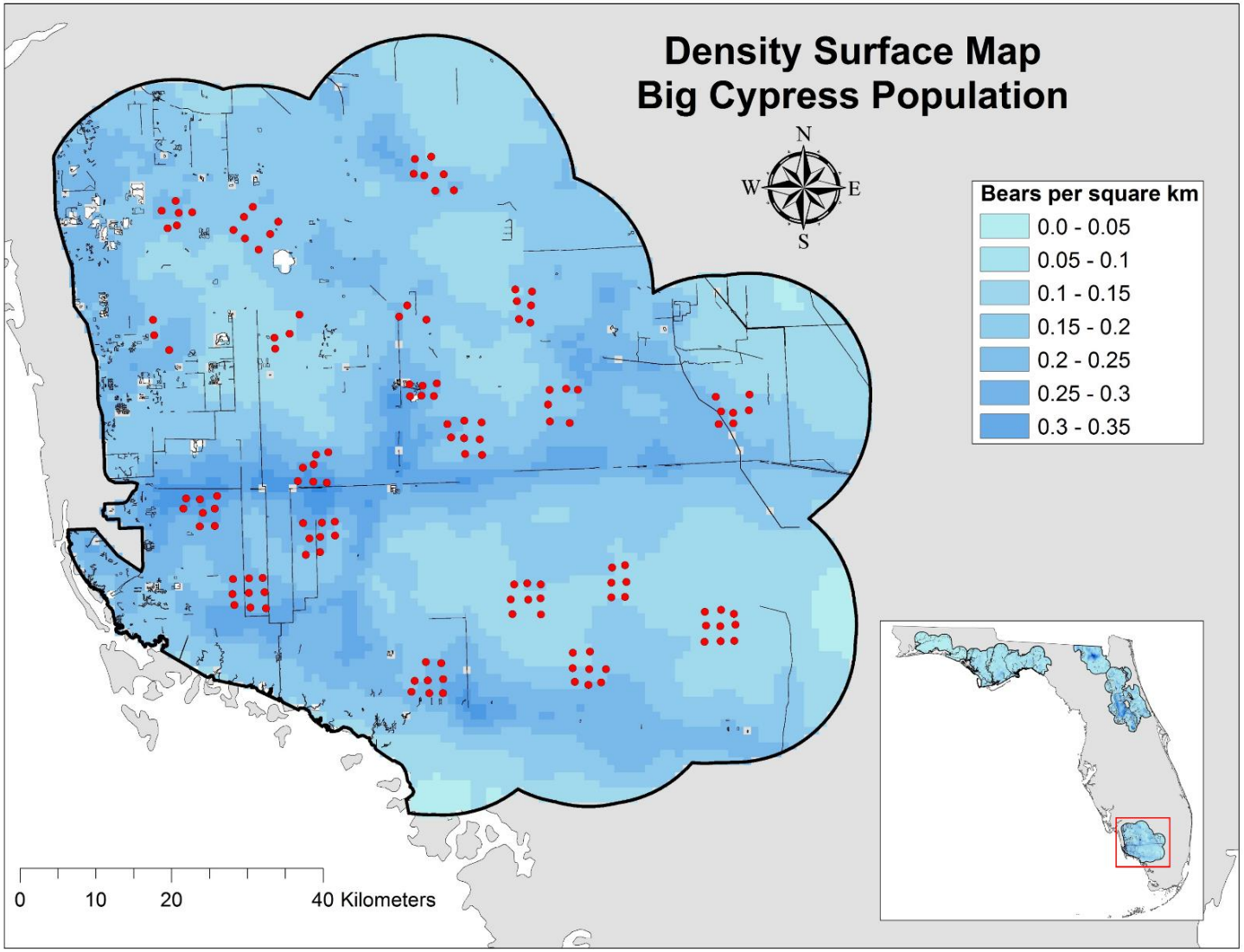

Figure 5. Model-averaged density surface map of the Big Cypress subpopulation, Florida, 2015. The red dots represent hair snare locations.

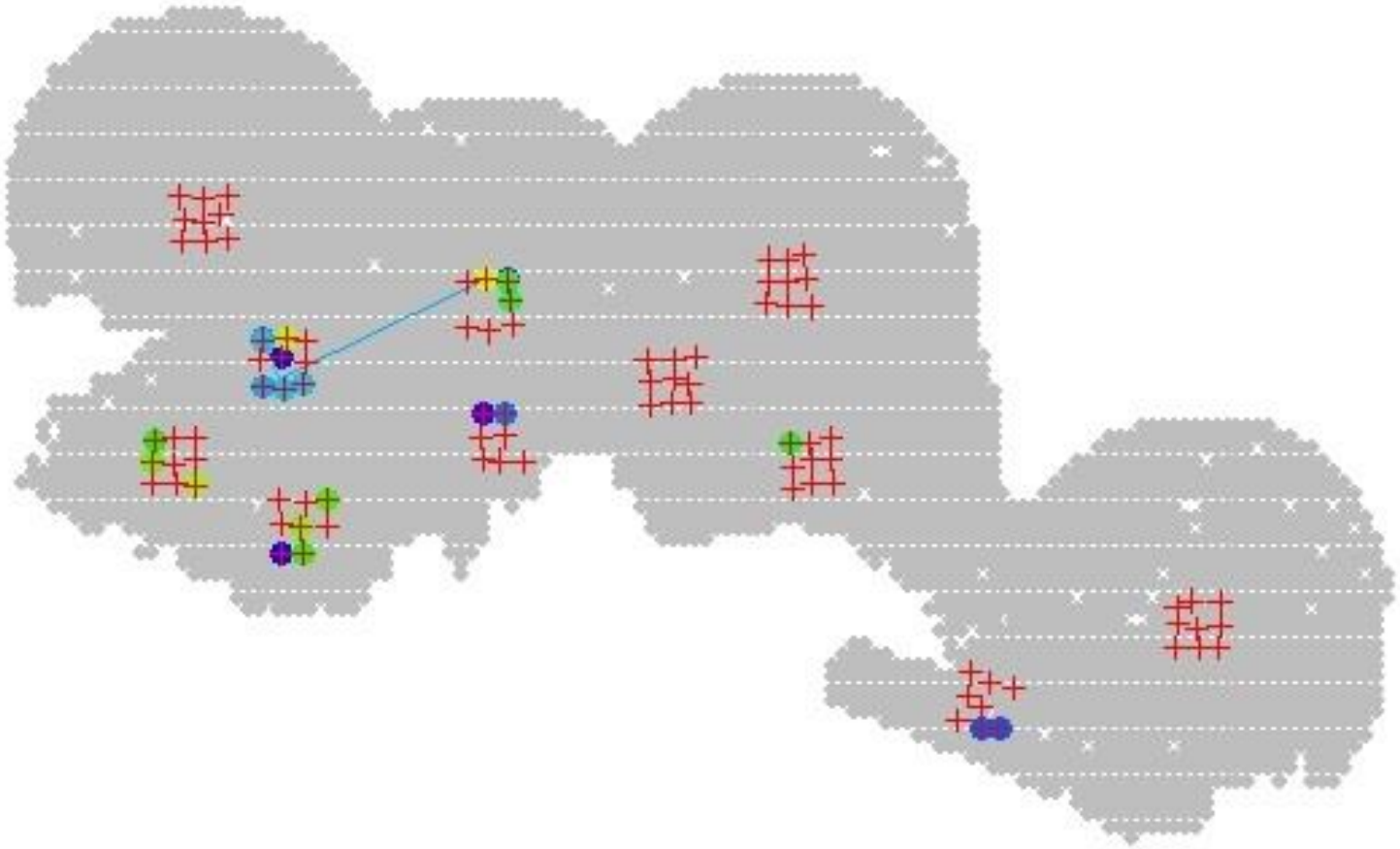

Figure 6. Trap sites and bear detections in the Eglin study area, Florida, 2015. The crosses represent hair traps and the colored dots within each trap cluster represent a different bear. Dots of the same color within a cluster represent the same animal. Lines between dots represent consecutive detections of the same animal.

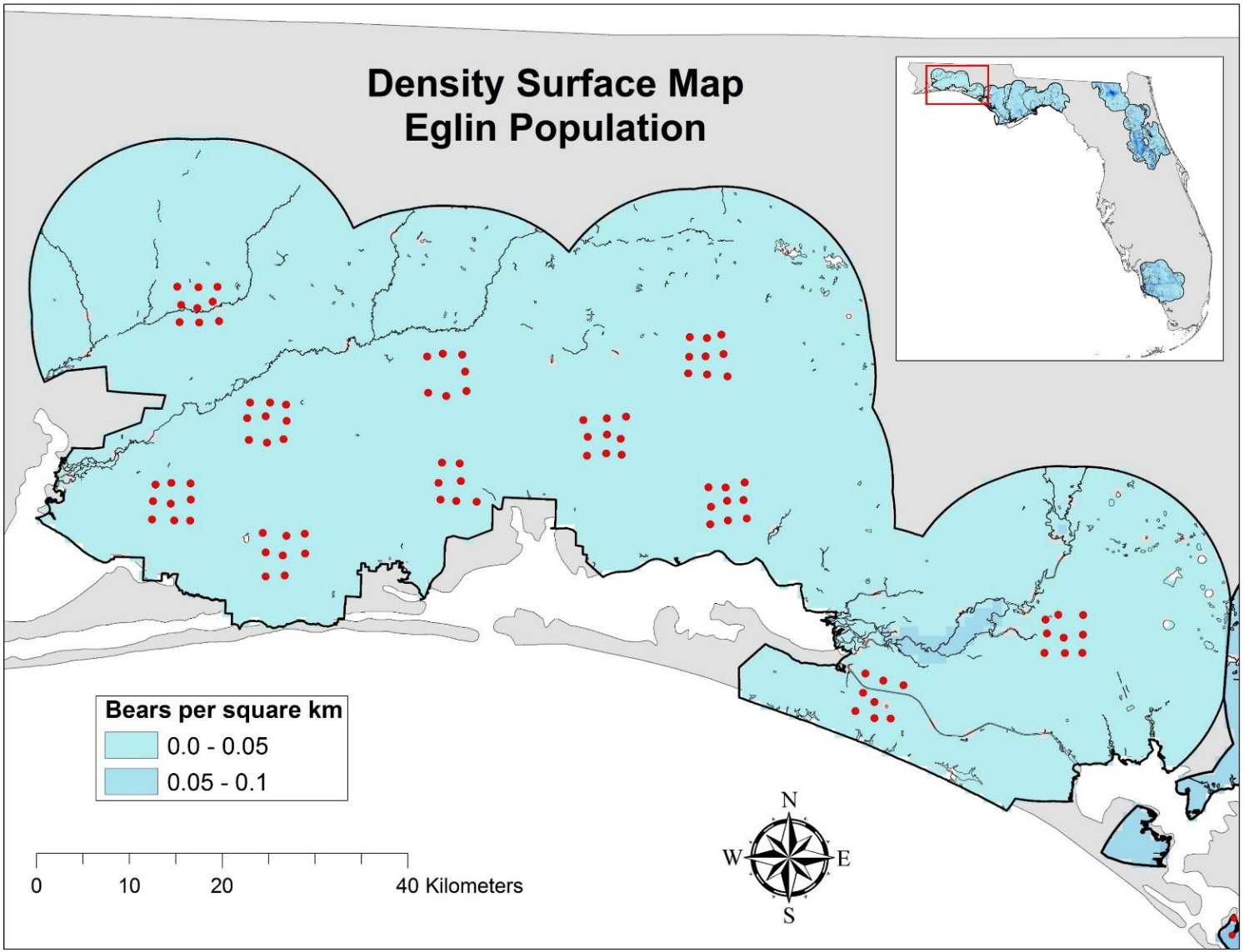

Figure 7. Model-averaged density surface map of the Eglin subpopulation, Florida, 2015. The red dots represent hair snare locations.

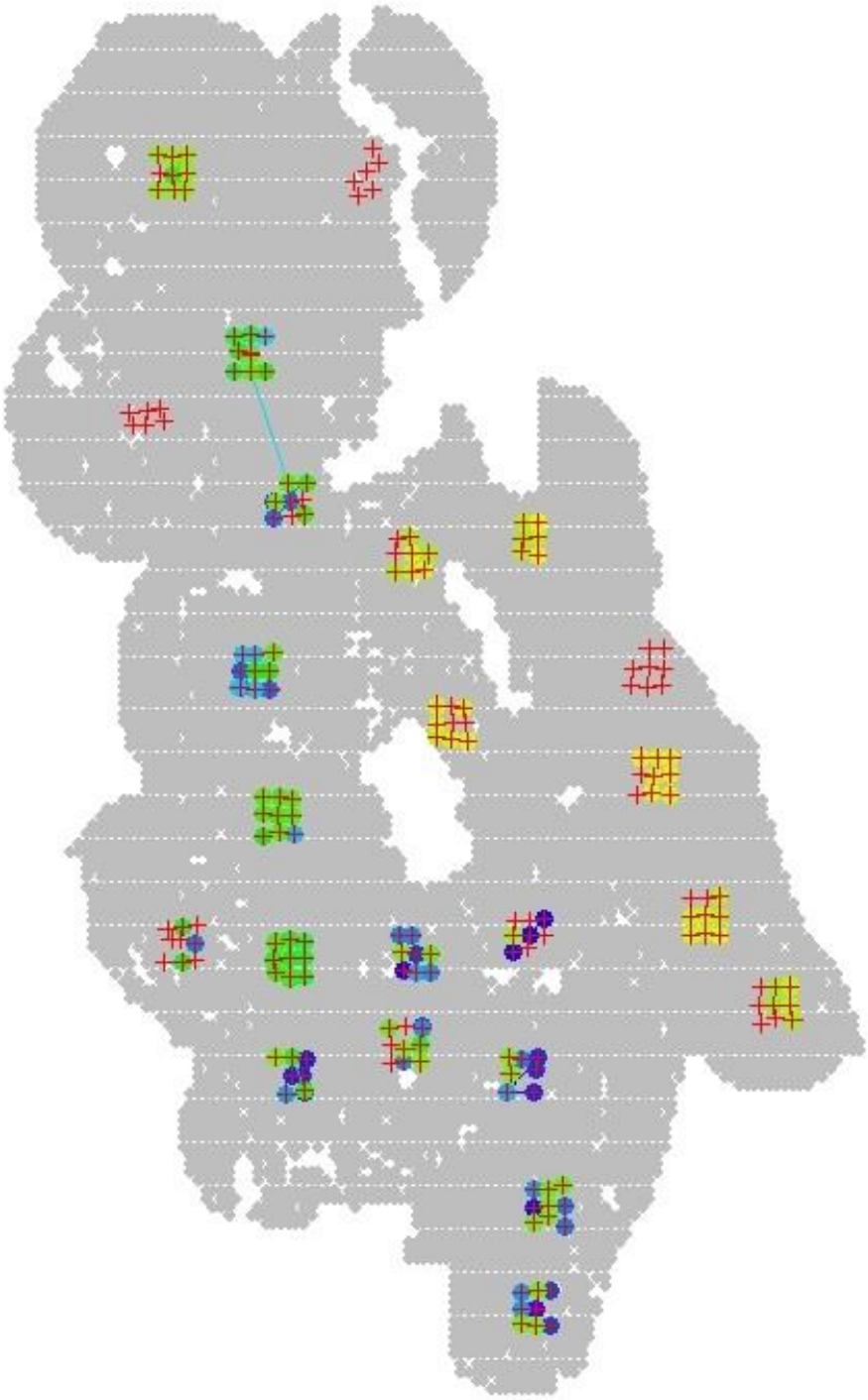

Figure 8. Trap sites and bear detections in the Ocala/St. Johns study area, Florida, 2014. The crosses represent hair traps and the colored dots within each trap cluster represent a different bear. Dots of the same color within a cluster represent the same animal. Lines between dots represent consecutive detections of the same animal.

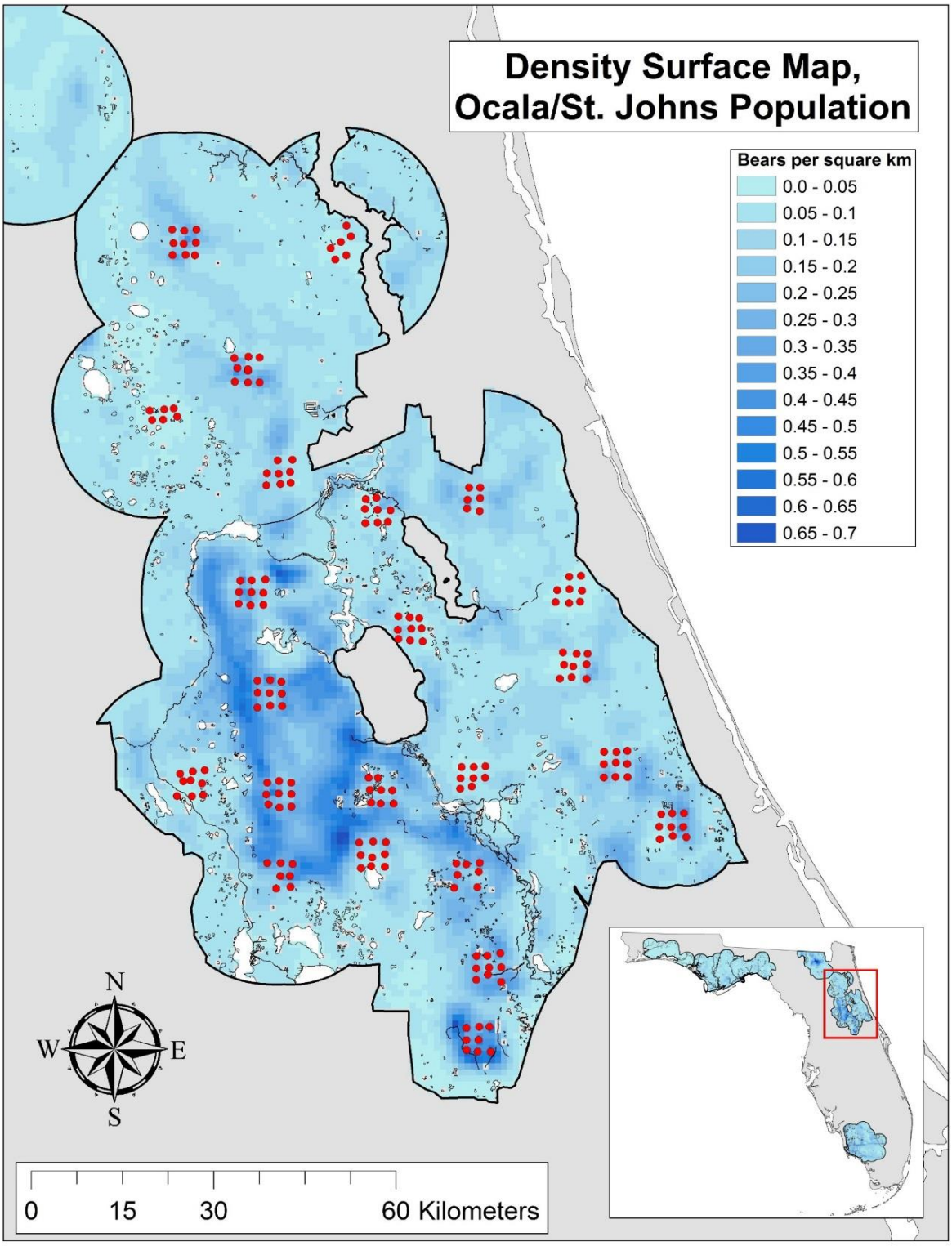

Figure 9. Model-averaged density surface map of the Ocala/St. Johns subpopulation, Florida, 2014. The red dots represent hair snare locations.

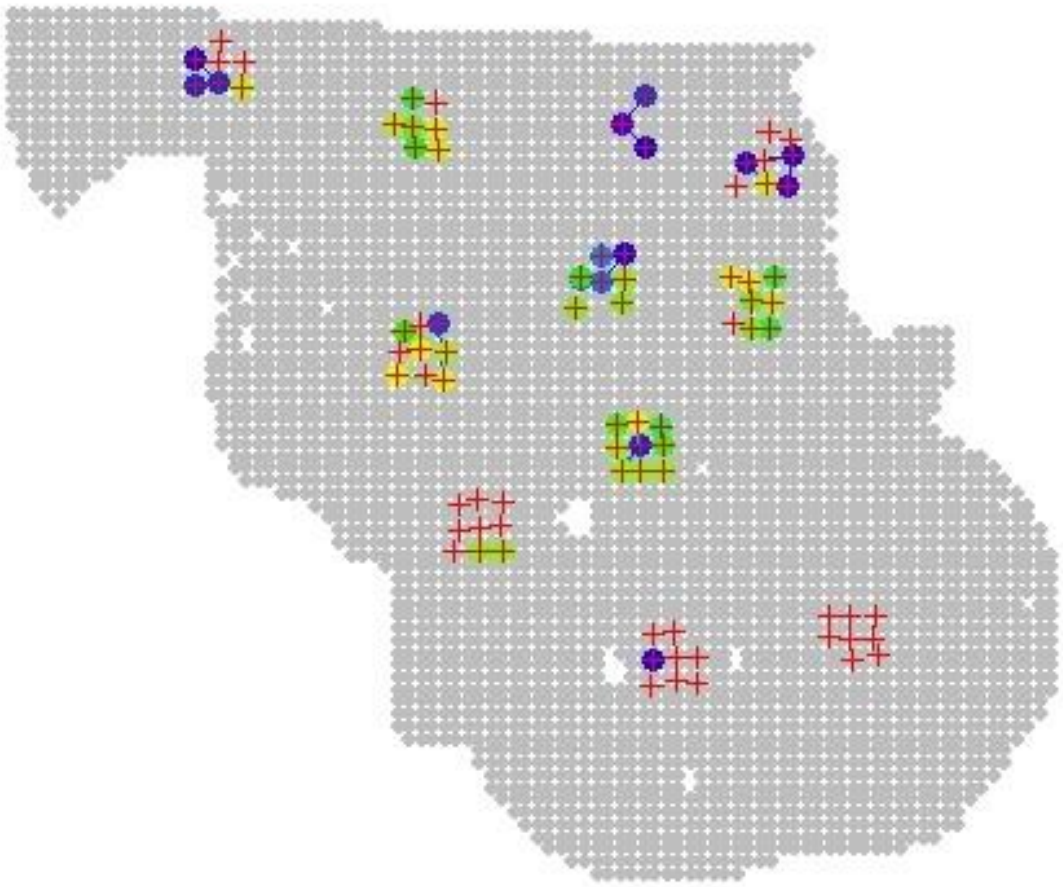

Figure 10. Trap sites and bear detections in the Osceola study area, Florida, 2014. The crosses represent hair traps and the colored dots within each trap cluster represent a different bear. Dots of the same color within a cluster represent the same animal. Lines between dots represent consecutive detections of the same animal.

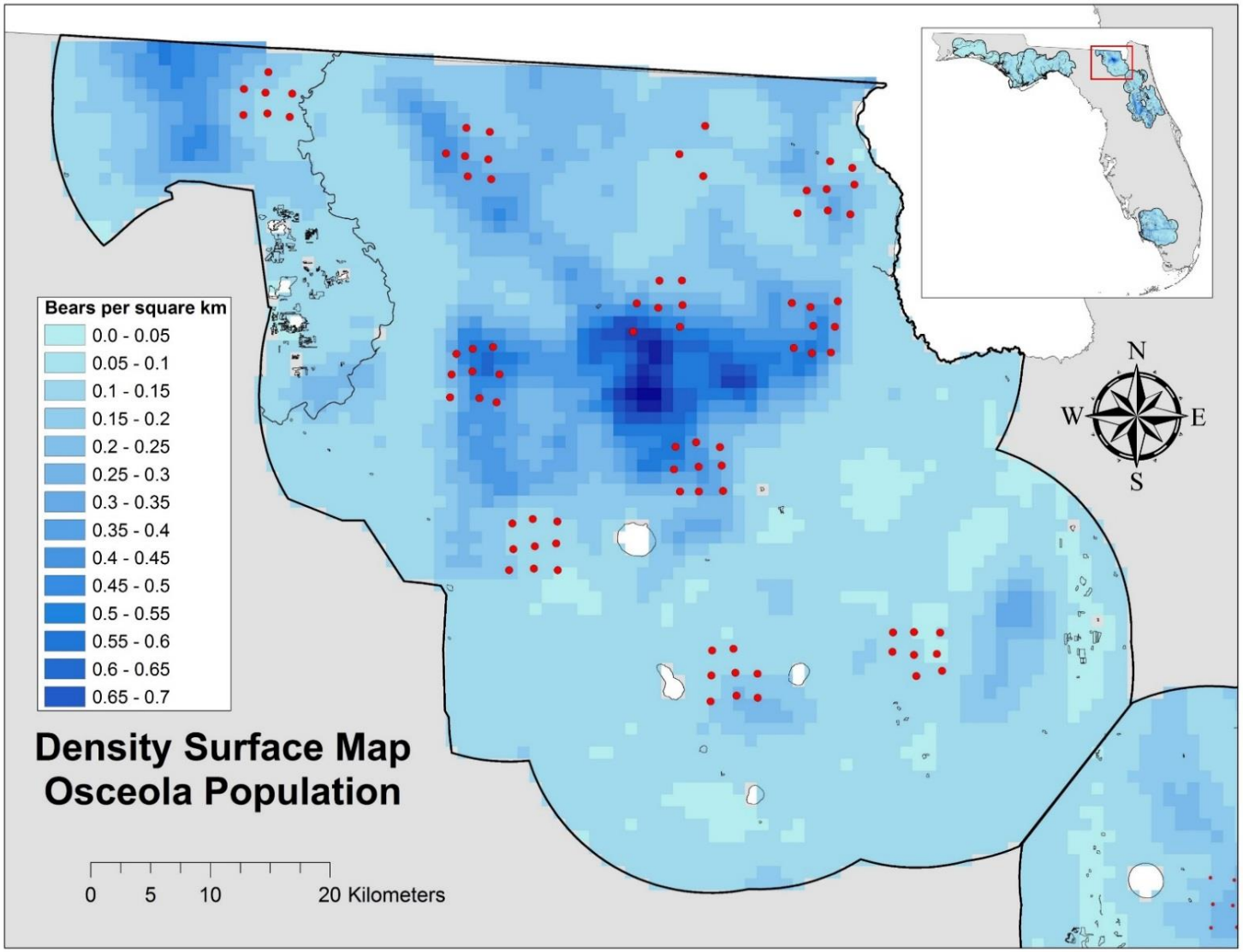

Figure 11. Model-averaged density surface map of the Osceola subpopulation, Florida, 2014. The red dots represent hair snare locations.

Vita

Jacob Humm is a Maryland native-turned-wanderer. He has lived in 7 states since he first left Maryland for new work experience. While traveling, Jacob has participated in conservation efforts under a wide range of disciplines; they include a prairie warbler behavior study and a Karner blue butterfly population study in New York, a black bear movement study and a red wolf reintroduction study in coastal North Carolina, a Mexican gray wolf reintroduction study in the White Mountains of eastern Arizona and western New Mexico, a Louisiana black bear population study in north-central and south-central Louisiana; a waterfowl monitoring study in northern California, and a mammal habitat-use study in central California. Jacob earned a B.S. in Biological Sciences from the University of Maryland, Baltimore County in 2009, and later a B.S. in Wildlife Science from Frostburg State University in 2013. After much deliberation on the merit of furthering his education, Jacob applied for a Master's degree program at the University of Tennessee studying population dynamics of the Florida black bear. He earned his Master's Degree in Wildlife Science with a Minor in Statistics from the University of Tennessee in May 2017. Jacob enjoys long walks on the beach and shouting obscenities at shorebirds while flapping his arms in a parody of fervent pursuit.