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

Journal of the Southeastern Association of Fish and Wildlife Agencies 8: 101–107

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 use corridors to travel long distances 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, they provide black bears daily access to food sources, water, cover, and day beds (Rudis and Tansey 1995). Finally, black bears are prone to genetic isolation due to their solitary nature and low reproductive rate (Eiler et al. 1989) and therefore corridors are critical for connecting reproductively mature individuals during the breeding season, both within and among nearby populations. Thus, connectivity provided by corridors at multiple spatial scales is critical for black bears. 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 the presence of roads and 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; however, their importance may 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 has 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 in southern Alabama that is genetically isolated from both 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 for both Alabama bear populations and the genetic isolation is a lack of corridors. 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; Johnson 1980). The second objective was to evaluate a corridor suitability model to determine if there were barriers to black bear movements among populations in Alabama and to 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, USA). 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. ameri-*

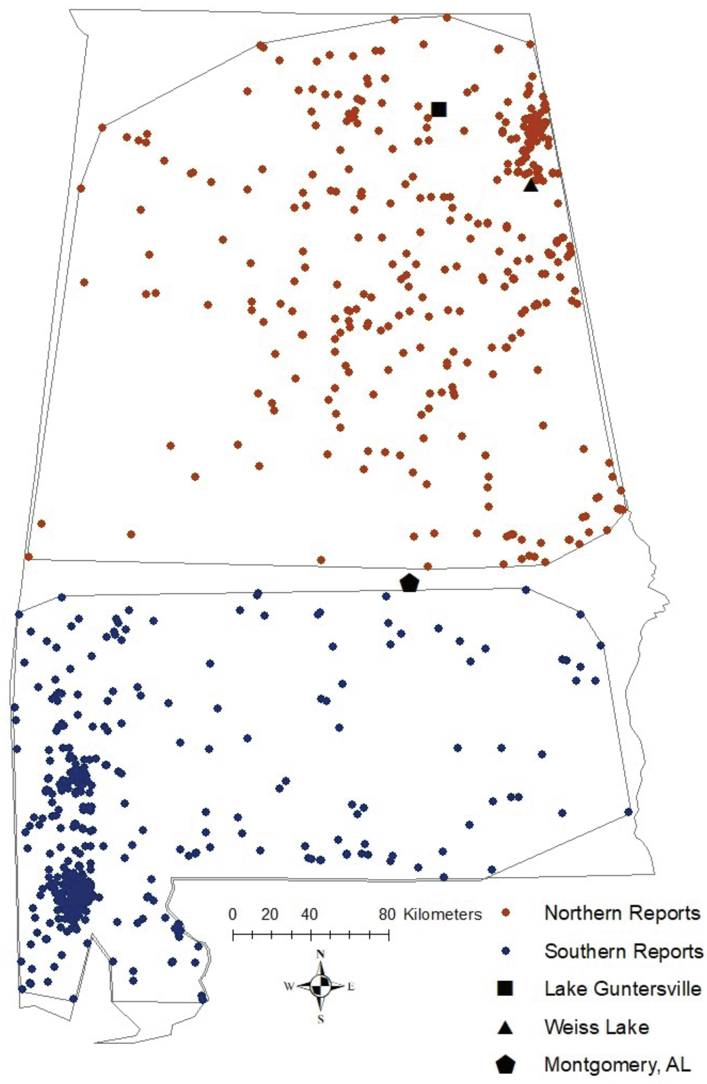

Figure 1. Locations of reported black bear sightings in Alabama. Northern reports are those north of Montgomery, Alabama, and southern reports are those south of Montgomery, Alabama.

canus 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, we added 600-m buffers around water bodies (U.S. Geological Survey 2020) 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 to 733 m in the northern region, and –12 to 218 m in the southern region. Slope ranged from 0 to approximately 38 degrees in the northern region, and from 0 to approximately 19 degrees in the southern region. Aspect was categorized into four cardinal directions: north, south, east, and west. 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, trail camera photos, tracks, and scat, 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. 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:

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

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 $P < 0.0001$ 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.

Table 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

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

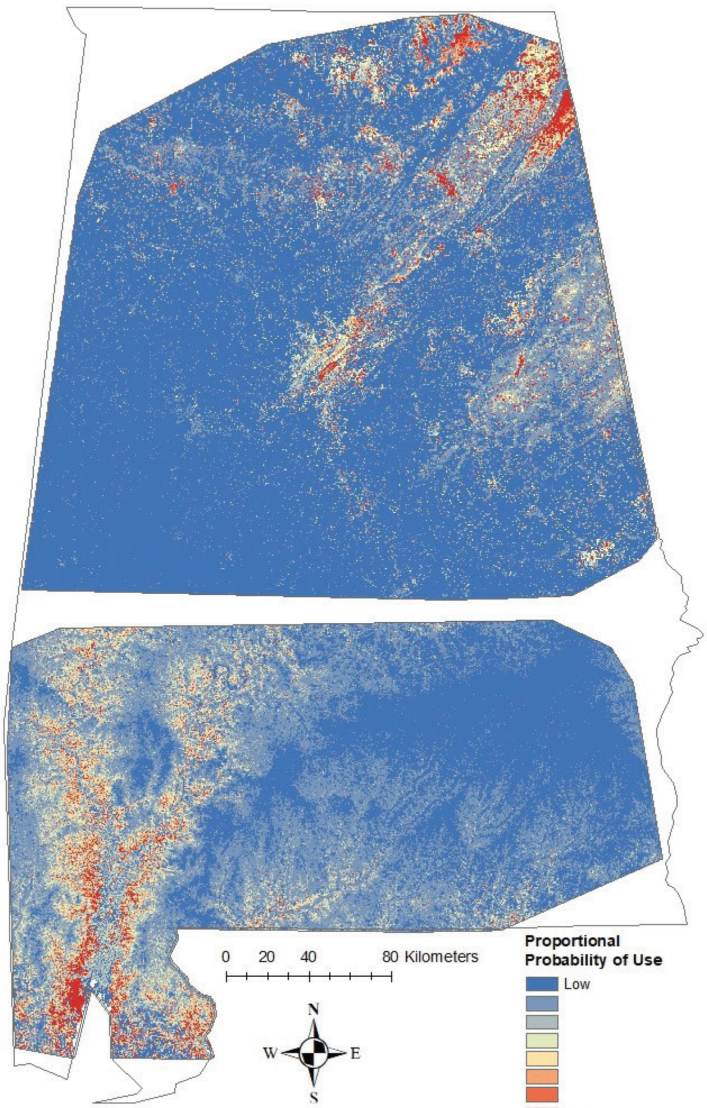

Figure 2. Black bear corridor suitability model (RSF) for northern Alabama and southern Alabama. Low (blue) to high (red) proportional probability of use.

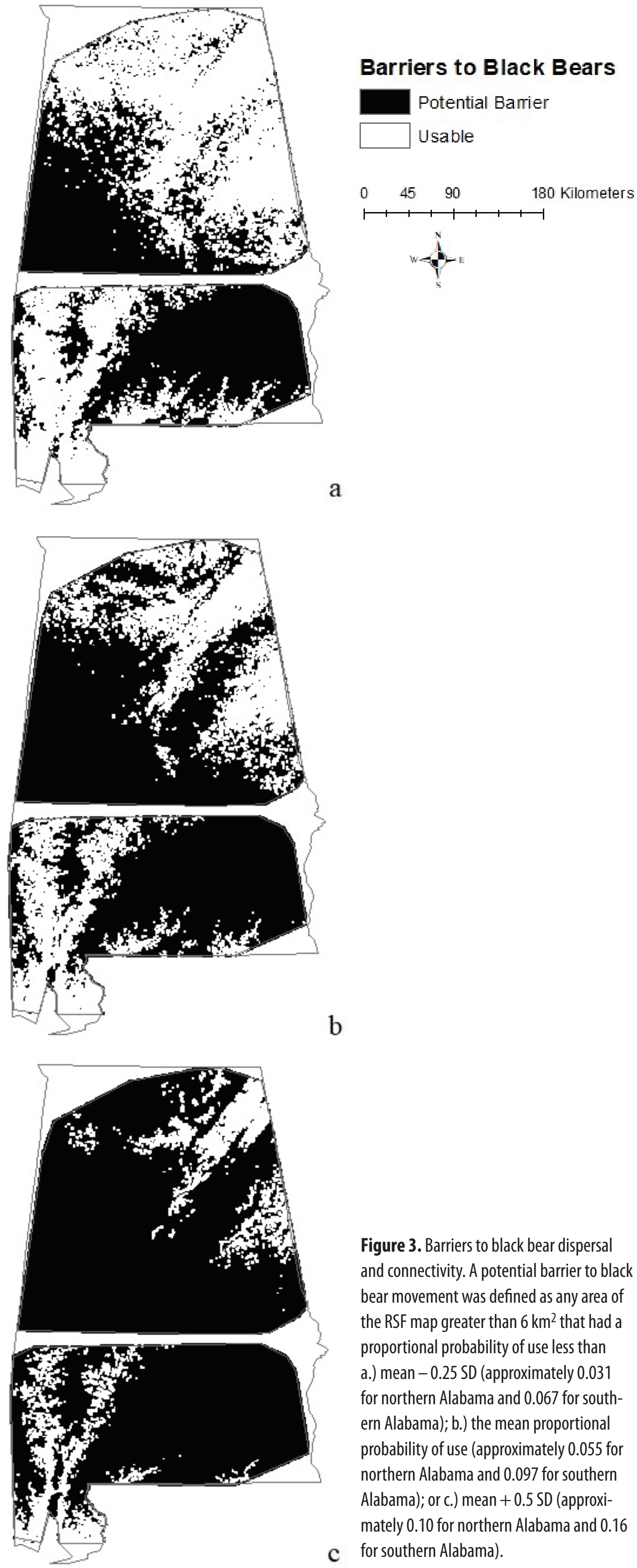

Figure 3. Barriers to black bear dispersal and connectivity. A potential barrier to black bear movement was defined as any area of the RSF map greater than 6 km^2 that had a proportional probability of use less than a.) mean – 0.25 SD (approximately 0.031 for northern Alabama and 0.067 for southern Alabama); b.) the mean proportional probability of use (approximately 0.055 for northern Alabama and 0.097 for southern Alabama); or c.) mean + 0.5 SD (approximately 0.10 for northern Alabama and 0.16 for southern Alabama).

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).

Differences in available land cover types existed 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. 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 limited human presence. As defined by Homer et al. (2016) in the NLCD, evergreen forests are "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."

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 other kinds of 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.

Acknowledgments

We are grateful to the Alabama Department of Conservation and Natural Resources, Alabama Natural Heritage Program, and the Alabama Wildlife Federation for compiling sightings and reports data, and especially Traci Wood for providing the database for our analyses. Funding for this project was provided, in part, by the Alabama Department of Conservation and Natural Resources Division of Wildlife and Freshwater Fisheries.

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