Resource Selection at Different Spatial Scales by Black Bears in Alabama

by

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Abstract

Black bears are native throughout Alabama; however, historic populations have diminished, in part from decreased connectivity and habitat degradation. At present, only two small populations of black bears occur in Alabama. One population is growing quickly in number, while the other is genetically isolated from other black bear populations in the southeastern U.S. Neither population exhibits the spatial growth patterns characteristic of what small populations could achieve. The observed limited spatial growth and genetic isolation could be explained by a lack of corridors, resulting in decreased connectivity, or limited population expansion could be caused by human development and a lack of suitable habitat. Therefore, we created first- and second-order habitat selection models using a Geographic Information System (GIS) for black bears in Alabama in order to understand resource selection at these two spatial scales. The objective of the first-order selection model was to identify potential spatial barriers and areas of population connectivity in Alabama. Models indicated that a lack of available corridors in south Alabama may be limiting gene flow with black bear populations in Florida. Conversely, potential corridors in north Alabama may be facilitating population connectivity and expansion. The objectives of the second-order selection model were to understand how black bears use human dominated landscapes in Alabama and to understand more about the potential for population range expansion despite widespread human presence. We found that much of Alabama has a relatively low potential for population expansion; however, there are areas that could provide opportunities for population growth, allowing bear populations to approach their historic distribution. Understanding potential spatial barriers and population expansion in Alabama could help to inform wildlife managers who are seeking to enhance bear populations and prepare for potential bear population growth in the state and elsewhere in the U.S.

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NAL	Northern Alabama
MRB	Mobile River Basin

Chapter 1: Potential Spatial Barriers to Black Bear Dispersal and Population Connectivity in Alabama

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Abstract:

Corridors are important for many species, especially black bears (*Ursus americanus*), which use corridors for juvenile dispersal and connectivity among local and regional populations. Black bears are native throughout Alabama; however, historic populations have diminished, in part from habitat degradation and decreased connectivity. At present, only two small populations of black bears occur in Alabama. One is a newly recolonized population in northern Alabama, whose numbers are growing quickly. The other is a remnant population in the Mobile River Basin that is genetically isolated from other black bear populations in the southeastern U.S. Neither population exhibits the spatial growth patterns characteristic of what small populations could achieve. One proposed explanation for the observed limited spatial growth and genetic isolation is a lack of corridors, resulting in decreased connectivity. In this study, we created Geographic Information System (GIS) models of corridor suitability for black bears in Alabama. We used reports and sightings of bears from 1911 to 2020 to parameterize and test the model. ROC curves confirmed that the GIS models were good predictors of proportional probability of use of a location by black bears. Models indicated that a lack of available corridors in south Alabama may be limiting gene flow with black bear populations in Florida. Conversely, potential corridors in north Alabama may be facilitating population connectivity and expansion.
Key words: Geographic Information System, *Ursus americanus*, model building

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Corridors have several important and interrelated functions to wild animals, each of which is critical for population persistence and species conservation (Soule and Gilpin 1991, Larkin et al. 2004). For example, dispersing individuals in many species travel long distances by utilizing corridors before establishing a new home range (Soule and Gilpin 1991). Additionally, corridors create linkages between habitat patches, allowing animals to travel among food sources, resting grounds, and areas of cover (Rudis and Tansey 1995, Dixon et al. 2006). Corridors connecting local and regional populations also aid in gene flow by providing pathways for movement of reproductively mature animals (Dixon et al. 2006, Cushman and Lewis 2010). Thus, geographically isolated populations that would be prone to genetic bottlenecks can benefit from corridors (Larkin et al. 2004). Conversely, a lack of corridors on the landscape can hinder animal movements, lead to genetic isolation, and geographically restrict populations (Larkin et al. 2004). Thus, understanding, creating, and maintaining the corridors available for any given species is important for its management and conservation.

Corridors are especially critical for black bears (*Ursus americanus*) due to the species' tendency to travel long distances and inhabit large tracts of land. For example, juvenile male black bears disperse from their natal area, sometimes traveling hundreds of kilometers before establishing a new home range (Dixon et al. 2006). During these dispersal movements, juveniles travel along corridors from one suitable habitat patch to the next, utilizing corridors at the landscape scale (Dixon et al. 2006). Corridors are also used at the home range scale; for example, by providing black bears daily access to food sources, water, cover, and day beds (Rudis and Tansey 1995). Thus, connectivity among different habitat patches provided by corridors at multiple spatial scales is critical for black bears. Finally, black bears are prone to genetic isolation due to their solitary nature and low reproductive rate (Eiler et al. 1989). Therefore, corridors are critical for connecting reproductively mature individuals during the breeding season, both within and among nearby populations. Thus, to manage for black bears, we must understand black bear movements in a variety of spatial contexts.

Black bear movements are influenced by several environmental features, including roads, bodies of water, human development, land cover type, elevation, slope, and aspect (Clark et al. 1993, Van Manen and Pelton 1997, Costello et al. 2013, Sollmann et al. 2016, Tri et al. 2016). In populations that are not hunted, vehicle collisions can be a major source of black bear mortality, and roads can additionally cause habitat fragmentation and increase human activity (Rudis and Tansey 1995, Costello et al. 2013). Therefore, black bears generally avoid roads and other areas of human development (Reynolds-Hogland and Mitchell 2007, Cushman and Lewis 2010, Atwood et al. 2011, Tri et al. 2016), while simultaneously selecting for dense land cover types such as forests and woody wetlands (Clark et al. 1993, Atwood et al. 2011, Costello et al. 2013, Sollmann et al. 2016, Tri et al. 2016). Black bears also tend to select for areas near water because these areas provide travel routes and access to food (Sollmann et al. 2016). Mid-range elevations and intermediate slopes are generally preferred by black bears because these areas tend to contain the greatest food availability while exhibiting lower levels of human development (Clark et al. 1993, Van Manen and Pelton 1997, Sollmann et al. 2016). Lastly, southern aspects provide seasonal food sources, resulting in black bears spending more time on southern aspects (Clark et al. 1993, Atwood et al. 2011). Given that traits that make for good permanent habitat for bears also tend to make for good corridors (Clark et al. 1993, Van Manen and Pelton 1997, Tri et al. 2016), each of these factors may also affect corridor quality but their importance can vary based on geographic location or behavioral differences in subpopulations.

In Alabama, black bears historically occurred throughout the state; however, the extent of their distribution diminished at least in part from habitat degradation and decreased connectivity (Scheick and McCown 2014). Currently, there are only two small populations of black bears in Alabama. The first population is a newly recolonized population in northern Alabama that is growing quickly in numbers (Draper et al. 2017), and the second is a remnant population in the Mobile River Basin and is genetically isolated from the northern population and bear populations in neighboring states (Rudis and Tansey 1995, Draper et al. 2017). Neither population exhibits the spatial growth patterns indicative of healthy, growing populations (unpublished data). One proposed explanation for the observed limited spatial growth and genetic isolation is a lack of corridors, resulting in decreased connectivity. Potentially, barriers on the landscape may be inhibiting dispersal and movement of black bears in these populations. However, more information is needed to know how black bears are using the landscape in Alabama, and if their movements are being hindered by geographic barriers.

This study had two main objectives. The first objective was to create a suitability model using a Geographic Information System (GIS) of black bear corridors in Alabama parameterized using data from black bear sightings and reports. The goal of the model was to describe black bear corridors at the population level (i.e., first-order selection as described by Johnson 1980), as opposed to corridors used to connect individual bears in a breeding population or used by individual bears within their home range (second- and third-order selection, respectively). The second objective was to evaluate the corridor suitability model to determine if there were barriers to black bear movements among populations in Alabama and in neighboring states. Based on previous studies of the population genetics of bears in Alabama (Draper et al. 2017), we hypothesized that there would be one or more geographic barriers between the Mobile River Basin population and black bears in the Florida panhandle but that no barriers would exist between the northern Alabama population and black bears in northern Georgia. The results of this study could serve to inform managers of limitations to black bear expansion and population connectivity in Alabama.

METHODS

We created corridor suitability models for black bears in Alabama using ArcMap 10.6 (ESRI, Inc., Redlands, California). Two different models were created, differentiated by areas north or south of Montgomery, Alabama (Figure 1). We divided the state this way because bear populations in the northern and southern regions appear to be from two different subspecies (*U. a. americanus* and *U. a. floridanus*, respectively) and because bears from the two populations appear to be more closely connected to bear populations in other states than each other (Draper et al. 2017). Variables considered for inclusion in the models included proximity to primary and secondary roads, proximity to water, land cover type, elevation, slope, and aspect. These variables were found to be significant predictors in previously published black bear habitat use models (Clark et al. 1993, Van Manen and Pelton 1997, Tri et al. 2016).

Primary and Secondary roads (TIGER/Line Shapefile, Primary and Secondary Roads n.d.) were buffered by 800 m (Reynolds-Hogland and Mitchell 2007, Atwood et al. 2011), based on previous studies that showed bears' tendency to avoid roads because of human activity, motorists, and increased perceived danger. Similarly, water (U.S. Geological Survey 2020) was buffered by 600 m based on previous studies that showed bears' tendency to select for areas within 600 m of water (Clark et al. 1993, Van Manen and Pelton 1997, Atwood et al. 2011, Tri et al. 2016). Roads and water were binary categorical variables, in which locations were classified as either being within or outside of the buffered areas. Land cover types were derived from the National Land Cover Database (NLCD; Homer et al. 2016). Slope and aspect were both derived from elevation data from the Consortium for Spatial Information (Reuter et al. 2007). Because black bears typically prefer intermediate slopes and elevations (Clark et al. 1993, Van Manen and Pelton 1997, Sollmann et al. 2016), we considered non-linear (i.e., quadratic) relationships for these variables. Elevation ranged from 8 m to 733 m in the northern region, and -12 m to 218 m in the southern region. Slope ranged from 0 degrees to approximately 38 degrees in the northern region, and from 0 degrees to approximately 19 degrees in the southern region. Aspect was categorized into four cardinal directions. Roads, water, and land cover variables had a 30 m resolution; elevation, slope and aspect (and thus final analyses) had a resolution of approximately 87 m.

We parameterized the corridor suitability models using location data from black bear sightings and reports compiled by Alabama Department of Conservation and Natural Resources, Alabama Natural Heritage Program, and the Alabama Wildlife Federation (i.e., reported locations; Figure 1). The compiled reports include data in the form of sightings and trail camera photos (approximately 40%), tracks (approximately 33%), scat (approximately 22%), and unknown (approximately 5%), and have been collected from 1911 to 2020, though most of the reports (approximately 78%) are from 2012 to present. These data typically come from citizens who have spotted a bear in an area where bears are uncommon. Although reports are more numerous near current black bear population range, these data are a representative sample of black bear habitat use when individuals are moving outside the range of the breeding population. In the northern region, approximately 23% of reports fall within current black bear range, and in the southern region, approximately 68% of reports fall within current black bear range. In addition to reports from locations known to have resident bears, there are also reports that fall within current range that appear to be from areas that bears are not regularly present. Each report is associated with a GPS location, though the validity of each location could not be verified as most of the reports come from the general public. A minimum convex polygon (MCP) was created around both the northern and southern regions to represent the area of habitat that is putatively ‘available’ to bears for use as corridors. A sample of 50,000 random locations from the available habitat was generated within each MCP. Values from each GIS layer were extracted for both reported and random locations. Reported and random locations were then divided into model building (75%) and model testing data (25%). Land cover types that had fewer than five report locations in the model building data were removed from the analysis. Specifically, locations within land cover types that were removed from the analysis were classified such that the value of that location would deem it “unusable,” regardless of the other parameter values of that location. We removed those land cover types because such a limited number of locations can cause problems for convergence of statistical models. Thus, given the relatively limited number of reported locations associated with those land cover types, we simply assumed that they largely were not used by bears. A logistic regression was run on the model building data from each region. A user-driven, backwards stepwise regression was used for variable selection in order to generate a model that fit the data well, but was also parsimonious (Murtaugh 2009, Hosmer et al. 2013). Specifically, in each step of the model building process, the most non-significant variable was removed from the model until all variables in the model were statistically significant ($P < 0.05$). Linear terms were not removed - even if non-significant - if squared terms were retained in the model. Categorical variables, such as aspect and land cover, were either left in the model or removed as a whole, rather than attempting to combine categories that were not significantly different.

Parameters from the models generated via the logistic regression were used to create models with a Poisson form that were proportional to our response variable of the probability of habitat use (i.e., resource selection functions; Manly et al. 2002, Keating and Cherry 2004, Johnson et al. 2006). Specifically, beta estimates for each variable were used to calculate the proportional probability of use for each cell on the corridor suitability map, using the following equation:

$$\hat{Y} = \exp(\beta_1 x_1 + \cdots + \beta_k x_k)$$

where the x variables are habitat variables and the β are coefficient estimates provided from the logistic regression analysis. The ability of each model to distinguish between report and random locations for both the building and testing data was evaluated using the area under a ROC curve (receiver operating characteristic) in the ROCR package (Sing et al. 2005) in R (R Core Team 2020).

The Poisson regression models described above (RSF) were used to generate corridor suitability maps via the Raster Calculator (ESRI, Inc., Redlands, California) in GIS. We considered a potential blockage to black bear movement to be any square area of the map of 6 km^2 (about the size of an average female bear home range; Clark et al. 1993, Edwards 2002) where the maximum proportional probability of use of the area was less than the mean for the respective region. While bears should be able to cross areas of such size during dispersal movements, we assumed an area of poor habitat of that size could at least be a stronger deterrent to bear movement. Potential barriers to movement were calculated using the Focal Statistics function in the Spatial Analyst toolbox in ArcMap 10.6 (ESRI, Inc., Redlands, California).

RESULTS

Our model describing the proportional probability of black bear use was best fit by the same variables for both datasets (Table 1). A partial likelihood ratio test showed that there was a significant improvement in fit to the data when slope was treated as quadratic rather than linear for both regions (P = 0.011 and <0.0001 for north and south, respectively). Both models included water, land cover, elevation, and slope (Table 1). Neither roads nor aspect were included in either model. A final check of the model indicated that no variables removed from the model explained a significant amount of variation in the data (all $P > 0.25$). In the northern region, land cover types of high intensity development (one report location), barren land (one report location), cultivated crops (two report locations), woody wetlands (four report locations), and emergent herbaceous wetlands (zero report locations) were removed from the analysis as they had fewer than five reports of bears using those land cover types. In the southern region, land cover types of high intensity development (one report location), barren land (zero report locations), cultivated crops (four report locations), and emergent herbaceous wetlands (one report location) were removed from the analysis, again because they had fewer than five reports of bears using those land cover types.

The area north of Montgomery, Alabama contained 395 report locations. By exponentiating the beta coefficients from the model, in the north, we found that locations that were within 600 m of water were 2.39 (1.86 – 3.05; 95% CL) times as likely to be used by a bear compared to those that were not within close proximity to water ($P < 0.0001$). Low intensity development appeared to be the land cover type with the highest probability of use and was 6.96 (4.24 – 11.12; 95% CL) times as likely to be used as our reference category of deciduous forest ($P < 0.0001$). Conversely, evergreen forest appeared to have the lowest probability of use for land cover types in the north, with evergreen forest being 0.13 (0.072 – 0.22; 95% CL) times as likely to be used as low intensity development ($P < 0.0001$). For each 100-m increase in elevation, a location was 2.33 (2.08 – 2.60; 95% CL) times as likely to be used ($P < 0.0001$). As slope increased above zero degrees, proportional probability of use increased until about six degrees of slope, then use decreased as slope continued to increase.

The area south of Montgomery, Alabama contained 692 report locations. In the south, we found that locations that were further than 600 m from water were 2.87 (2.18 – 3.86; 95% CL) times as likely to be used by a bear relative to locations in close proximity to water ($P < 0.0001$). Open space appeared to be the land cover type with the highest probability of use and was 4.74 (2.46 – 10.31; 95% CL) times as likely to be used as deciduous forest ($P < 0.0001$). Open space was 12.32 (6.62 – 25.57; 95% CL) times as likely as pasture to be used ($P < 0.0001$), with pasture appearing to have the lowest probability of use for land cover types in the south. For each 100-m decrease in elevation, a location was 44.01 (30.71 – 63.70; 95% CL) times as likely to be used ($P < 0.0001$). As slope increased above zero degrees, proportional probability of use increased until about four degrees of slope, then use decreased as slope continued to increase.

The ROC curves indicated that both models were adequate predictors of black bear corridor suitability, with the areas under the curves equaling 0.79 and 0.76 with building and testing datasets, respectively, for the northern region, and 0.82 and 0.83 for the southern region. The black bear corridor suitability models (Figure 2) indicated that much of Alabama had a relatively low proportional probability of use. Furthermore, our corridor analysis (Figure 3) indicated physical geographic barriers that would inhibit black bear movement in both regions. For example, in support of our hypothesis, there were barriers of low corridor suitability between the Mobile River Basin black bear population and black bears in the Florida panhandle. The model showed additional barriers throughout Alabama, such as potential barriers at Lake Guntersville and the area around Weiss Lake in northern Alabama. However, both regions of the state also appear to contain suitable corridors beyond current population extent, indicating that black bear populations could potentially spread in the state, occupying many areas of available habitat and approaching the historic distribution (Scheick and McCown 2014). These qualitative results were relatively robust to the exact definition used of a barrier to movement (Figure 3). Ultimately, however, whether any location on the map represents a true barrier to movement should be a function of an individual bear's motivation to cross relatively poor-quality habitat.

DISCUSSION

The results from our black bear corridor suitability models suggest that suitability is influenced by similar variables in different geographic locations. Analysis of both datasets indicated that bears' use of habitat was most influenced by water, land cover type, elevation, and slope; roads and aspect did not appear to be important determinants of bear habitat use. Previously published black bear habitat use models (Clark et al. 1993, Van Manen and Pelton 1997, Tri et al. 2016) found differing results, though most tended to include some variation of roads, water, land cover type, elevation, slope, and aspect. The differences we observed among our models and previously published models could have several explanations. First, topography in Alabama changes drastically from the northern to the southern regions, which could explain the positive relationship between use and elevation in the north and the negative relationship in the south observed in our study. Northern Alabama is characterized by rugged, mountainous terrain, while southern Alabama has a flatter landscape. However, elevation was a significant predictor variable for both models, despite the lack of topographic variation in southern Alabama. The negative relationship between use and elevation in the south observed in our study could additionally be explained by the higher concentration of reports around the Mobile area, which has a low elevation of only about 3 m. The concentration of reports decreases further inland, where elevation begins to increase. Similarly, in both regions we found a significant improvement in fit to the data when slope was treated as quadratic. Optimal slope peaked at a relatively gentle slope – about six degrees in the north and about four degrees in the south, which differs from other previously published studies that found that bears selected steep slopes (Costello et al. 2013, Sollmann et al. 2016). However, because our model was parameterized using sightings and reports, the limited human presence on steep slopes could be biasing the results towards gentler slopes.

Differences in available land cover types exist between north and south Alabama. In the northern region, proportional probability of black bear use was higher within 600 m of water, while in the south, it was higher outside of the 600-m water buffer. Typically, bears tend to select for areas in close proximately to water because these areas generally have cooler temperatures, increased food availability, and easier travel routes (Clark et al. 1993, Van Manen and Pelton 1997, Atwood et al. 2011, Tri et al. 2016). In both regions, the land cover types with the highest probability of use were in developed areas – low intensity in the north (35 out of 395 report locations; 8.86%) and open space in the south (95 out of 692 report locations; 13.73%). However, these results could be caused by the accessibility and easier viewing opportunities in these land cover types, or one or a few bears that have been reported repeatedly could be biasing these results. Additionally, these results could be an artifact of where bears and humans are more likely to interact, though more research is needed to understand bear use of these developed areas, especially use of developed areas by young, dispersing bears. Interestingly, we found that evergreen forest was the land cover type with the lowest probability of use in the north, while previously published studies have found different types of forests to be important for black bear use (Clark et al. 1993, Van Manen and Pelton 1997, Tri et al. 2016). Again, this could be an artifact of the difficulty of viewing bears in an evergreen forest and the limited human presence. As defined by Homer et al. (2016) in the NLCD, evergreen forests are “areas dominated by trees generally greater than five m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.”

Using location data from black bear sightings and reports could bias results towards areas where bears and humans are more likely to interact, such as developed land cover types and areas closer to roads. However, proximity to roads was not a significant predictor variable of black bear habitat use in either region of our study. Additionally, approximately only 30% of reports in the north and approximately only 21% of reports in the south were within 800 m of roads. If most reports were from sightings along roadsides, we believe that roads would have been a significant predictor variable. But because the reports are a mixture of road-side sightings, back yard sightings, trail camera photos, tracks, and scat, the data appear to be an accurate representation of black bear habitat use, both within and outside of the 800 m road buffer that we used.

Additionally, our results indicate that developed areas had the highest probability of use in both regions. We believe that the apparent selection for developed areas could be an artifact of what category of bears are being reported. Bears that are being reported from areas outside of current breeding population ranges are more likely to be young males that are dispersing. As young males disperse from their natal territory, they are more likely to pass through areas of open space or low intensity development, where there are more anthropogenic food sources available. Therefore, while developed areas are not beneficial for bears, developed areas certainly are used by bears, especially young, dispersing males that are most likely just passing through the area. Although most reports (68%) in the southern region fall within current bear range, our results are still indicative of resource selection by dispersing bears, since both dispersing bears and resident bears are likely to select for similar resources. Ultimately, both young, dispersing males and resident adults need food and water sources and cover. Furthermore, the limited number of reports outside of current bear range in the southern portion of Alabama could be further evidence of the potential spatial barriers that are hindering population connectivity between the Mobile River basin black bear population and black bears in neighboring states.

Because location data of resource selection by black bears outside of current population ranges are limited, our results are influenced by the probability of a bear using a location, and the probability of a human reporting bears’ use of that location. Therefore, caution should be taken when using the results from this study for broad-scale management of black bears. While these results could be representative of first-order resource selection of corridors by dispersing black bears in Alabama, more research is needed to understand resource selection of non-dispersing bears, and what potential exists for bear population expansion outside of current range.

In support of our hypothesis that black bears in the southern black bear population are isolated from black bears in the Florida panhandle due to lack of corridors, our corridor suitability model appeared to show physical, geographic barriers on the landscape. The apparent lack of available suitable corridors is confounded by anecdotal observations of black bears from Florida moving throughout south Alabama each year, including movements into the southeastern Alabama black bear population (Figure 1; C. Seals, Auburn University, personal communication). Thus, the low genetic diversity and apparent genetic isolation of the southern Alabama black bear population may additionally be due to other factors, such as bear behavior.

Indeed, one hypothesis that explains the genetic isolation could be that a few large males are monopolizing all the breeding in the population. More research is needed to test this hypothesis.

Ultimately, the apparent availability of corridors and few barriers could mean that black bears have the potential to re-colonize portions of the state, approaching historic black bear distributions. However, currently neither population in Alabama appears to be taking advantage of the lack of barriers (unpublished). The lack of population expansion may have more to do with the asymmetric dispersal between the sexes (Rogers 1987, Dixon et al. 2006) and barriers to resettlement by females such as lack of denning habitat (C. Seals, Auburn University, personal communication), which is not as important to males (Weaver and Pelton 1994, Oli et al. 1997). Additionally, if a population is below carrying capacity, resource competition may be low enough that density-dependent dispersal may not be occurring, hence limiting spatial expansion. Thus, more research is needed into the dispersal rates and characteristics of juvenile bears in both populations. When obvious barriers to movement are not apparent, only through more nuanced understanding of the interaction between habitat and black bear behavior can we hope to understand a lack of spatial growth in a species.

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TABLES

Table 1.1: Final models describing proportional probability of use of a habitat by black bears (*Ursus americanus*) as a function of variables chosen to remain in the model. Models were parameterized using a comparison of random locations to sightings and reports of black bears in Alabama, compiled from 1911 to 2020. Land cover type comparisons are in reference to Deciduous Forest for both regions.

Region	Variable	Coefficient	Confidence Limits	*P*
North	Water	0.87	(0.62 – 1.12)	< 0.01
North	Developed, Open Space	1.80	(1.45 – 2. 16)	< 0.01
North	Low Intensity Development	1.94	(1.45 – 2.41)	< 0.01
North	Evergreen Forest	-0.13	(-0.61 – 0.32)	0.58
North	Mixed Forest	0.33	(-0.15 – 0.78)	0.16
North	Shrub/Scrub	0.04	(-0.78 – 0.72)	0.92
North	Grassland/Herbaceous	0.64	(-0.01 – 1.21)	0.04
North	Pasture/Hay	-0.08	(-0.50 – 0.34)	0.73
North	Elevation	0.01	(0.01 – 0.01)	< 0.01
North	Slope	0.11	(0.00 – 0.22)	0.05
North	$Slope^2$	-0.01	(-0.02 – -0.00)	0.02
South	Water	-1.06	(-1.35 – -0.78)	< 0.01
South	Developed, Open Space	1.56	(0.90 – 2.33)	< 0.01
South	Evergreen Forest	0.40	(-0.22 – 1.15)	0.25
South	Mixed Forest	0.17	(-0.50 – 0.96)	0.64
South	Shrub/Scrub	0.34	(-0.36 – 1.15)	0.37

South	Grassland/Herbaceous	0.12	(-0.62 – 0.95)	0.76
South	Pasture/Hay	-0.95	(-1.87 – -0.02)	0.04
South	Woody Wetlands	-0.30	(-0.95 – 0.47)	0.40
South	Elevation	-0.04	(-0.04 – -0.03)	< 0.01
South	Slope	0.68	(0.46 – 0.91)	< 0.01
South	$Slope^2$	-0.09	(-0.13 – -0.05)	< 0.01

FIGURE CAPTIONS

Figure 1.1: Locations of reported black bear sightings in Alabama. Northern reports are those north of Montgomery, Alabama and southern reports are those south of Montgomery, Alabama.

Figure 1.2: Black bear corridor suitability model (RSF) for northern Alabama and southern Alabama. Low (blue) to high (red) proportional probability of use.

Figure 1.3: Barriers to black bear dispersal and connectivity. A potential barrier to black bear movement was defined as any area of the RSF map greater than 6 km^2 that had a proportional probability of use less than a) mean – 0.25 SD (approximately 0.031 for northern Alabama and 0.067 for southern Alabama); b) the mean proportional probability of use (approximately 0.055 for northern Alabama and 0.097 for southern Alabama); and c) mean + 0.5 SD (approximately 0.10 for northern Alabama and 0.16 for southern Alabama).

FIGURES

Figure 1.1:

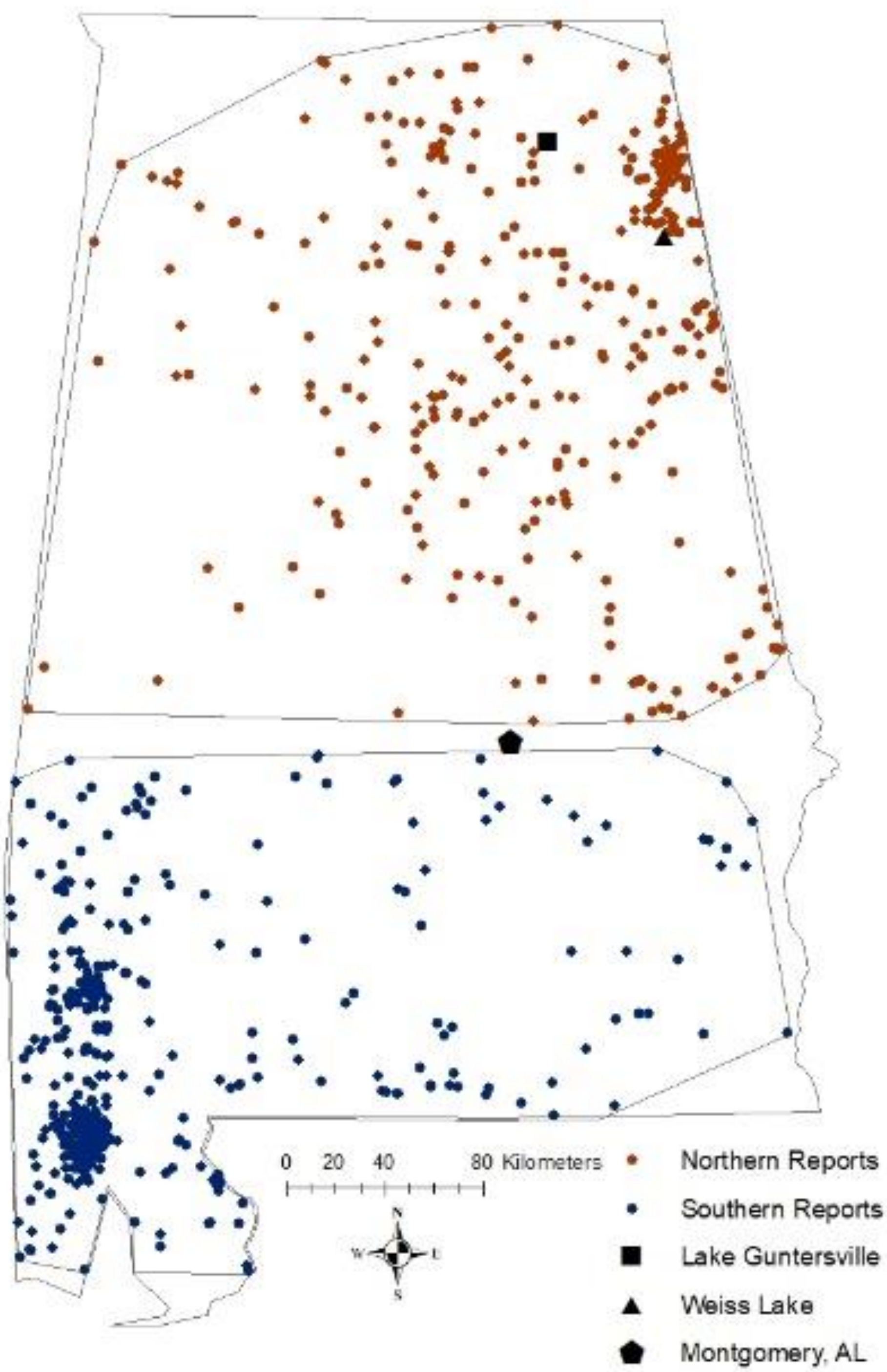


Figure 1.2:

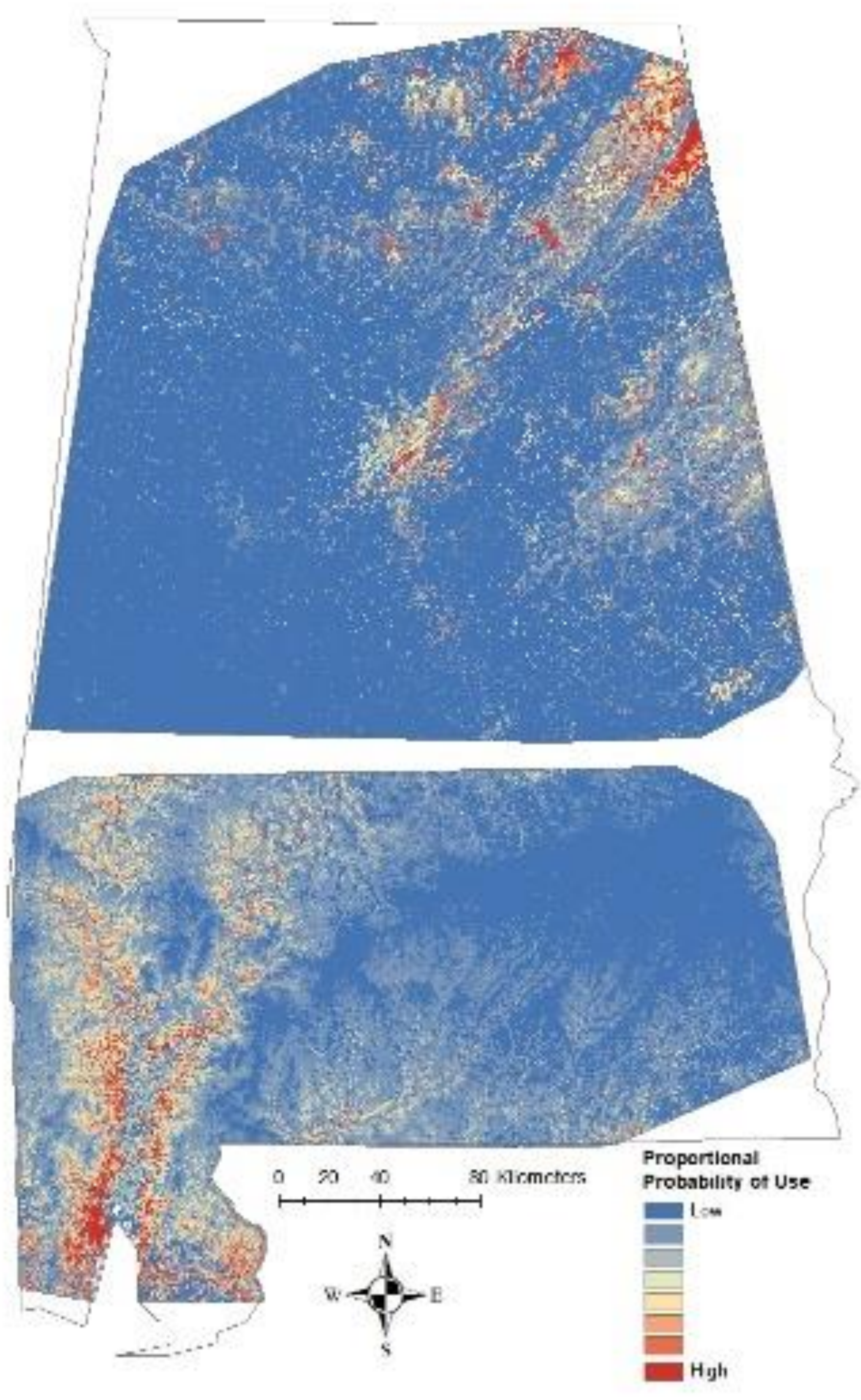
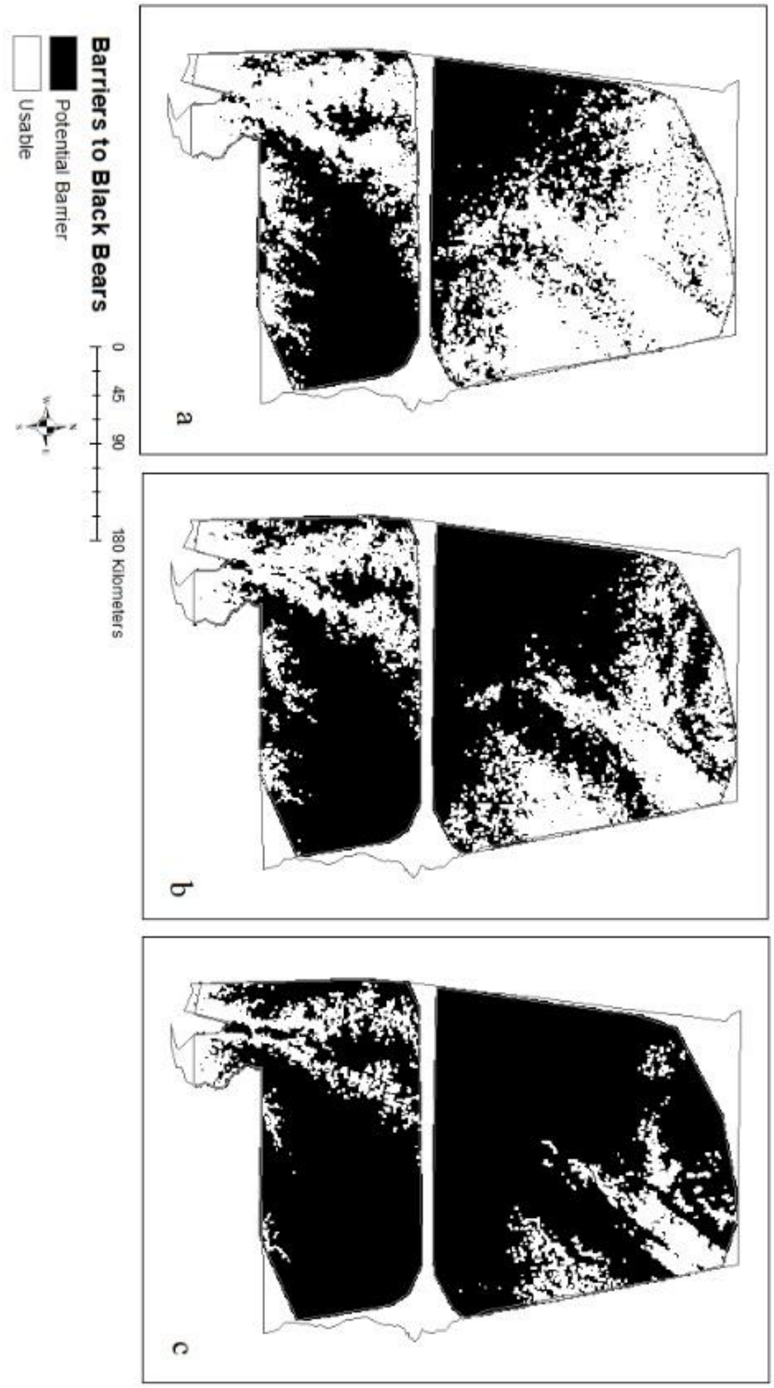

0 20 40 80 Kilometers
Proportional
Probability of Use
Low
High
N
W
E
S

Figure 1.3:


Barriers to Black Bears
Potential Barrier
Usable
0 45 90 180 Kilometers
a
b
c

Chapter 2: Potential for Population Expansion by Black Bears in Alabama

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Abstract:

Human development and lack of suitable habitat can impede spatial population growth for many species. Because black bears have large home ranges, the amount of habitable area available to the species has been drastically reduced, especially in the southeastern U.S., causing some populations to face possible extirpation. Recently, some black bear populations in the U.S. have begun to recover and recolonize portions of historic black bear range, despite human-dominated landscapes. The relationship between black bear population expansion and human development is especially apparent in Alabama. The Mobile River Basin black bear population has persisted through the development of Mobile and the surrounding area, but it does not appear to be growing spatially or numerically. Conversely, black bears have recently recolonized northern Alabama from a nearby northern Georgia black bear population and this northern Alabama population appears to be growing numerically at a fast rate. This study sought to understand how black bears use human dominated landscapes in Alabama and to understand more about the potential for population range expansion despite widespread human presence. We created resource selection models for black bears via a Geographic Information System and location data from GPS-collared black bears in Alabama. We hypothesized that the area around the Mobile River Basin population would have low potential for population expansion of habitat because of higher human density and an urbanized landscape. Conversely, we hypothesized that the area around the northern Alabama population would have high potential for bear population expansion because of lower human density and a more rural landscape with large tracts of undeveloped, forested land cover. We found that much of Alabama has a relatively low potential for population expansion; however, there are areas that could provide opportunities for population growth, allowing bear populations to approach their historic distribution.

Understanding potential bear population expansion in Alabama could help to inform wildlife managers who are seeking to enhance bear populations and prepare for potential bear population growth in the state and elsewhere in the U.S.

INTRODUCTION

Historic population ranges of many animal species have been reduced, at least in part, as a result of over-harvest, habitat manipulation, and human settlement (Woodroffe 2000). While the effects of overharvest often can be reversed by simply allowing the population to grow once again, the population effects of habitat loss typically cannot be overcome unless the lost habitat is restored. Thus, due to alterations to the landscape, many species have experienced permanent reductions in their range. The effects of habitat alteration, disturbance, and human development across the landscape are especially apparent in large carnivore species because of their greater potential for negative interactions with humans, extensive home ranges, and increased resource requirements (Woodroffe 2000). Thus, when the conservation goal for a large carnivore species is to expand its range and restore population sizes, lack of suitable habitat and human development can critically impede those population expansion efforts.

In the early half of the 20th century, black bear (*Ursus americanus*) populations across the U.S. decreased severely in range and size in part due to loss of habitat and the expansion of human populations (Cowan 1970, Woodroffe 2000, Scheick and McCown 2014). The decrease in bear populations was particularly dramatic in the southeastern U.S., where bear populations experienced an 80% reduction in range (Pelton and Van Manen 1997, Scheick and McCown 2014). Like many large mammals, black bears have extensive home ranges and prefer large tracts of forested land (Clark et al. 1993, Tri et al. 2016). Consequently, increased human development had caused a decrease in available black bear habitat (Cowan 1970). However, more recently, many black bear populations appear to have experienced a resurgence (Bales et al. 2005, Sollmann et al. 2016, Draper et al. 2017). For example, bear populations in Florida, which were once considered endangered at the state level, have recovered to the point that hunting of the species was recently allowed in the state for a short period (Dixon et al. 2006; Florida Fish and Wildlife Conservation Commission 2019). Other bear populations in the southeastern U.S. and beyond have experienced similar expansions in both size and range (Bales et al. 2005, Sollmann et al. 2016, Draper et al. 2017). Yet, some local black bear populations still appear to experience limitations to their growth and expansion (e.g. northern Georgia, Little et al. 2017; Missouri, Sollmann et al. 2016). Consequently, more information is needed to understand how black bears use human-dominated landscapes and how - or even if - black bears are capable of expanding their population range considering the near-ubiquitous presence of humans.

An example of black bear populations that may be limited from growth and spatial expansion due to habitat loss and human encroachment are those found in the state of Alabama. While historically native throughout the state, black bears were nearly extirpated from Alabama in the early part of the 20th century (Cowan 1970, Scheick and McCown 2014). For several generations, the only remaining black bears consisted of a small population around the Mobile River Basin (MRB). However, this population has been highly genetically isolated and does not appear to be connected with any other nearby black bear populations in neighboring states (Draper et al. 2017). Putatively, the isolation of the MRB population may be a result of the high level of human development and inadequate habitat around Mobile and the surrounding area.

Conversely, a new population of black bears has recently repatriated northern Alabama (NAL) when immigrant bears from North Georgia settled in the area (Draper et al. 2017). The

NAL population appears to be growing quickly and expanding further into Alabama. The rapid expansion of the NAL population could be facilitated by the lower level of human development in the area compared to MRB. Ultimately, however, more information is needed on how black bears use landscapes in Alabama and what potential exists for bear populations to expand spatially in the state.

In this study, we created habitat selection models for black bears, parameterized using location data from GPS-collared black bears in Alabama, via a Geographic Information System (GIS; ESRI, Inc., Redlands, California). We then extrapolated these models to generate predictions about the relative probability of habitat use of various landscape attributes available in Alabama and the potential for black bear expansion throughout the rest of the state. We hypothesized that there would be low potential for bear population expansion into habitat surrounding the MRB population because of higher human density and an urbanized landscape. Conversely, we hypothesized that there would be high potential for bear population expansion into habitat surrounding the NAL population because of lower human density and a more rural landscape with large tracts of undeveloped, forested land cover. Ultimately, understanding how and where bear populations may expand in the state should be very useful to wildlife managers who seek to enhance bear populations and prepare for bear population growth in the state and elsewhere in the U.S.

METHODS

Research efforts were focused on two distinct populations of black bears in Alabama: the northeastern Alabama population (NAL), and the Mobile River Basin population (MRB) in the southwest corner of the state (Figure 1). The NAL population (34°30'N, 85°36'W) is centered in

DeKalb and Cherokee counties, including the federally managed Little River Canyon National Preserve and DeSoto State Park. In addition, many large tracts of privately managed hunting land and stands managed for timber harvest blanket the landscape. Dominant habitat types in NAL include deciduous and evergreen forests, and pasture and hay, with steep topography and mountainous terrain (Homer et al. 2016, Draper et al. 2017). Homer et al. (2016) define deciduous forests as “areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change;” and evergreen forests as “areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.” Pasture includes “areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle. Pasture/hay vegetation accounts for greater than 20% of total vegetation” (Homer et al. 2016). Elevation ranged from approximately 164 m to approximately 600 m, and slope ranged from zero degrees to approximately 35 degrees. Conversely, the MRB population (31°12'N, 88°06W) is centered in Mobile and Washington counties in the southwest corner of Alabama. Dominant habitat types include mixed and evergreen forests, and woody wetlands (Homer et al. 2016, Draper et al. 2017). Homer et al. (2016) define mixed forests as “areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of total tree cover;” and woody wetlands as “areas where forest or shrub land vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.” Elevation ranged from approximately 0 m (sea level) to approximately 117 m, and slope ranged from zero degrees to approximately 10 degrees. Human population density is higher in MRB than it is in NAL (Draper et al. 2017), creating a landscape mosaic and higher proportion of bears occupying suburban areas.

We created second-order (sensu Johnson 1980) habitat selection models for black bears in Alabama using ArcMap 10.6 (ESRI, Inc., Redlands, California). Two different models were created: one for the north Alabama population (NAL), and one for the population around the Mobile River Basin (MRB; Figure 1). We divided the state in this way because northern and southern bear populations appear to be from two different subspecies (*americanus* and *floridanus*, respectively) and because bears from the two populations appear to be more closely connected to bear populations in other states than each other (Draper et al. 2017).

Variables considered for inclusion in the models included proximity to water, proximity to primary and secondary roads, land cover type, elevation, slope, aspect, stewardship, and human density. These variables were found to be significant predictors in previously published black bear habitat use models (Clark et al. 1993, Van Manen and Pelton 1997, Tri et al. 2016).

Proximity to primary and secondary roads (TIGER/Line Shapefile, Primary and Secondary Roads n.d.) was considered (as both categorical and continuous variables) based on previous studies that showed bears' tendency to avoid roads because of human activity, motorists, and increased perceived danger. To create a binary categorical road variable, roads were buffered by 800 m (Reynolds-Hogland and Mitchell 2007, Atwood et al. 2011), in which locations were classified as either being within or outside of the buffered areas. To create a continuous variable, Euclidean distance to roads was calculated (ESRI, Inc., Redlands, California), and we also examined potential non-linear (i.e., quadratic, third-order polynomial) relationships with this variable. Similarly, proximity to water (U.S. Geological Survey 2020) was tested as both categorical and continuous variables. To create a binary categorical water variable, water was buffered by 600 m based on previous studies that showed bears' tendency to select for areas within 600 m of water (Clark et al. 1993, Van Manen and Pelton 1997, Atwood et al. 2011, Tri et al. 2016). To create a continuous variable, Euclidean distance to water was calculated (ESRI, Inc., Redlands, California). Land cover types were derived from the National Land Cover Database (NLCD; Homer et al. 2016). Slope and aspect were both derived from elevation data from the Consortium for Spatial Information (Reuter et al. 2007). Because black bears typically prefer intermediate slopes and elevations (Clark et al. 1993, Van Manen and Pelton 1997, Sollmann et al. 2016), we considered non-linear relationships for these variables. Elevation in Alabama ranges from -24 m to 733 m, and slope in Alabama ranges from 0 degrees to approximately 50 degrees (Reuter et al. 2007). Aspect was categorized into the four cardinal directions. Stewardship was classified into four groups, with "1" being highly protected and managed for biodiversity, to "4" having no known mandate for biodiversity protection (U.S. Geological Survey (USGS) 2018). Human density was calculated as the number of people per square kilometer, and was also tested for potential non-linearities (U.S. Census Bureau 2010). Roads, water, land cover, stewardship, and human density variables had a 30 m resolution; elevation, slope and aspect had a resolution of approximately 89 m.

We parameterized the habitat selection models using location data from GPS-collared black bears collected from 2014 to 2020 (i.e. used locations; Figure 1). Adult black bears (>1.5 years old) were trapped from May through November using Cambrian style traps baited with corn, pastries, and commercial bear attractants. Captured black bears were anaesthetized intramuscularly using a jab stick (Dan-Inject, Austin, TX), with 4 mg/kg of body weight of Telazol (Fort Dodge Laboratories, Fort Dodge, IA; Hebblewhite et al. 2003, Garrison et al. 2007, Tri et al. 2016). Each bear was weighed, sexed, marked with a unique passive integrated transponder (PIT; Biomark, Boise, ID) tag subcutaneously injected between their shoulder blades, marked with unique ear tags, morphologically measured (body length, chest circumference), had a sample of hair taken for genetic analyses, and fitted with a motion-sensitive GPS collar (Vectronics, Berlin, Germany; Telonics, Inc., Mesa, AZ). Collars were designed such that collars entered mortality mode after a 12-hour stationary period. Collar locations were acquired every 1-2.5 hours. Iridium satellite collars allowed remote monitoring of movements, without the need to relocate the bear and download the GPS locations from the collar. Any one GPS location from a collar could be up to approximately 86 m from the true location, though most locations were within approximately 20 m. We determined collar accuracy by measuring the distance of acquired GPS fixes from a collar that was placed at a known location.

Used locations were divided into those from the NAL population and those from the MRB population. A minimum convex polygon (MCP) was created around each population and then buffered by one km to represent the area of habitat that was putatively 'available' to bears for use during the study period. A sample of random ('available') locations from the available habitat equal to the number of used locations was generated within each MCP (n = 40,765 for NAL, n = 92,851 for MRB). Values from each GIS layer were extracted for both used and available locations. Any land cover types that had fewer than five used locations or fewer than five available locations were removed from the analysis due to problems they would cause with model convergence. Instead, we simply considered those land cover types as unusable. In NAL, low intensity development, medium intensity development, high intensity development, and barren land were removed from the analysis as they had fewer than five used locations in those land cover types. In MRB, high intensity development and cultivated crops were removed from the analysis, again because they had fewer than five used locations in those land cover types. Similarly, human densities above which there were no used locations were removed from the analysis; we considered those higher human densities as unusable by bears. In NAL, densities above 134.7 humans per square km, and in MRB, densities above 2048 humans per square km were removed from the analysis. The MRB population did not have any locations with a stewardship ranking of 1.

Logistic regression was used to build a model for each dataset (MRB and NAL). Models were built using a backwards stepwise procedure. Specifically, a model containing all terms was fit to the data. Potential non-linearities in Euclidean distance to water, Euclidean distance to roads, elevation, slope, and human density were then considered by adding – one at a time – higher order terms to the model and evaluating their significance and effect. Subsequently, a directed approach was used to remove model terms; the most non-significant variable was removed from the model until all variables remaining in the model were significant ($P < 0.05$). Linear terms were not removed - even if non-significant - if squared terms or cubed terms were retained in the model. Categorical variables, such as aspect and land cover, were either left in the model or removed as a whole, rather than attempting to combine categories that were not significantly different.

Parameters from the models generated via the logistic regression were used to create models with a Poisson form that represented proportional probability of habitat use (i.e., resource selection functions; Manly et al. 2002, Keating and Cherry 2004, Johnson et al. 2006). Specifically, the model had the form:

$$Y = \exp(\beta_1 X_1 + \cdots + \beta_k X_k)$$

where *Y* is proportional to the probability of use, *X* is the habitat attribute, and β is the coefficient estimate for that habitat attribute generated via the logistic regression for *k* parameters. The RSF models were used to generate potential population expansion maps via the Raster Calculator in ArcMap 10.6 (ESRI, Inc., Redlands, California).

The predictive ability of each model was evaluated using the k-fold cross validation method described by Johnson et al. (2006). Specifically, we randomly divided the data from each area (MRB and NAL) into 10 equally-sized groups (folds). For each of 10 evaluations, a different group was designated as the testing dataset, while the remaining 9 groups were combined to represent the training dataset. The logistic regression model chosen for that area during the procedures outlined previously was fit to each training dataset. The coefficients from each logistic regression were used to create models with a Poisson form, as described above. The Poisson models, or RSF's, were used to assign proportional probability of use values to pixels in a GIS, with an extent equal to the MCP's described previously. The pixels were ranked by RSF value and equally divided into 10 groups by number of pixels in the MCP. For example, the lowest 10% of the ranked RSF values comprised the first bin, second lowest 10% of ranked RSF values comprised the second bin, and so on. We then calculated the expected number of used locations within each bin via the utilization function described in Johnson et al. 2006. Finally, we compared the expected number of used locations with the observed number of used locations within each bin via linear regression and chi-square tests.

RESULTS

We acquired location data from 48 different bears in Alabama; 19 (5 M:14 F) bears in the NAL population and 29 (10 M:19 F) bears in the MRB population. The distribution of these bears adequately represents current black bear range in Alabama. Number of locations per bear ranged from 150 to 8043.

We found that the model to predict proportional probability of black bear use of a location, and thus potential for population expansion, was best fit by the global models for both the NAL and MRB datasets. Variables in the global models included distance to water, distance to roads, land cover type, elevation, slope, aspect, stewardship, and human density (Table 1). AIC scores indicated that both distance to water and distance to roads were better treated as continuous (Euclidean distance) rather than categorical (buffered) variables. Partial likelihood ratio tests indicated that there was a significant improvement in fit to the data when Euclidean distance to water, Euclidean distance to roads, elevation, slope, and human density were treated as third-order polynomial rather than linear or quadratic for both datasets (all $P < 0.0001$). The RSF models indicated relatively low proportional probability of use, and thus low potential for population expansion, throughout the state for both models (Figure 4).

In the NAL population, we found that as both distance to water and distance to roads increased, relative probability of use increased, albeit in non-linear manners (Figure 2). Cultivated crops appeared to be the land cover type with the highest relative probability of use and were 2.85 (2.44 – 3.34; 95% C.L.) times as likely to be used as mixed forests ($P < 0.0001$). Conversely, open space development appeared to be the land cover type with the lowest relative probability of use in the NAL population, with open space development being 0.38 (0.32 – 0.44; 95% C.L.) times as likely to be used as mixed forests ($P < 0.0001$). As elevation increased, relative probability of use decreased until about 232 meters of elevation, then use increased as elevation increased until about 445 meters of elevation; then use decreased as elevation increased further (Figure 2). As slope increased above zero degrees, relative probability of use decreased until about two degrees of slope, then use increased as slope increased until about 18 degrees of slope; then use decreased as slope increased further (Figure 2). East-facing aspects appeared to have the highest relative probability of use and were 1.07 (1.01 – 1.14; 95% C.L.) times as likely to be used as south-facing aspects ($P = 0.018$). Conversely, west-facing aspects appeared to have the lowest relative probability of use in the NAL population, with west-facing aspects being 0.88 (0.83 – 0.93; 95% C.L.) times as likely to be used as south-facing aspects ($P < 0.0001$). Areas with a stewardship ranking of 1 had the highest relative probability of use for bears in the NAL population, and were 2.64 (1.84 – 3.73; 95% C.L.) times as likely to be used as areas with a stewardship ranking of 3 ($P < 0.0001$). Conversely, areas with a stewardship ranking of 2 had the lowest relative probability of use, and were 0.26 (0.18 – 0.39; 95% C.L.) times as likely to be used as areas with a stewardship ranking of 3 ($P < 0.0001$). A stewardship ranking of 3 was used as the reference group because it had neither the highest nor lowest relative probability of use; therefore, the stewardship rankings that had the highest and lowest relative probability of use could both be compared to stewardship rankings of 3. As human density increased, relative probability of use decreased until about 56 people per square km, then use increased as human density increased and appeared to stabilize.

When we combined the results from each fold, the cross-validation analysis of the model for NAL indicated that the regression line (Figure 3) had a slope of 0.97 (0.94 – 1.00; 95% C.L.), which was significantly different from 0, indicating that the model was better than a random or neutral model. Additionally, the slope was not significantly different from 1, suggesting that the model provides predictions that are proportional to the probability of use. The estimate of the intercept was 10.55 (-17.55 – 38.66; 95% C.L.), which was not significantly different from 0 ($P = 0.46$); a result that again indicates that the model provides predictions that are proportional to the probability of use (Johnson et al. 2006). The multiple R^2 value was 0.98. The chi-square test indicated significant deviation between observed and expected values ($X^2 = 2336$, $P = 0$). Chi-square tests of individual bins confirmed that the number of observed locations in all ten bins was significantly different from expected.

In the MRB population, we found that as distance to water increased, relative probability of use decreased until about 27 meters to water, then use increased as distance to water increased until about 1598 m, then use decreased as distance to water continued to increase (Figure 2). As distance to roads increased, relative probability of use increased until about 3805 m to roads, then use decreased as distance to roads continued to increase (Figure 2). For land cover type, woody wetlands appeared to be the land cover type with the highest relative probability of use and were 1.67 (1.59 – 1.76; 95% C.L.) times as likely to be used as mixed forest ($P < 0.0001$). Conversely, barren land appeared to be land cover type with the lowest relative probability of use in the MRB population, with barren land being 0.13 (0.092 – 0.19; 95% C.L.) times as likely to be used as mixed forest ($P < 0.0001$). As elevation increased above zero meters, relative probability of use decreased, albeit in a non-linear manner (Figure 2). As slope increased above zero degrees, relative probability of use increased until about four degrees of slope, then use decreased as slope continued to increase (Figure 2). East-facing aspects appeared to have the highest relative probability of use and were 1.11 (1.08 – 1.15; 95% C.L.) times as likely to be used as south-facing aspects ($P < 0.0001$). Conversely, south-facing aspects appeared to have the lowest relative probability of use in the MRB population, with north-facing aspects being 1.04 (1.01 – 1.08; 95% C.L.) times as likely to be used as south-facing aspects ($P = 0.014$). Areas with a stewardship ranking of 4 had the highest relative probability of use for bears in the MRB population, and were 9.12 (4.69 – 19.57; 95% C.L.) times as likely to be used as areas with a stewardship ranking of 3 ($P < 0.0001$). Conversely, areas with a stewardship ranking of 2 had the lowest relative probability of use, and were 0.12 (0.035 – 0.36; 95% C.L.) times as likely to be used as areas with a stewardship ranking of 3 ($P = 0.00028$). As human density increased, relative probability of use decreased until about 1329 people per square km, then use increased as human density increased.

When we combined the results from each fold, the cross-validation analysis of the model for MRB indicated that the regression line (Figure 3) had a slope of 1.07 (1.03 – 1.11; 95% C.L.), which was significantly different from both 0 and 1. Additionally, the intercept, -64.44 (-121.10 – -7.78; 95% C.L.), was significantly different from 0 ($P = 0.026$). However, the multiple R^2 value was 0.97. The chi-square test indicated significant deviation between observed and expected values ($X^2 = 3322.26$, $P = 0$). Again, chi-square tests of individual bins confirmed that the number of observed locations in all ten bins was significantly different from expected.

DISCUSSION

Our analyses indicated that bears' use of habitat was similar in both populations. In both populations, we found a significant improvement in fit to the data when distance to water, distance to roads, elevation, slope, and human density were treated as third-order polynomial, rather than linear or quadratic. In both populations, the lowest relative probability of use was at locations closest to water. However, this result differed from other previously published studies that have found that bears tend to select for areas closer to water because these areas generally have cooler temperatures, increased food availability, and easier travel routes (Clark et al. 1993, Van Manen and Pelton 1997, Atwood et al. 2011, Tri et al. 2016). Similarly, we found that relative probability of use increased as distance to roads increased. While some roads can provide travel routes and easier access to food sources (Reynolds-Hogland and Mitchell 2007), the increased human activity and associated habitat fragmentation likely increase the perceived danger affiliated with roads. Bears in the MRB population appear to select for areas within intermediate distance to roads. Potentially, bears may want to stay far enough away from roads to avoid the perceived danger, but close enough to utilize easier travel corridors provided by roads. In the NAL population, relative probability of use reached a low point at approximately 232 meters of elevation, and was highest at approximately 445 meters of elevation (Figure 2), which are both intermediate elevations as elevation in the NAL population ranged from approximately 164 m to approximately 600 m. In the MRB population, proportional probability of use decreased as elevation increased (Figure 2). Elevation in the MRB population ranged from approximately 0 m (sea level) to approximately 117 m. Selection for certain elevations by bears is likely a factor of human activity, seasonal food availability, and accessibility to travel corridors (Clark et al. 1993, Van Manen and Pelton 1997, Sollmann et al. 2016). Previously published studies suggest that bears select steep slopes, while our results indicate that bears tend to select intermediate slopes (Costello et al. 2013, Sollmann et al. 2016; Figure 2). However, the MRB region had a much flatter landscape than the NAL region; thus, a slope that might be considered gentle in the NAL population could be considered relatively steep in the MRB population.

A previous study that analyzed black bear resource selection at the first-order scale in order to identify potential corridors and barriers in Alabama (Leeper and Steury, in press) had some differing results to this study that analyzed black bear resource selection at the second-order scale. Low intensity development was removed from analysis for the NAL population in this study which analyzed resource selection at the second-order habitat selection scale (Johnson

1980). Conversely, first-order resource selection by potentially dispersing black bears in Alabama found low intensity development to be the land cover type with the highest relative probability of use in the northern region of Alabama (Johnson 1980; Leeper and Steury, in press). Similarly, cultivated crops were removed from the analysis for having fewer than five reported locations in the northern region when analyzed at the first-order scale (Leeper and Steury, in press), but cultivated crops were the land cover type with the highest probability of use when analyzed at the second-order scale. However, results from the first-order habitat selection study may have been influenced by using location data from black bear sightings and reports. Thus, the locations may have been biased towards areas with easier viewing opportunities and where bears and humans were more likely interact, such as low intensity development land cover types. Additionally, bears may not be visible to humans when using cultivated crops, either because of visual obstruction, or because bears may use cultivated crops at night.

Interestingly, both the first-order selection model for the southern region (Leeper and Steury, in press) and the second-order selection model for the MRB population confirm that relative probability of use was highest at lower elevations, and that optimal slope peaked at a relatively gentle slope- four degrees. Again, these results could be explained by the food availability, human presence, and accessibility to travel corridors at certain elevations and slopes.

While there are similarities and differences between the first- and second-order selection models, each set of models serve a purpose. The first-order selection models are likely more accurate at predicting dispersal areas and potential corridors for young males that are leaving their natal territory. The second-order selection models are likely more accurate for predicting population expansion outside of current range. Additionally, the RSF maps for the southern portion of the state for both first- and second-order selection models appear fairly similar, which could be an indicator that our RSF's are robust, especially in the areas that show higher probability of use. However, because the second-order selection models use location data from GPS-collared black bears, while the first-order selection models use location data from black bear sightings and reports, the results from the second-order selection models should be used to predict how bears will use individual environmental attributes for population expansion.

Not surprisingly, areas with a stewardship ranking of 1 had the highest relative probability of use for the NAL population, indicating that protected areas are important for bear use. Similarly, our results suggest that intermediate human densities have lower relative probability of use, while lower and higher human densities have higher relative probability of use by bears in both populations. The higher relative probability of use at higher human densities could indicate bears' reliance on anthropogenic food sources, which should be considered as bear populations continue to grow and potentially expand towards areas with more human-provided food sources. As human densities continue to increase in Alabama and other states with recovering bear populations, which resources bears use and how they use them will likely change. Additionally, just as bear use changes in response to increasing human densities, bear use will likely change as bear density increases as well. The NAL population is newly recolonized, and the area has likely not yet reached carrying capacity. As the population continues to grow in number and increase in density, resource use and allocation will likely begin to shift. Understanding more about how resource selection changes in response to changing bear and human population density could help to predict future population trends for growing or declining species. As animal populations grow and expand outwards from protected areas with low human density, population ranges may begin to encroach towards more human-dominated landscapes.

Counter to our hypothesis that there is relatively low potential for population expansion surrounding the MRB population, our RSF appears to show high relative probability of use throughout the southern portion of the state (Figure 4). Conversely, the NAL model suggests relatively low potential for population expansion around the NAL population, which differs from our hypothesis that there would be higher potential for population expansion around the NAL population because of lower human density and larger tracts of undeveloped, forested land. Interestingly, both models generate fairly similar predictions of relative probability of use throughout the state, which could indicate that our RSF's are robust. Additionally, while both second-order habitat selection models indicate that much of Alabama has a relatively low proportional probability of use, and thus low potential for population expansion, both models do appear to indicate that there are areas of the state that could support spatial population growth. However, currently neither population in Alabama appears to be growing spatially. The MRB population does not appear to be limited by poor quality habitat surrounding the population, so there must be other factors that are hindering population expansion. For example, the lack of numeric population growth would likely limit spatial growth as well. In the NAL population, the apparent lack of spatial growth could be explained by the fact that this population has newly recolonized the area, and thus not yet reached carrying capacity. As population density increases, individuals may be pushed out of current population range, thus expanding the NAL population throughout Alabama. Both black bear populations in Alabama should continue to be monitored for indicators of spatial and numeric population expansion throughout the state in order to prepare for the future of managing the species. Understanding population growth of black bear populations in Alabama can help managers predict if or when a population could support a harvest season or predict when human-bear interactions are likely to increase.

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TABLES

Table 2.1: Coefficients from logistic regression models for both regions. Distance to water, distance to roads, and elevation are measured in meters; slope is measured in degrees; and human density is measured in people per square km. The reference group for land cover type is Mixed Forest; and for stewardship is a ranking of 1 in NAL, and a ranking of 2 in MRB.

Region	Variable	Coefficient	Confidence Interval	*P*
NAL	Water	0.0019	(0.0015 – 0.0022)	< 0.0001
NAL	$Water^2$	-2.85e-6	(-3.30e-6 – -2.40e-6)	< 0.0001
NAL	$Water^3$	1.52e-9	(1.37e-9 – 1.68e-9)	< 0.0001
NAL	Roads	0.00029	(0.00020 – 0.00038)	< 0.0001
NAL	$Roads^2$	4.08e-8	(1.55e-8 – 6.60e-8)	0.0015
NAL	$Roads^3$	-3.44e-12	(-5.46e-12 – -1.41e-12)	0.00086
NAL	Cultivated Crops	1.048	(0.89 – 1.21)	< 0.0001
NAL	Deciduous Forest	0.15	(0.088 – 0.21)	< 0.0001
NAL	Developed, Open Space	-0.97	(-1.13 – -0.81)	< 0.0001
NAL	Emergent Herbaceous Wetland	-0.73	(-1.74 – 0.32)	0.17
NAL	Evergreen Forest	0.18	(0.096 – 0.26)	< 0.0001
NAL	Grassland/Herb	0.29	(0.16 – 0.42)	< 0.0001
NAL	Pasture/Hay	-0.92	(-1.02 – -0.81)	< 0.0001
NAL	Shrub/Scrub	0.27	(0.14 – 0.40)	< 0.0001
NAL	Woody Wetland	-0.56	(-1.79 – 0.46)	0.33
NAL	Elevation	-0.17	(-0.18 – -0.15)	< 0.0001
NAL	$Elevation^2$	0.00055	(0.00051 – 0.00059)	< 0.0001

NAL	Elevation^3	-5.43e-7	(-5.77e-7 – -5.09e-7)	< 0.0001
NAL	Slope	-0.033	(-0.061 – -0.0045)	0.023
NAL	Slope^2	0.0086	(0.0057 – 0.012)	< 0.0001
NAL	Slope^3	-0.00028	(-0.00036 – -0.00020)	< 0.0001
NAL	North	-0.12	(-0.18 – -0.061)	< 0.0001
NAL	West	-0.13	(-0.19 – -0.069)	< 0.0001
NAL	East	0.071	(0.012 – 0.13)	0.018
NAL	Stewardship 2	-2.31	(-2.51 – -2.11)	< 0.0001
NAL	Stewardship 3	-0.97	(-1.32 – -0.61)	< 0.0001
NAL	Stewardship 4	-0.63	(-0.70 – -0.56)	< 0.0001
NAL	Human Density	-0.087	(-0.093 – -0.082)	< 0.0001
NAL	Human Density^2	0.0011	(0.00095 – 0.0013)	< 0.0001
NAL	Human Density^3	-3.90e-6	(-4.95e-6 – -2.84e-6)	< 0.0001
MRB	Water	-0.00017	(-0.00031 – -0.000025)	0.022
MRB	Water^2	3.12e-6	(2.94e-6 – 3.30e-6)	< 0.0001
MRB	Water^3	-1.28e-9	(-1.34e-9 – -1.22e-9)	< 0.0001
MRB	Roads	0.00053	(0.00048 – 0.00057)	< 0.0001
MRB	Roads^2	-4.65e-8	(-5.86e-8 – -3.44e-8)	< 0.0001
MRB	Roads^3	-3.98e-12	(-4.94e-12 – -3.02e-12)	< 0.0001
MRB	Barren ground	-2.02	(-2.38 – -1.66)	< 0.0001
MRB	Deciduous Forest	0.45	(0.23 – 0.69)	0.0001
MRB	Developed, Low Intensity	-1.69	(-1.93 – -1.46)	< 0.0001
MRB	Developed, Medium Intensity	-1.57	(-1.88 – -1.26)	< 0.0001

MRB	Developed, Open Space	-0.57	(-0.67 – -0.47)	< 0.0001
MRB	Emergent Herbaceous Wetland	-0.24	(-0.38 – -0.11)	0.00040
MRB	Evergreen Forest	0.42	(0.37 – 0.47)	< 0.0001
MRB	Grassland/Herb	-0.25	(-0.32 – -0.19)	< 0.0001
MRB	Pasture/Hay	-0.36	(-0.50 – -0.23)	< 0.0001
MRB	Shrub/Scrub	0.075	(0.0099 – 0.14)	0.024
MRB	Woody Wetland	0.52	(0.47 – 0.57)	< 0.0001
MRB	Elevation	-0.17	(-0.18 – -0.16)	< 0.0001
MRB	Elevation^2	0.0023	(0.0021 – 0.0025)	< 0.0001
MRB	Elevation^3	-1.42e-5	(-1.58e-5 – -1.26e-5)	< 0.0001
MRB	Slope	0.058	(-0.020 – 0.14)	0.14
MRB	Slope^2	0.053	(0.018 – 0.087)	0.0027
MRB	Slope^3	-0.011	(-0.015 – -0.0067)	< 0.0001
MRB	North	0.042	(0.0087 – 0.075)	0.013
MRB	West	0.022	(-0.011 – 0.055)	0.19
MRB	East	0.11	(0.074 – 0.14)	< 0.0001
MRB	Stewardship 3	2.12	(1.01 – 3.34)	0.00028
MRB	Stewardship 4	4.33	(3.54 – 5.37)	< 0.0001
MRB	Human Density	-0.0024	(-0.0032 – -0.0017)	< 0.0001
MRB	Human Density^2	-8.30e-6	(-1.15e-5 – -5.3e-6)	< 0.0001
MRB	Human Density^3	4.62e-9	(3.13e-9 – 6.37e-9)	< 0.0001

FIGURE CAPTIONS

Figure 2.1: Black bear populations in Alabama. Locations are from GPS-collared bears from 2014 – 2020. a) used locations from GPS-collared black bears in Alabama; b) used locations from GPS-collared black bears in the NAL population; c) used locations from GPS-collared black bears in the MRB population.

Figure 2.2: Relationships between proportional probability of use and a) distance to water in NAL, b) distance to roads in NAL, c) elevation in NAL, d) slope in NAL, e) human density in NAL, f) distance to water in MRB, g) distance to roads in MRB, h) elevation in MRB, i) slope in MRB, and j) human density in MRB.

Figure 2.3: Cross validation linear regression for a) NAL and b) MRB using 100 expected and 100 observed locations. For NAL, the slope of the line was 0.97 (0.94 – 1.00; 95% C.L.), and the intercept was 10.55 (-17.55 – 38.66; 95% C.L.). For MRB, the slope of the line was 1.07 (1.03 – 1.11; 95% C.L.), and the intercept was -64.44 (-121.10 – -7.78; 95% C.L.).

Figure 2.4: Resource Selection Functions for a) NAL and b) MRB as a function of distance to water, distance to roads, land cover type, elevation, slope, aspect, stewardship, and human density.

FIGURES

Figure 2.1:

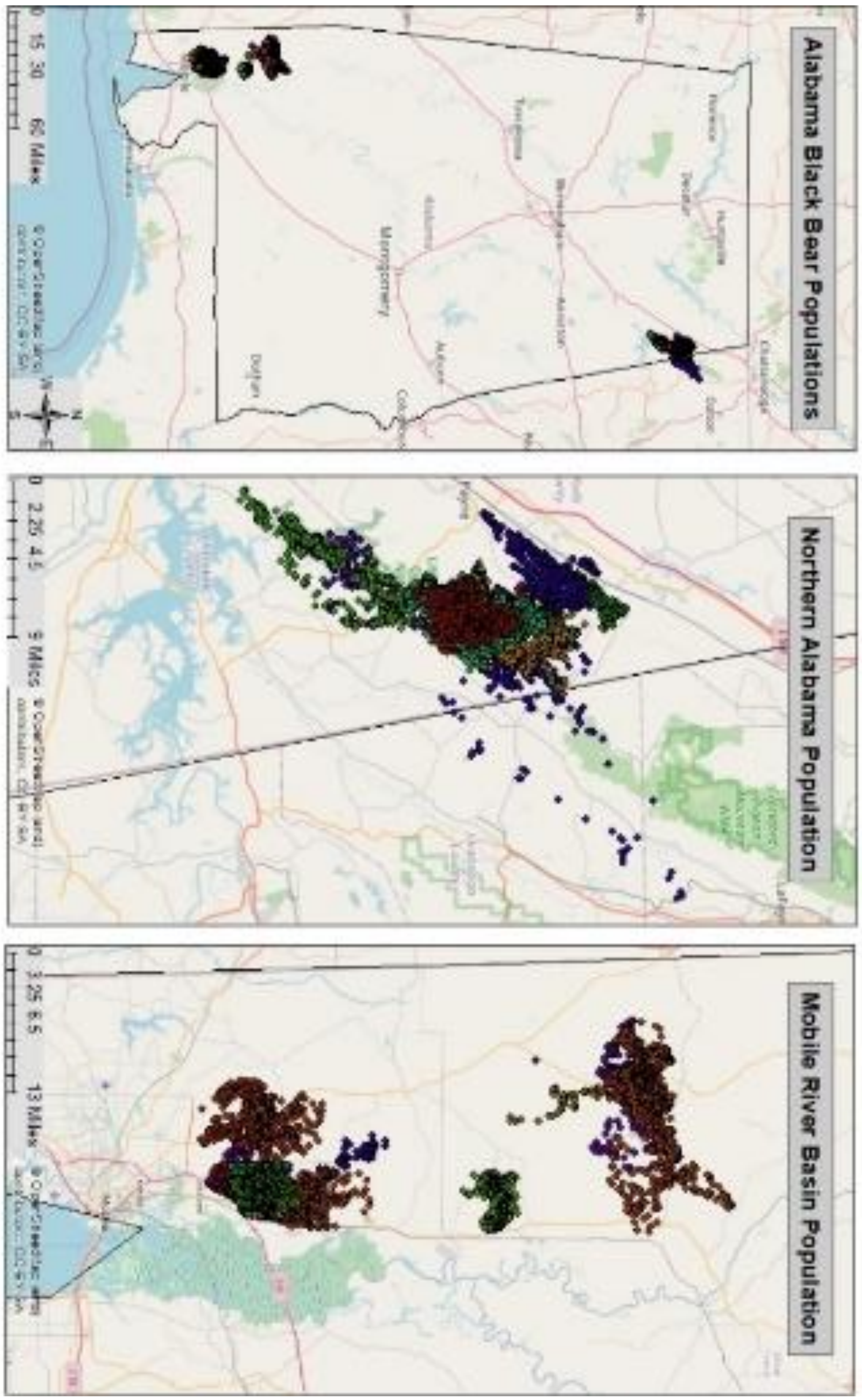


Figure 2.2:

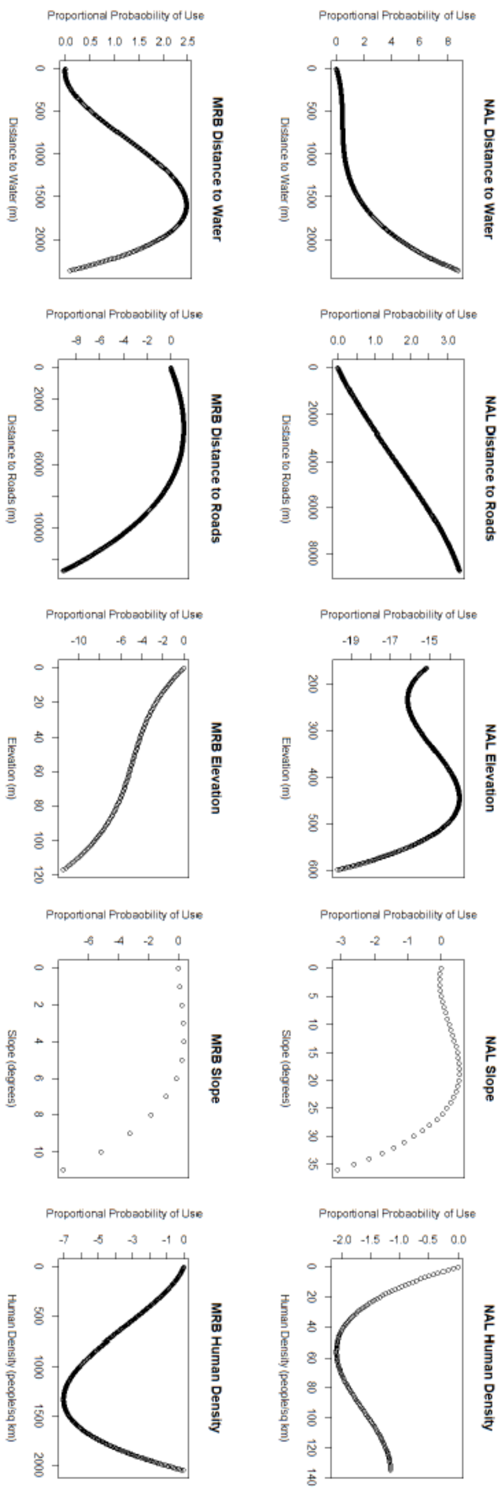

MRB Distance to Water
NAL Distance to Water
Distance to Water (m)
MRB Distance to Roads
NAL Distance to Roads
Distance to Roads (m)
MRB Elevation
NAL Elevation
Elevation (m)
MRB Slope
NAL Slope
Slope (degrees)
MRB Human Density
NAL Human Density
Human Density (people/sq km)
Proportional Probability of Use

Figure 2.3:

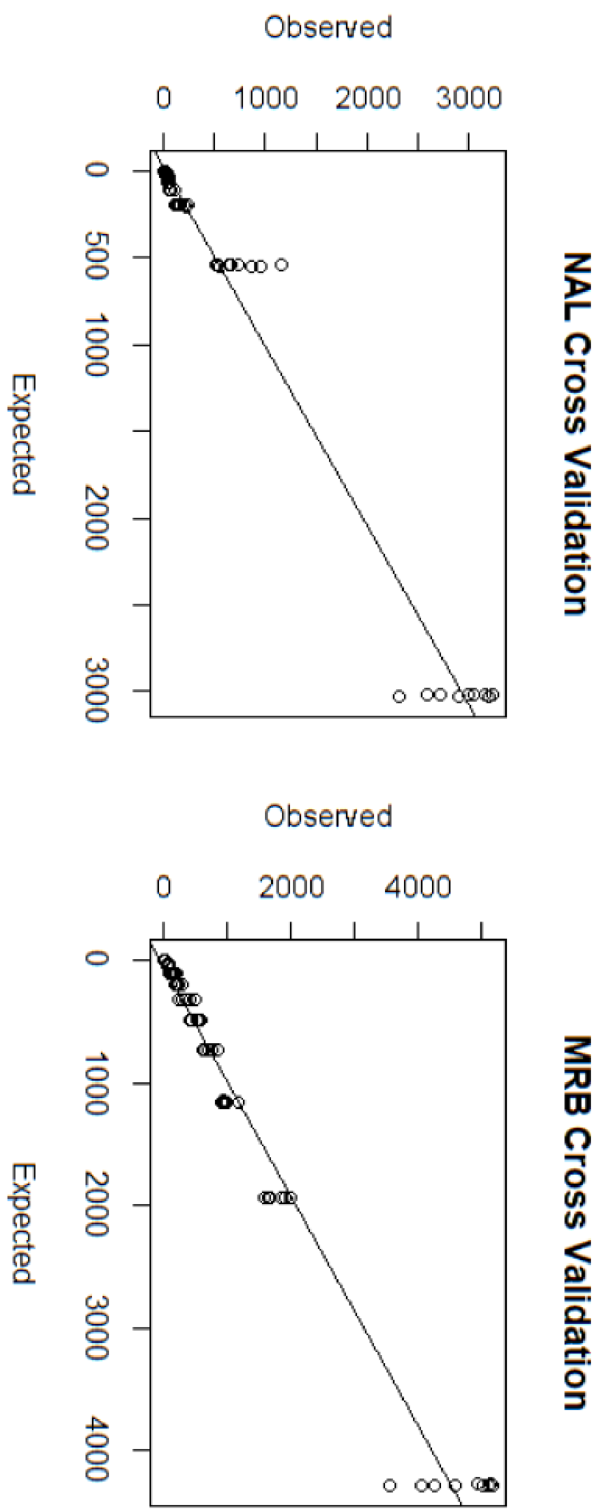
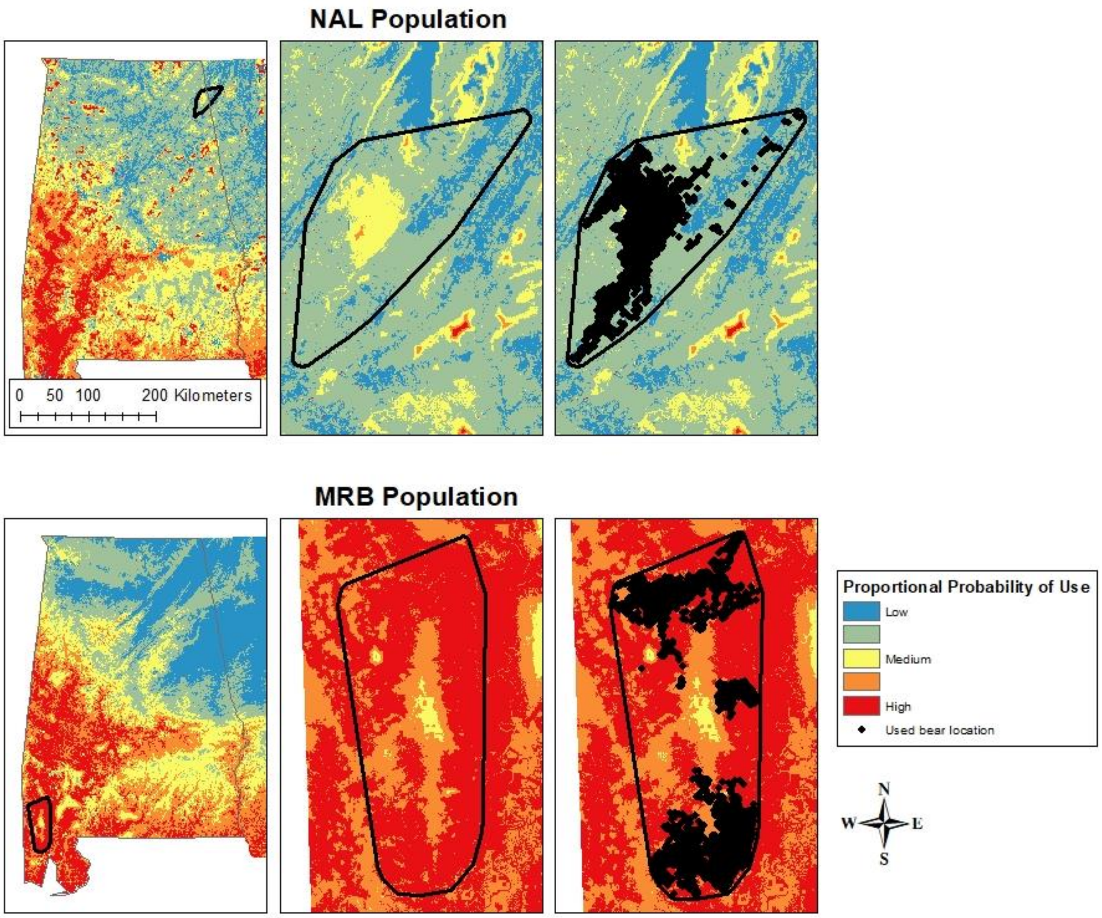

NAL Cross Validation
Observed
0
1000
2000
3000
Expected
0
500
1000
2000
3000
MRB Cross Validation
Observed
0
2000
4000
Expected
0
1000
2000
3000
4000

Figure 2.4:


NAL Population
0 50 100 200 Kilometers
MRB Population
Proportional Probability of Use
Low
Medium
High
Used bear location
N
W
E
S