

MOVEMENT, GENETIC STRUCTURE, AND SPACE USE OF CENTRAL
GEORGIA BLACK BEARS (*URSUS AMERICANUS*) AS INFLUENCED BY A
HIGHWAY CORRIDOR

by

MICHAEL JAMES HOOKER

(Under the Direction of Michael J. Chamberlain)

ABSTRACT

Georgia, USA has 3 American black bear populations. The least abundant of these is the Central Georgia Bear Population. Relatively low abundance, isolation from neighboring bear populations, and a proposed plan to widen a highway which bisects the range of the Central Georgia Bear Population are cause for concern. I used movement and genetic data to address these issues. I used GPS-tracking and dynamic Brownian bridge analysis to identify black bear highway crossings in Central Georgia and recommend placement for wildlife underpasses. I used microsatellite genotypes of Georgia black bears to determine the level of genetic separation among Georgia's bear populations. Results suggest a high degree of separation and low genetic diversity within the Central Georgia Bear Population. Lastly, I used GPS-tracking data to develop a step selection function of bear movement across Georgia's landscape and predict the likelihood of bears migrating to the Central Georgia Bear Population.

INDEX WORDS: American black bear, connectivity, dynamic Brownian bridge, genetic diversity, Georgia, microsatellite, step selection function, wildlife underpasses, *Ursus americanus*

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DEDICATION

I dedicate this dissertation to all the Hookers who encouraged me throughout this endeavor.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

The American black bear (*Ursus americanus*) is the most common and widely distributed North American member of the family Ursidae (Pelton 2003). However, the current range of the black bear represents only approximately 62% of its historic range (Pelton and van Manen 1994, Scheick and McCown 2014). The conservation status and densities of black bear populations vary widely across this range. In some areas of North America, black bears are abundant, sustain high levels of harvest and are sometimes considered a pest. Conversely, other regions of North America, including the southeastern United States (hereafter Southeast) maintain only small, isolated, remnant populations of black bears or have experienced black bear extirpation (Pelton 2003).

Bartram (1791) described bears, qualitatively, at several locales in the Southeast, as being ‘numerous enough’ (p. 46) and ‘yet too numerous’ (p. 282). Roughly 2 centuries later, Maehr (1984) estimated that bears inhabited only 10% of their historic range in the Southeast due to habitat loss and historic overexploitation. However, due to conservation efforts, changes in bear harvest regulations, and protection and/or restoration of bear habitat, many states in the eastern United States have experienced growing bear populations and expansion of bear distribution in recent times (Pelton 2001).

Wooding et al. (1994) reported at least 13 black bear populations within the Coastal Plain geophysical region of the Southeast. Combined, these populations represent 3 of the 16 black

bear subspecies reported by Hall (1981): the eastern black bear (*U. a. americanus*), the Louisiana black bear (*U. a. luteolus*), and the Florida black bear (*U. a. floridanus*). The Florida black bear and the Louisiana black bear are endemic to the Coastal Plain (Wooding et al. 1994).

Within Georgia (GA) there are 3 black bear populations; the North GA Bear Population (NGBP), the South GA Bear Population (SGBP) and the Central GA Bear Population [CGBP, (Carlock 1999)]. The least abundant and most geographically isolated of these populations is the CGBP. Jenkins (1953) stated that there were only roughly 650 bears in all of Georgia with ≤ 40 bears in the CGBP. About 30 years later, Grahl (1985) reported a population estimate of 64 for the CGBP. Sanderlin (2009) used a web-design, noninvasive capture-mark-recapture (CMR) to derive annual, seasonal estimates ranging from 106 to 213. More recently, Hooker et al. (2015) and Ashley (2016) used spatially explicit, capture-recapture methods to estimate density over 2 different extents and derived abundance estimates of ~ 240 and ~ 430 bears, respectively, in the CGBP.

In addition to relatively low abundance, a number of interrelated factors have potential to negatively impact conservation of the CGBP and are, therefore, of special interest to bear managers. Sanderlin (2009) documented that the CGBP had low within-population genetic diversity. The full extent of the level of genetic drift between the 3 GA bear populations is, however, unknown. Likewise, it is unclear if any genetic (or demographic) exchange occurs between the CGBP and either of the other GA bear populations. Populations are subject to combinations of deterministic (e.g., habitat loss and overexploitation) and stochastic (e.g., demographic and genetic) factors (Shaffer 1981). Small populations, relative to larger populations, tend to have decreased rates of persistence due to stochastic demographic processes (MacArthur and Wilson 1967, Shaffer 1987, Lande 1993). Smaller populations are also more

prone to negative impacts of stochastic genetic processes such as fixation of deleterious alleles, genetic drift, and inbreeding depression (Mills 2012).

Additionally, the Georgia Department of Natural Resources (GDNR) restructured harvest regulations governing bear hunting in central GA. From 1984 through 2010, the CGBP experienced a mean annual harvest of ~1 bear/year, restricted to public lands only (B. Bond, Georgia Department of Natural Resources, unpublished data). In 2011 harvest was allowed to occur on private lands in several counties within the CGBP and 34 [17 male (M): 17 female (F)] bears were harvested that year. Since 2011, CGBP bear harvest has averaged ~8 bears/year and most years is > 50% female. From a conservation standpoint, the interpretation of this increased CGBP harvest is quite different depending on whether or not the CGBP is demographically and genetically isolated or is functionally a part of a meta-population with neighboring bear populations [e.g., the NGBP and SGBP; (Hanski 2005)].

Finally, the widening of Georgia State Route 96 (SR 96), a 2-lane highway which bisects the area inhabited by the CGBP, has potential to impact the CGBP. The U.S. Department of Transportation's Federal Highway Administration (FHWA) and the Georgia Department of Transportation (GDOT) are implementing a plan to widen a 24 km-long stretch of SR 96 between Bonaire, GA and the intersection of SR 96 and U. S. Interstate 16 (I-16). The proposed widening is intended to facilitate traffic flow between I-16 and U.S. Interstate 75 (I-75). The section of SR 96 being widened bisects an area of forest land associated with the Ocmulgee River drainage and in doing so, bisects the CGBP. The planned widening project calls for the inclusion of 7 wildlife underpasses. The underpasses are intended to minimize occurrences of wildlife on the highway surface, while allowing local wildlife the ability to cross the highway

corridor. It is unknown if SR 96, in its current form, is having an impact on black bear movement and bear population genetic structure.

OBJECTIVES

My objectives were to monitor black bear movement, space use, habitat selection and population genetic structure near SR 96 during the pre-construction and construction phase of the widening project. Likewise, I assessed genetic differentiation among all 3 Georgia bear populations and predicted the likelihood of interchange among populations. The anticipated research results will be a valuable baseline with which post-construction monitoring can be compared and offer wildlife managers insight regarding conservation of the CGBP.

DISSERTATION FORMAT

This dissertation is presented in manuscript format. Chapter 1 is introductory material regarding the American black bear in the Southeast; more specifically, the bear populations of Georgia and management concerns regarding bears in Central Georgia. Chapter 2 quantifies bear crossings of SR 96 and evaluates habitat characteristics associated with crossing locations. I used fine-scale temporal GPS data and a dynamic Brownian Bridge Movement Model [dBBMM; (Kranstauber et al. 2012)] to determine crossing locations and assess habitat characteristics associated with crossings. General Linear Mixed Models (GLMM) compared habitat characteristics of crossing locations to random locations along SR 96. Chapter 3 evaluates population genetic structure among the 3 Georgia bear populations and within the CGBP relative to SR 96. Bear hair, tissue, and blood samples were used to develop multi-locus genotypes identifying individual bears. These genotypes were analyzed using factorial correspondence

analysis [FCA; (Benzecri 1992)] and Bayesian population clustering (Pritchard et al. 2000). I determined genetic metrics for each population and a measure of genetic distance among the 3 GA bear populations. Chapter 4 addresses connectivity between the CGBP and the other bear populations in GA. I used GPS movement data and a step selection function to model bear movement across the landscape. I then evaluated the likelihood of bears moving from NGBP and SGBP into the CGBP. I determined frequencies at which these events are likely to occur and highlight potential routes bears may use to immigrate to the CGBP. Chapter 5 discusses conclusions drawn from this study and management implications. Chapters 2–4 will be submitted to peer-reviewed journals for publication.

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CHAPTER 2

IDENTIFYING AMERICAN BLACK BEAR (*URSUS AMERICANUS*) HIGHWAY

CROSSING LOCATIONS IN CENTRAL GEORGIA, USA

Hooker, M. J., K. V. Miller, R. J. Warren, and M. J. Chamberlain. To be submitted to Journal of Wildlife Management.

ABSTRACT

The Central Georgia Bear Population (CGBP), the smallest of Georgia's 3 populations of American black bear (*Ursus americanus*), is of special concern due to its size and potential isolation from other bear populations. Plans to widen Georgia State Route (SR) 96, which bisects the CGBP, has potential to negatively impact the population. Highway underpasses are being planned to mitigate these impacts. During 2012–2014, we used global-positioning-system (GPS)-tracking of 63 bears and remote, infrared trail cameras to document bear crossings along SR 96. We evaluated landscape characteristics associated with 212 (210 by 11 GPS-collared bears plus 2 photographs) bear crossings using a resource selection function approach and generalized linear mixed-models. Closer distances between State Route 96 and forest edge were positively associated with bear crossings. Bear crossings were generally concentrated with 169 (79.7%) crossings generated by 7 bears occurring within a 2.5-km section of SR 96. We recommend placement of an underpass within this section. Likewise, we recommend that vegetation management be used to connect underpass openings to forest edges along the highway rights-of-way.

INDEX WORDS: American black bear, dynamic Brownian bridge movement model, GPS-tracking, highway crossing, *Ursus americanus*, wildlife underpass

INTRODUCTION

The CGBP black bear population (Fig. 2.1) has an estimated 430 animals inhabiting about 1,127 km² of forested land along the Ocmulgee River, roughly 150 km southeast of Atlanta (Ashley 2016). This area is almost completely surrounded by human development and fragmented agricultural land. Relatively low abundance and potential isolation from other bear populations make conservation of the CGBP of special concern. The CGBP is separated from the other Georgia bear populations by distances of ~150 km (Hooker et al. 2015), resulting in little dispersal and poor connectivity among the populations. Between the CGBP and the North Georgia Bear Population is the city of Atlanta, characterized by considerable urban sprawl and several interstate highways. Extensive tracts of agricultural properties with sparse forest cover lie between the CGBP and the bear population in South Georgia. Although bears are occasionally reported in areas between the 3 populations, the level of demographic and genetic separation among these populations is uncertain.

Human encroachment in the form of roads, rights-of-way, railroads, and pipelines have potential to influence bear behavior (Mattson et al. 1987, Brody and Pelton 1989, Beringer et al. 1990, Kaczensky et al. 2003, McCown et al. 2004), and these anthropogenic features can fragment and degrade habitat for various species (Andrews 1990, Jackson 2000, Primack 2006, Laurance et al. 2009, Latham et al 2011). Roads, in particular, impact wildlife populations through direct loss of habitat, increased mortality, and potential limitation of access to resources (Trombulak and Frissell 2000, Jaeger et al. 2005). Likewise, roads can contribute to fragmentation of populations both demographically (Trombulak and Frissell 2000, Hostetler et al. 2009) and genetically (Thompson 2003, Thompson et al. 2005, Riley et al. 2006), resulting in smaller, more vulnerable subpopulations (Jaeger et al. 2005, Beckmann and Hilty 2010).

Populations of species maintaining large home ranges and exhibiting wide-ranging movement patterns, such as many carnivores, can be especially affected by highways [e.g., Florida panther (*Puma concolor coryi*; Maehr et al. 1991, Foster and Humphrey 1995), bobcats (*Lynx rufus*; Litvaitis et al. 2015, Poessel et al. 2014), ocelot (*Leopardus pardalis*; Haines et al. 2005), American black bear (Brody and Pelton 1989, Wooding and Maddrey 1994), grizzly bears (*Ursus arctos*; Waller & Servheen 2005), and wolves (*Canis lupus*; Mech 1989)].

The United States contains an estimated 6.7 million km of roads (Federal Highway Administration 2014). Furthermore, it is estimated that the ecology of approximately one fifth of the country's total area is affected by roads (Forman 2000, Cerulean 2002). In addition to wildlife conservation issues, the interaction of wildlife and highways has a human cost in the form of vehicle damage, personal injury, and in extreme cases human fatality (Conover et al. 1995, Groot et al. 1996, Romin and Bissonette 1996.)

Since the 1970s, wildlife managers and road engineers have increased efforts to develop methods to mitigate negative effects of roads on wildlife and reduce (or eliminate) the human cost of wildlife-vehicle collisions (Kroll 2015). Numerous methods have been used to reduce wildlife-vehicle collisions, including the use of underpasses to allow wildlife to pass beneath the road.

Bisecting the area inhabited by the CGBP is SR 96, a 2-lane highway with a mean daily traffic load of >8,000 vehicles, 12% of which are large commercial trucks (Georgia's State Traffic and Report Statistics 2012). To accommodate increasing traffic loads, the Georgia Department of Transportation (GDOT) is widening SR 96 into a 4-lane divided highway, and is mandated to investigate potential ecological impacts. Because bear-vehicle collisions occur annually on SR 96, the widening project plan includes installation of underpasses and roadside

fencing to reduce wildlife-vehicle collisions while allowing wildlife movement across the highway. At the request of the GDOT, we evaluated incidences and locations of bear crossings of SR 96 prior to the highway widening project. Our objectives were to quantify bear crossings of SR 96, evaluate habitat and landscape features associated with crossing locations, and quantify incidences of bear roadkill on SR 96 and other roads within the geographic extent of the CGBP.

STUDY AREA

We conducted research along a 27-km section of SR 96, and adjacent bear habitat, within Houston and Twiggs counties, Georgia (Fig. 2.2). Predominant forest types adjacent to this section of SR 96 were bottomland hardwood forests within the Ocmulgee River flood plain and planted pine (*Pinus* spp.), natural pine, and mixed pine-hardwood in the uplands. Common overstory tree species included loblolly pine (*Pinus taeda*), red and white oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), water tupelo (*Nyssa aquatica*), and bald cypress (*Taxodium distichum*). Clear-cutting, tree thinning, and prescribed burning of the understory were common forestry practices in the study area.

Most forested land in the area was managed for seasonal, recreational hunting. Common large and medium-sized mammals included white-tailed deer (*Odocoileus virginianus*), feral pigs (*Sus scrofa*), black bear (*Ursus americanus*), coyote (*Canis latrans*), grey fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*) opossum (*Didelphis virginianus*) and armadillo (*Dasypus novemcinctus*).

The Ocmulgee River flowed through the study site from north to south and was a defining geographical feature. Nearby human population centers included Macon (pop. 91,234),

Warner Robins (pop. 72,531), Bonaire (pop. 13,999), Cochran (pop. 5150), and Hawkinsville (pop. 4589, U.S. Census Bureau 2010). Much land west of the study area was dominated by human development, whereas land to the south and east was primarily agricultural land. Major crops included cotton (*Gossypium hirsutum*), corn (*Zea* spp.), peanut (*Arachis hypogaea*), sorghum (*Sorghum* spp.) and other grain crops.

East of Bonaire, SR 96 crossed the flood plain of the Ocmulgee River, and the span of highway within the flood plain was on a levee approximately 6 m high. SR 96 was bridged over the Ocmulgee River and 4 ephemeral drainages associated with the river (Fig. 2.3). In contrast, SR 96 east of the Ocmulgee River flood plain was mostly at the same level as the surrounding ground and there were no bridges within this section of highway. There were numerous culverts of various design along SR 96, but only 3 were large enough to allow bears to pass beneath the highway (Fig. 2.4).

Between Bonaire and Tartersville, land adjacent to SR 96 was mostly forested. East of Tartersville, SR 96 was adjoined by a mix of woodlots and agricultural fields. Paralleling SR 96 directly to the north, between Bonaire and Tartersville, was an electric-power transmission line devoid of trees, and vegetation under the line was maintained at a height of <1m. The western half of the right-of-way was approximately 140 m wide whereas the eastern half was 55 m.

METHODS

GPS Tracking

During summers 2012–2014, we captured bears with modified Aldrich foot snares (Johnson and Pelton 1980) using soured corn and artificial flavoring (Mother Murphy's, Greensboro, North Carolina, USA) to attract bears to the snares. We focused our trapping efforts within the SR 96 corridor (i.e., within ~2 km either side of the highway) and along the full 27 km

of SR 96 we defined as our study area. We anesthetized captured bears with Telazol[®] (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) or large animal xylazine (100mg/ml) combined with Telazol[®] (XZT). We reversed bears anesthetized with XZT using atipamazol hydrochloride (Antisedan[®], Orion Pharma, Orion Corporation, Espoo, Finland) and diazepam approximately 45 minutes after initial anesthesia. We monitored rectal temperature throughout the anesthesia event, and bears exhibiting elevated rectal temperatures were cooled by having cold water poured on their extremities. We monitored pulse and blood oxygen saturation levels using pulse-oximeters, and bears with blood oxygen levels below ~90% received supplemental oxygen via nasal cannula.

We ear-tagged all captured bears with paired, numbered button tags (All American[®], Y-Tex Corporation, Cody, Wyoming, USA), and tattooed the inside of the right upper lip with a number corresponding to the ear-tag number. We implanted a passive integrated transponder (PIT) sub-cutaneously along the mid-line of the back between the scapulae. We recorded sex, weight, and a series of standard morphometric measurements, and extracted the first upper premolar (UPM1) using an apical 301 dental elevator. Collected teeth were used for cementum-annuli aging (Willey 1974). Our capture and handling methods were approved by the University of Georgia Institutional Animal Care and Use Committee (Protocol Number A2011 10-004-A1).

We collared bears with WildCell[®] (Lotek Wireless Inc., Newmarket, Ontario, Canada) Global Positioning System (GPS)/General System for Mobile (GSM) collars (hereafter GPS-collar). For bears weighing ~45.4 kg or greater, we used WildCell[®] MG series collars, whereas we used WildCell[®] SG collars on bears in the ~22.7–45.4 kg range. In 2012, all collars were equipped with a timed, mechanized release programmed to release 52 weeks after activation, and

a leather break-away (Garshelis and McLaughlin. 1998). After 2012, collars had only a leather break-away.

We programmed each collar to collect a location every 20 minutes, and collars also had virtual fence technology. When the collar (i.e., a collared bear) was within the area outlined by the virtual fence, the GPS location acquisition rate increased to one location every 5 minutes. Upon leaving the virtually fenced area, the collar reverted to the 20-minute location acquisition rate. The virtually fenced area was ~250 m either side of the SR 96 centerline between the intersection of SR 96 and Houston Lake Road west of Bonaire, GA and the intersection of SR 96 and GA 358, south of Jefferson, GA (Fig. 2.5). All location data were transmitted to a desk-top base station via GSM and stored.

Collar battery life is a function of many variables, including location acquisition rate. A more frequent acquisition rate depletes batteries faster and shortens functional longevity. Because we were interested in collecting fine temporal scale data when bears were near SR 96, and because bears become less active in winter, we opted to only collect fine temporal scale data during spring, summer and fall months (May–November).

Camera Surveys

During summer and fall 2012 and 2014, we used infrared trail cameras (Bushnell®, 5.0 Megapixel Trophy Cam, Overland Park, Missouri, USA) to monitor wildlife activity under 4 of 5 SR 96 bridges and at one end of culverts large enough to allow passage of a bear. Persistent flooding during summer and fall 2013 precluded camera surveys. We excluded the first bridge east of the Ocmulgee River (i.e., Bridge 4) and the west end of the Ocmulgee River Bridge (i.e., Bridge 3) from the survey due to high human activity in these areas. We placed cameras in

series, facing one to the next, so that the full span of ground under a given bridge was within camera view (Fig. 2.6).

We placed cameras approximately 1 m above the ground and spaced them at the effective distance of the camera motion sensitive trigger (~7.5m). We painted the first bridge pile in front of each camera with a number corresponding to the camera identification number, and located painted numbers so they were visible in photographs. If a pile was not visible, such was the case at culverts, then we staked a numbered sign in front of the camera. We programmed each camera to take 3 photographs at 1-second intervals each time the camera was triggered. Following the third photograph in a series, cameras paused for 1 min before being capable of being triggered again. All photographs contained a date and time stamp.

Roadkill Monitoring

Throughout the study, we documented incidences of bears killed along roads throughout the CGBP. We investigated reports of road-killed bears provided by the Georgia Department of Natural Resources, local law enforcement agencies, and the general public. In each case, we attempted to locate the site of the road kill and record it with a handheld GPS unit. If a bear carcass was located, we collected it, examined it for markings (i.e., ear tags, tattoos, and PIT-tags), documented biological information (e.g., sex and body condition), and collected a premolar for cementum-annuli aging, and hair and tissue samples for genetic analysis.

Analysis

We screened GPS data using a multi-step approach. Initially, we plotted each bear's data and removed locations that were outside the study area or otherwise nonsensical. We then removed locations classified as 2 dimensional (2D) with dilution of precision values (PDOP) >5 (Lewis et al. 2007). Likewise, GPS location data have inherent error from a number of sources

(D'Eon et al. 2002, D'Eon and Delparte 2005, Frair et al. 2004), so we evaluated location error by placing GPS collars in the field and collecting a minimum of 24 hours of locations while collars remained stationary. We staked test collars in place approximately 0.5 m high with the GPS receiving unit oriented skyward. We placed collars throughout the study area in varied habitat types (e.g., planted pine forest, bottomland hardwood forest, open field, and standing corn crops) and along various topographical features (i.e., ridgelines and drainage bottoms). At each test collar, we used a handheld GPS unit to acquire ≥ 100 GPS locations and considered the mean of these locations the known location of the test collar. We then estimated collar error by comparing location data collected by each collar to each respective collar's known location.

We visually inspected location data for each bear to identify crossings of SR 96. For each crossing of SR 96, we selected a 24-hour subset of the bear's movement path temporally centered on the crossing event (i.e., 12 hours prior to crossing and 12 hours after crossing). Because some bears had a tendency to spend time directly adjacent to SR 96, collar error made it appear that the bear had crossed the road. Therefore we considered a bear to have crossed SR 96 only if there were 2 or more locations and a demonstrated movement path immediately after a crossing event. We used a dynamic Brownian Bridge Movement Model (dBBMM) in R to create a 95% utilization distribution (UD) for these 24-hour movement paths (R Core Team 2014; Kranstauber et al. 2012). We intersected the resulting probability distributions with the centerline of SR 96 using ArcMap[®] 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA) resulting in a segment of SR 96 within which the crossing most likely occurred. We then used Geospatial Modeling Environment (GME, Beyer 2015) to generate a random point along the centerline of SR 96 within each of the segments. We pooled locations at

which bears were photographed crossing under bridges with the crossing locations from within the UDs.

We used a resource selection function (RSF) approach to evaluate habitat characteristics associated with crossing locations (Manly et al. 2002). We used GME to generate random points along SR 96 within our study area so that each crossing point was paired with a random point. We analyzed habitat selection as a binomial response variable (1=crossing, 0=random location) yielding the proportional probability of use of locations (Boyce et al. 2002).

To describe landscape characteristics associated with crossing and random locations, we used ArcMap[®] 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA) to assign landscape variable values to both locations. We selected variables based on their potential to influence bear crossings of SR 96, and their potential to be of use to GDOT in placing and designing underpasses. First, we measured the distance from each location to the closest forest edge (DIST-FE), excluding single trees and narrow tree lines (i.e., rows of trees multiple trees in length but only the width of single trees). We also measured distance from each location to agricultural fields (DIST-AF), and to the intersection of SR 96 and major drainages (DIST-DI). We also categorized each location on whether it was within either bottomland or upland habitat (BU). We tested for correlation among continuous variables using Pearson's correlation coefficient.

We developed a candidate set of RSF models and fit models to our data using a General Linear Mixed Model (GLMM). We modeled individual bears as a random effect to account for inherent differences among individual bears (e.g., age and experience crossing roads). We then ranked candidate models using second-order Akaike Information Criterion (AIC_c , Burnham and Anderson 2002), and assessed model prediction using k-fold cross validation (Boyce et al. 2002).

RESULTS

We GPS-tracked 63 bears (33 M: 30 F) for a total of 8,965 bear-tracking days.

Combined, these bears exhibited use patterns all along the 27-km section of SR 96 we studied. Qualitatively, bear locations demonstrated that home ranges and movement patterns were clearly influenced by SR 96 (Fig. 2.7). From spring 2012 through winter 2014–2015, 38 bears (60.3%, 17 M: 21 F) were within the virtual fence (i.e., within 250 m of SR 96) long enough to derive at least one GPS location. However, only 11 GPS-collared bears (7 M: 4 F) crossed SR 96 210 times (Table 2.1) and 8 bears crossed 4 or fewer times each. Two males (Bears 105 and 140) accounted for 182 (86.7%) of the 210 total crossings. Of bears that crossed SR 96 and were tracked for multiple years ($n=3$, 27.3 %, 1 M: 2 F), all crossed the highway in some years but not others. For instance, Bear 117 maintained a home range adjacent to SR 96 and crossed the highway 4 times during fall 2012, but didn't cross again despite being monitored until the end of summer 2014 (Fig. 2.8).

Only 2 bears were photographed crossing beneath SR 96 bridges. A male bear was photographed beneath Bridge 5 in October 2012, and a female bear was photographed beneath Bridge 1 in October 2014. There was only one case of a bear being photographed at a culvert. A bear of undetermined sex was photographed approaching the mouth of Culvert 1 in 2012. It did not appear that the bear entered the culvert and subsequent inspection of the substrate within the culvert revealed no bear tracks.

Bear crossings of SR 96 were concentrated in the central portion of the roadway. The highest concentration, both in number of crossings and number of different bears that crossed, occurred near Tarversville and the intersection of SR 96 and SR 87 (Fig. 2.9). The highway segments identified by intersecting the dBBMM 95% UD's with SR 96, (i.e., segments within

which crossings by GPS marked bears most likely occurred) ranged from 10.0 m to 604.4 m, with a median of 92.7 m (Fig. 2.10).

We observed only moderate correlation between 2 of 3 continuous, fixed variables so we retained all 3 variables (Table 2.2). The global model was the most parsimonious and carried most model weight ($w_i > 0.99$, Table 2.3). Cross validation yielded a delta of 0.80, suggesting that the global model had suitable power to distinguish between crossing and random locations. All of the fixed-effect parameter estimates were significant, with 95% confidence intervals not bounding zero. We found that bears were more likely to cross SR 96 in upland habitat types (Table 2.4). Likewise, we noted an increase in bear crossings on sections of SR 96 that were closer to forest edge, agriculture fields, and intersections of drainages. We found that distance to forest edge was the most influential parameter in the model. Scaled odds ratio for distance to forest edge (0.68) indicated that the occurrence of bear crossings increased 32.2% for every 25 m closer SR 96 was to a forest edge.

During 2012–2014, we investigated 23 reports of bears struck by vehicles across our entire study area. Seven bears (5 M: 2 F), 5 bears (3 M: 2 F), and 8 bears (7 M: 1 F) were struck and killed in 2012, 2013, and 2014, respectively. In addition, in each year we documented one case where a bear was struck but no carcass was located. In 2 of these cases, we were able to use GPS location data or microsatellite genotyping of hair collected from a vehicle to identify the bears involved, and 5 (21.7%) cases involved bears we had previously live-captured. Only 5 (21.7%, 3 M: 1 F: 1 unk.) collisions occurred on SR 96. The remainder took place on several other highways in central Georgia: 8 (34.8%, 5 M: 3 F) on SR 87, 4 (17.4%, 4 M) on SR 247/247spur, 4 (17.4%, 3 M: 1 F) on I-16, one (0.04%, 1 M) at the Interstate 75/475 interchange south of Macon, GA, and one (0.04%, 1 F) on Moody Road within Bonaire, GA.

DISCUSSION

Our findings indicate that bears within the SR 96 corridor are affected by the highway. Bear home ranges adjacent to SR 96 were often bounded by the forest edge at highway verge or the forest edge adjacent to the powerline that parallels SR 96. Notably, most bears we tracked near SR 96 did not cross the highway, and those that did cross only crossed sporadically. Of the bears we documented crossing SR 96, most crossed few times and of those that we tracked for multiple years, all crossed in some years but not others. Both bears we documented crossing SR 96 the most (i.e., male Bear 105 and male Bear 140) were struck and killed by vehicles after we were no longer tracking them. Bear 105 was killed on SR 96, whereas Bear 140 was struck on a highway intersecting SR 96.

Bear crossings of SR 96 were concentrated within a 2.5-km section (i.e., 9.3% of the 27 km we monitored) that contained 167 of 212 (78.8%) crossings made by 7 of 11 bears that crossed (63.6%, 4 M: 3 F). The 3 females that crossed within this section did so after traveling distances of 3–5 km away from their apparent home ranges. This 2.5-km section of SR 96 also contained the locations of 3 of 5 (60.0%) vehicle-bear collisions we investigated, and has historically been the location of vehicle-bear collisions (B. Bond, Georgia Department of Natural Resources, unpublished data).

Of the 27-km study area along SR 96, 4 km was in bottomland forest, yet this section only contained 3 bear crossings; each crossing was by a different bear (1 M: 2 F). Each bear crossed SR 96 under a different bridge and we documented no bears crossing the SR 96 road surface within bottomland forest habitats. Most of the 4-km section of SR 96 that crosses the bottomlands (i.e., the Ocmulgee River flood plain) is upon a steep-sided levee, overgrown with thick stands of species such as greenbrier (*Smilax* spp.), and cane (*Arundinaria tecta*), which

forms a barrier between the road-side forest and SR 96. Along the base of the levee, especially near SR 96 bridges, we observed game trails that likely direct animal movement toward the underpasses as opposed to across the surface of the highway. Our camera surveys under the SR 96 bridges revealed extensive use of these trails and the underpasses by deer and feral pigs, but we only detected the 3 bear crossings. This diminished number of bear crossings, relative to number of bear crossings we observed in the uplands, is likely related to the fact that we observed little use of bottomlands throughout Central Georgia by our GPS-collared bears. Bottomland habitats in our study area often flood during winter and spring, which may in part explain the lack of use. Furthermore, many foods used by bears in summer and fall (coinciding with our monitoring of bear crossings of SR 96) are found primarily in upland habitats [e.g., blackberry and dewberry (*Rubus* spp.), agricultural crops].

Although several landscape variables influenced where bears crossed SR 96, the most influential variable was distance between the highway and forest edge (i.e., cover). Previous studies have noted similar relationships for a number of species including grizzly bear (*Ursus arctos*) and elk (*Cervus elaphus*; Clevenger and Waltho 2005, Waller and Servheen 2005). Lewis et al. (2011) suggested that shorter distance to forest cover was positively associated with black bear road crossings. However, they noted that the relationship between road crossings and distance to forest was not as strong as it might be in landscapes where high variability in distance between forest edge and roads occurred, as such variability didn't exist in their study area (Lewis et al. 2011). Conversely, we observed considerable variability in distances between forest edge and road throughout our study area.

Black bears, although highly adaptable, are ultimately a forest species and prefer areas of forest and thick understory (Pelton 2003). While black bears use more open habitats (e.g.,

agriculture fields and clear-cuts), their use of these features is often restricted to edges near forest cover (Lindzey and Meslow 1977). Black bears are adapted to climbing and from a young age will climb trees in response to threats, and to feed and loaf (Herrero 1972). We suspect this adaptation to forest cover may explain the correlation we found between bear crossing locations and distance to forest cover. When near or attempting to cross SR 96, bears may experience stress as a result of the unpredictability of traffic volumes and speeds, human presence, road noise, and vehicle lighting. When encountering these stressors, bears likely prefer to be in or near forest cover.

Although SR 96 influences bear movements within the CGBP, and bears are periodically struck and killed, SR 96 does not create an impermeable barrier to bear movement. We documented highway crossings by 29% of bears that maintained home ranges adjacent to, or overlapping, the highway corridor. Likewise, our findings suggest that the vehicle collisions with bears on SR 96 do not represent an excessive source of mortality for the CGBP, at least when compared to other highways in Central Georgia and to other sources of mortality such as harvest (B. Bond, Georgia Department of Natural Resources, unpublished data). During 2012–2014, we documented 20 bears being killed by vehicles in Central Georgia with only 4 (20%) being killed on SR 96.

From the standpoint of gene flow, the principle of >10 migrants per generation (Vucetich and Waite 2000) or the even more conservative estimate of one migrant per generation (Mills and Allendorf 1996), suggests it is unlikely that SR 96 (prior to widening) is a substantial barrier to gene flow within the CGBP. Indeed, van Manen et al. (2012) suggested that crossing rates similar to those we observed were sufficient to maintain genetic connectivity across a newly widened highway in North Carolina. However, they cautioned that their research was conducted

immediately after highway widening occurred. Because bears are long-lived with slow reproductive rates, their work may have been conducted too soon following highway construction to detect genetic effects influenced by the highway corridor. Although we documented male and female bears crossing SR 96, future work should quantify whether these periodic crossings actually equate to gene flow within the CGBP.

MANAGEMENT IMPLICATIONS

Based on our results, we recommend the elimination of 2 of the proposed bridges on SR 96 because these locations were in areas that either received very little use by our GPS-collared bears or had less suitable habitat features for bears. Furthermore, we recommend that GDOT add a new bridge to the proposed project in a 2.5-km section of SR 96 where we noted suitable bear habitat and a high incidence of bear-crossing activity (Fig. 2.11). We also recommend eliminating the proposed fencing design alongside SR 96 because it was not likely to decrease the potential of bears accessing the roadway. Furthermore, the proposed fence design had potential to allow bears to become entrapped within the highway right-of-way, which might increase the chance of a bear-vehicle collision if a bear was unable to easily escape the roadway because of the fencing. Rather than fencing, we recommend GDOT use vegetation management to ensure connectivity between the forest edge and the openings of all current and future SR 96 underpasses. We also recommend that GDOT ensures the highway verge is mowed and free of forest between underpasses, thus encouraging bears to travel the forest edge toward underpasses as opposed to crossing on the highway surface. GDOT adopted all 3 of these recommendations and saved \$1.18 million on the future construction costs for this project by removal of the one of the bridges, fencing, and gates (personal communication, Design Group Manager, Georgia Department of Transportation).

Future research should focus on monitoring potential changes to bear crossing rates of SR 96 after completion of the widening project. If bears fail to use highway underpasses, then the widened highway could exacerbate demographic separation and frustrate movements of bears maintaining home ranges along SR 96. Conversely, increased movements across the highway corridor associated with highway underpasses could help prevent genetic and demographic separation of the CGBP, thereby improving connectivity throughout the population.

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Table 2.1. Black bear crossings of Georgia State Route 96 documented via GPS-tracking and camera surveys, Central Georgia, USA 2012–2014.

Bear	Sex	Dates Tracked/ Date Photographed	Days Tracked	Crossings
105	M	11 June 2012–27 February 2013, 7 June 2014–27 November 2014	434	68
107	M	17 June 2012–13 November 2012	149	2
112	F	3 July 2012–11 March 2013, 8 May 2013–24 November 2013	451	1
116	F	25 July 2012–12 November 2012	110	9
117	F	3 August 2012–3 March 2013, 8 May 2013–12 November 2013, 21 March 2014–10 August 2014	542	4
119	M	19 August 2012–10 November 2012	83	2
140	M	27 May 2013–30 September 2013	126	114
165	M	3 June 2014–2 November 2014	152	2
166	M	5 May 2014–26 September 2014	113	4
169	F	14 June 2014–18 November 2014	157	2
181	M	12 July 2014–10 November 2014	121	2
P12 ¹	M	4 October 2012	-	1
P14 ¹	F	4 October 2014	-	1

¹ Bears P12 and P14 photographed crossing beneath bridges all other bears tracked via GPS.

Table 2.2. Correlation among fixed, continuous variables in resource selection function models for black bears, Central Georgia, USA 2012–2014.

	DIST-AF ¹	DIST-FE ²	DIST-DI ³
DIST-AF	1.0000000	-0.0507536	-0.4381734
DIST-FE	-0.0507536	1.0000000	0.0793556
DIST-DI	-0.4381734	0.0793556	1.0000000

¹ Distance to agriculture field

² Distance to forest edge

³ Distance to intersection of Georgia State Route 96 and drainage

Table 2.3. Summary of candidate general linear mixed-models with individual bear as a random effect for black bears, Central Georgia, USA 2012–2014.

Model	Log(L)	<i>K</i>	AIC _{<i>c</i>}	Δ_i	<i>w_i</i>
BU ¹ + DIST-AG ² + DIST-DI ³ + DIST-FE ⁴	-179.4948	6	371.1910	0.00000	0.999229
BU + DIST-AG + DIST-FE	-188.3696	5	386.8828	15.69174	0.000391
DIST-AG + DIST-FE	-189.4220	4	386.9394	15.74838	0.000380
BU + DIST-FE	-204.5818	4	417.2590	46.06794	0.000000
DIST-FE	-207.4816	3	421.0204	49.82933	0.000000
Null ⁵	-293.8944	2	591.8173	220.62627	0.000000

¹Categorical habitat variable; bottomland or upland forest

² Continuous variable; distance to agriculture field

³ Continuous variable; distance to drainage intersection with Georgia State Route 96

⁴ Continuous variable; distance to forest edge

⁵ Random effect only

Table 2.4. Parameter estimates of landscape-level parameters from top-performing model used to predict bear crossings of Georgia State Route 96, Central Georgia, USA 2012–2014.

Parameter	Estimate	Std. Error	<i>Z</i>	<i>p</i>
BU ¹	1.470481	0.685321	-2.146	0.0319
DIST-DI ²	-0.012055	0.002995	-4.025	<0.001
DIST-AF ³	-0.019361	0.003208	-6.035	<0.001
DIST-FE ⁴	-0.388514	0.051458	-7.550	<0.001

¹ Categorical habitat variable; bottomland or upland forest

² Continuous variable; distance to agriculture field

³ Continuous variable; distance to drainage intersection with Georgia State Route 96

⁴ Continuous variable; distance to forest edge

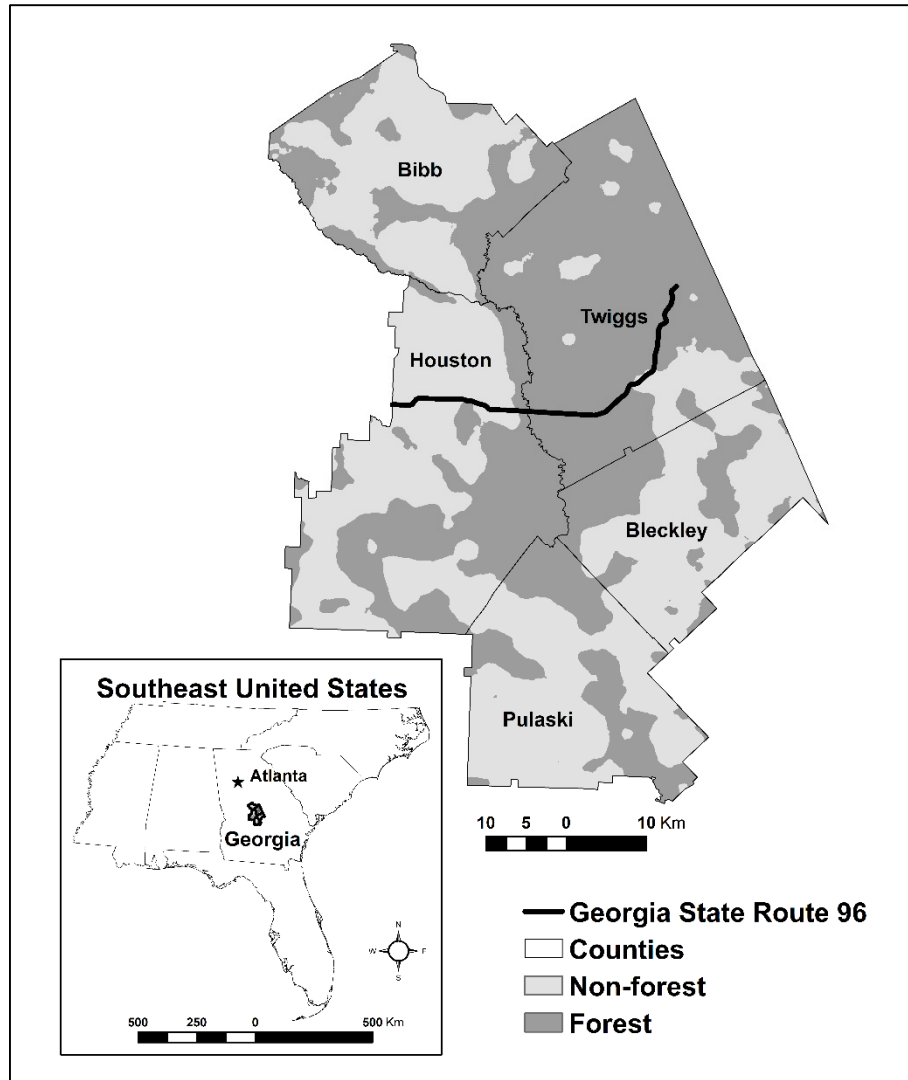


Figure 2.1. Central Georgia black bear study area with Georgia State Route 96, Georgia, USA, 2012–2014.

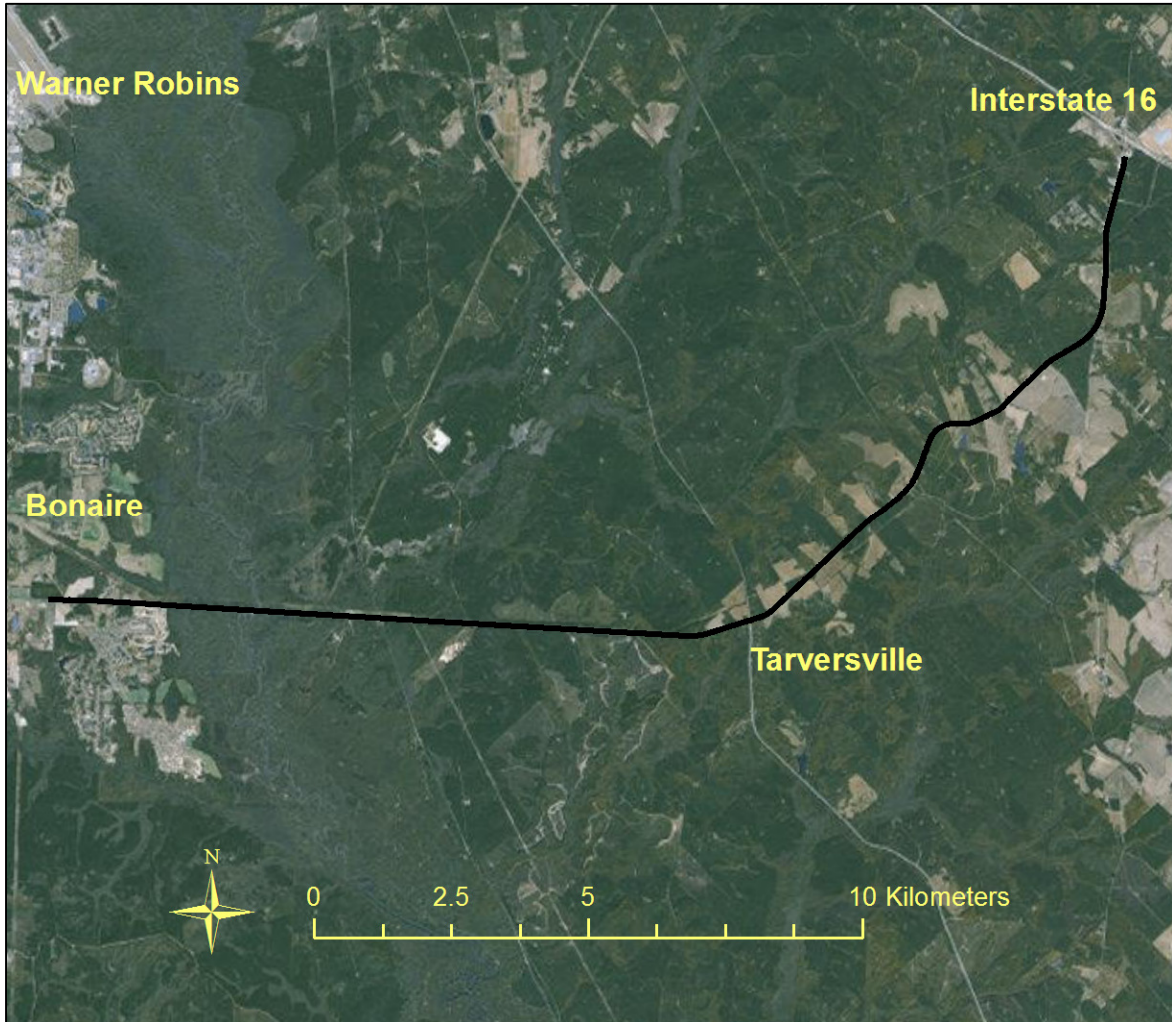


Figure 2.2. Section of Georgia State Route 96 (black line) used to evaluate black bear highway crossings, Georgia, USA, 2012–2014.

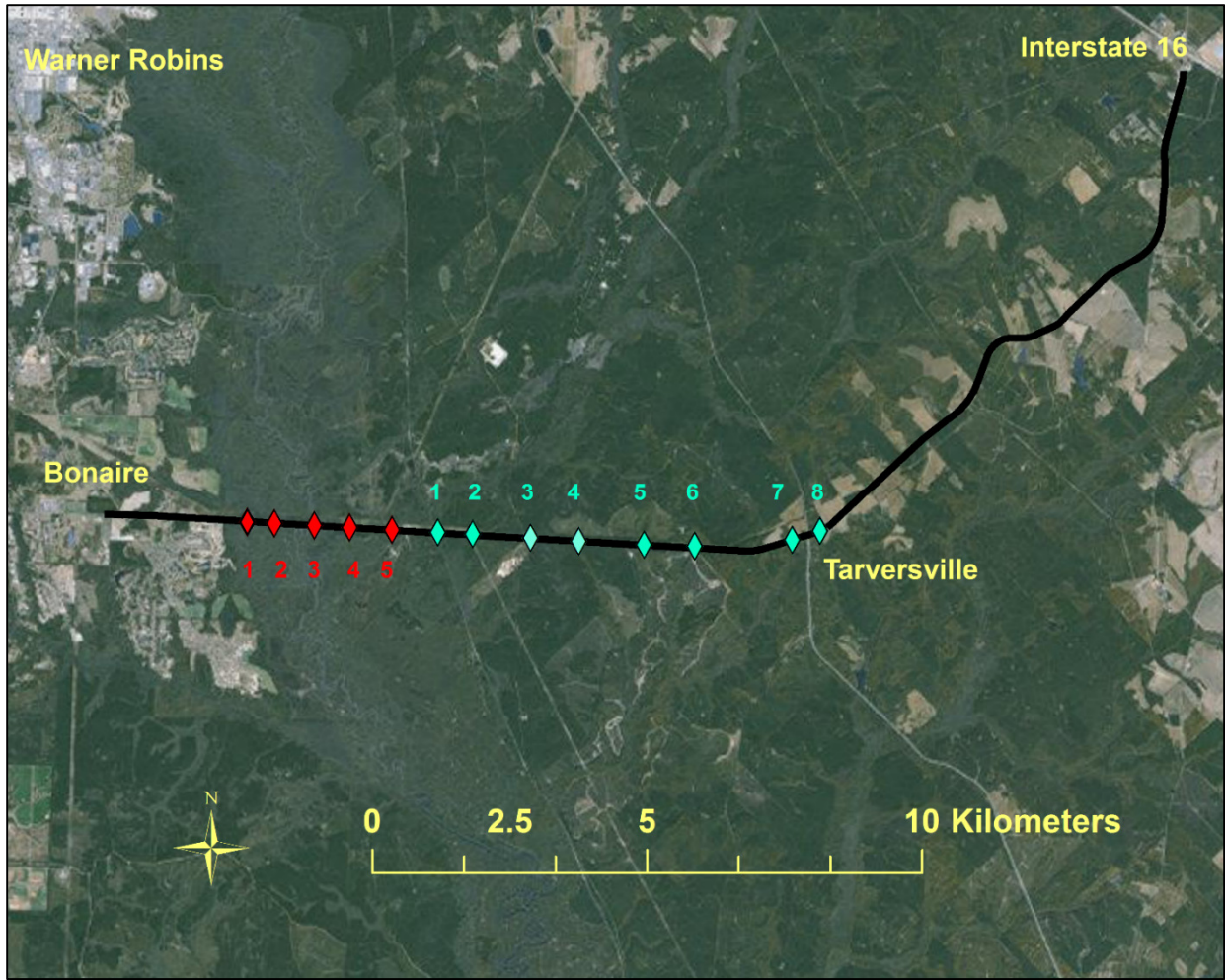


Figure 2.3. Section of Georgia State Route 96 (black line) used to evaluate black bear highway crossings, with existing bridges (red diamonds) and proposed underpasses (tourmaline diamonds), Georgia, USA, 2012–2014.

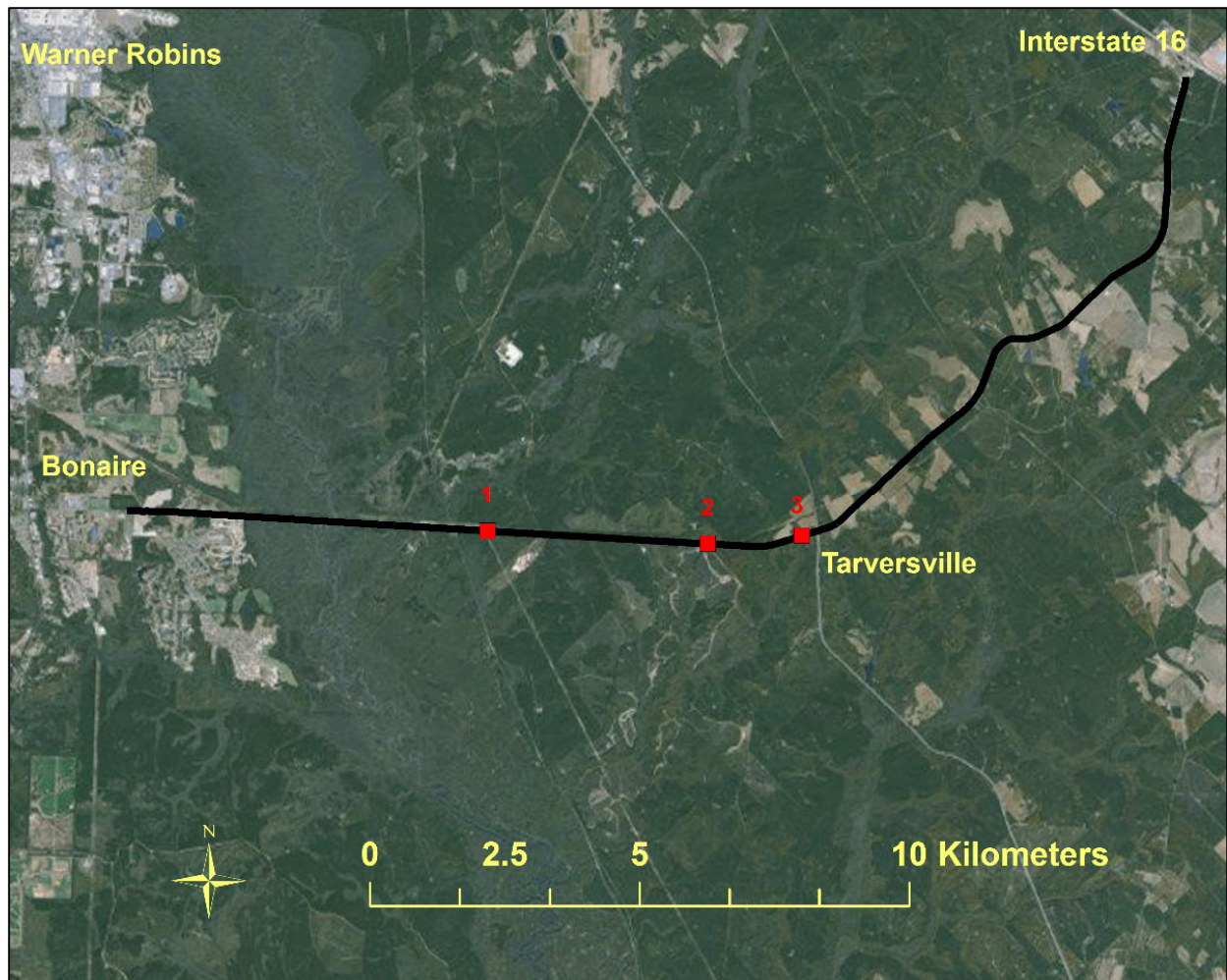


Figure 2.4. Section of Georgia State Route 96 (black line) with box culverts (red squares) monitored for bear activity via infrared trail camera, Georgia, USA, 2012–2014.

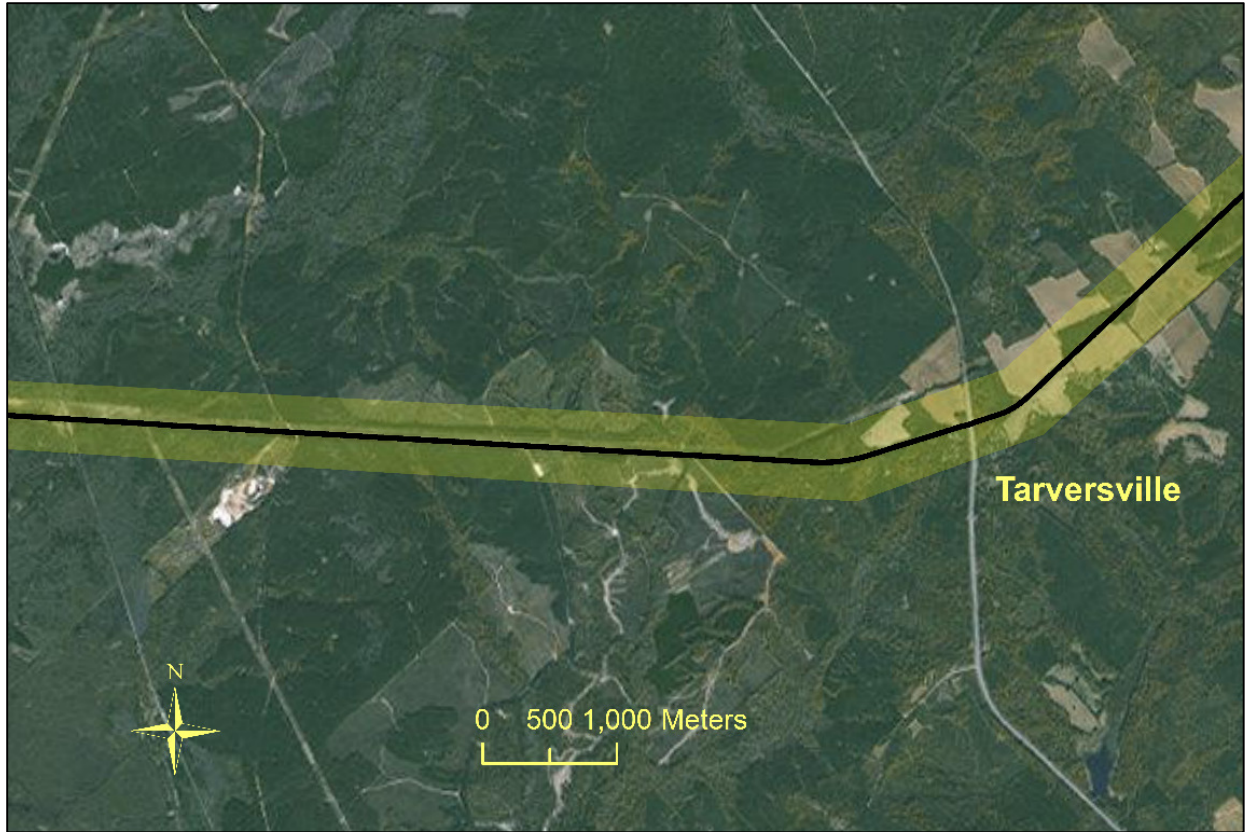


Figure 2.5. Section of Georgia State Route 96 (black line) used to evaluate black bear highway crossings, with depiction of virtual fence (yellow shaded area), Georgia, USA, 2012–2014.

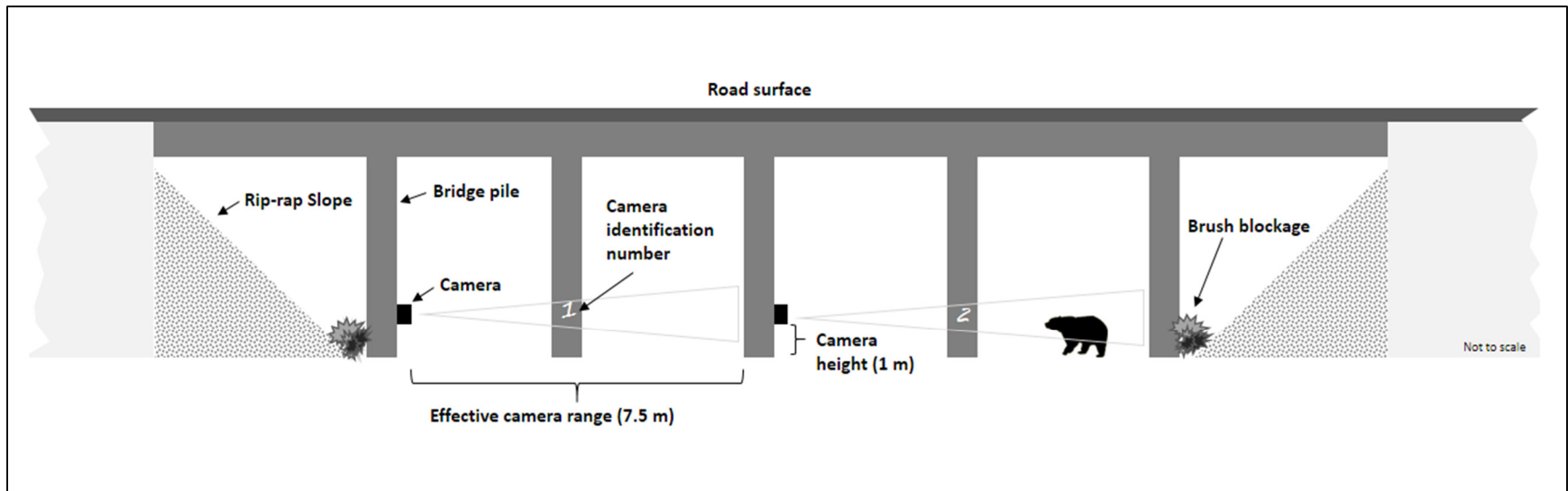


Figure 2.6. Schematic of camera survey setup used to monitor bear activity under Georgia State Route 96 bridges, Georgia, USA, 2012–2014.

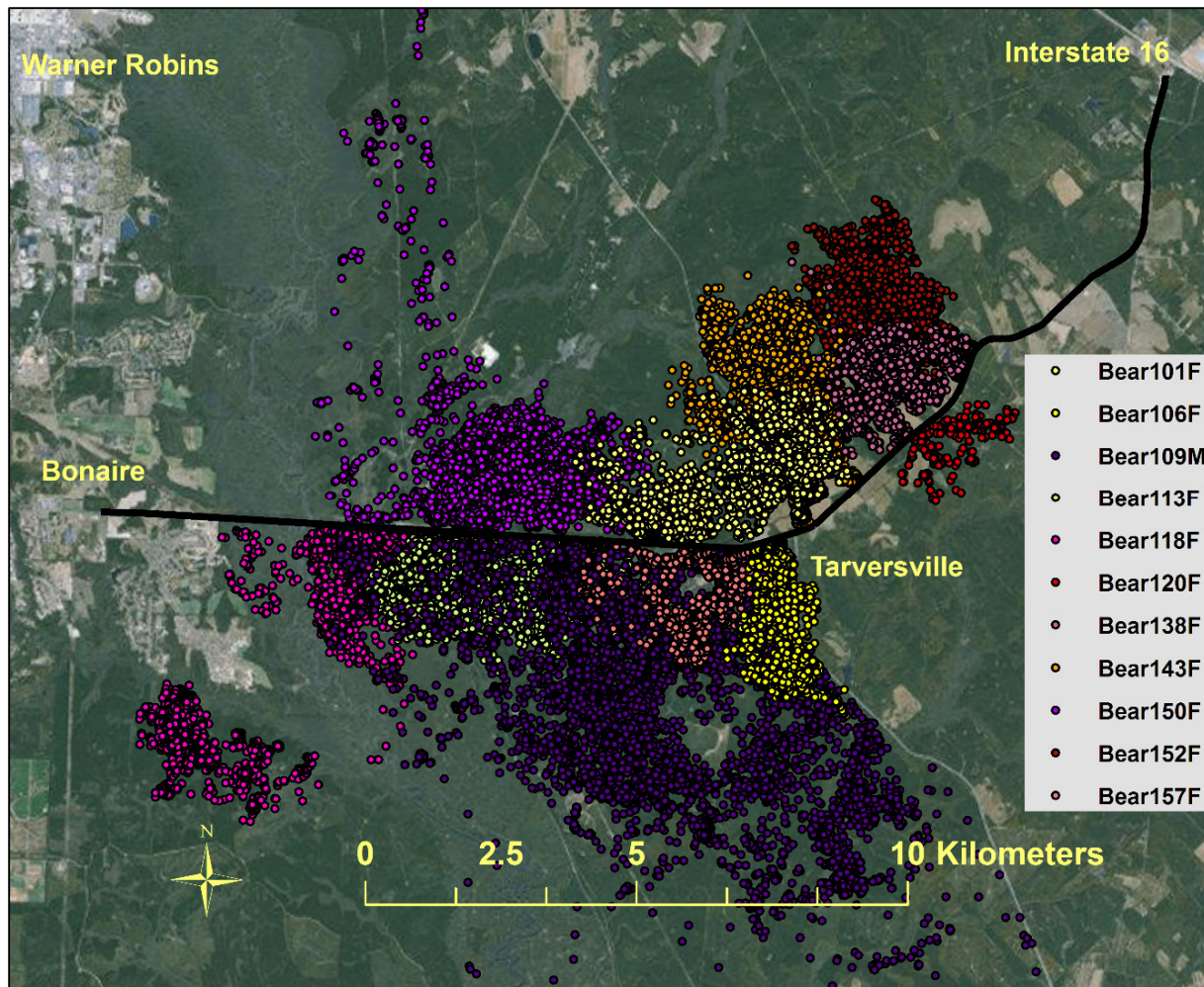


Figure 2.7. Section of Georgia State Route 96 (black line) and examples of black bear location data exhibiting bear activity adjacent to but not crossing Georgia State Route 96, Georgia, USA, 2012–2014.

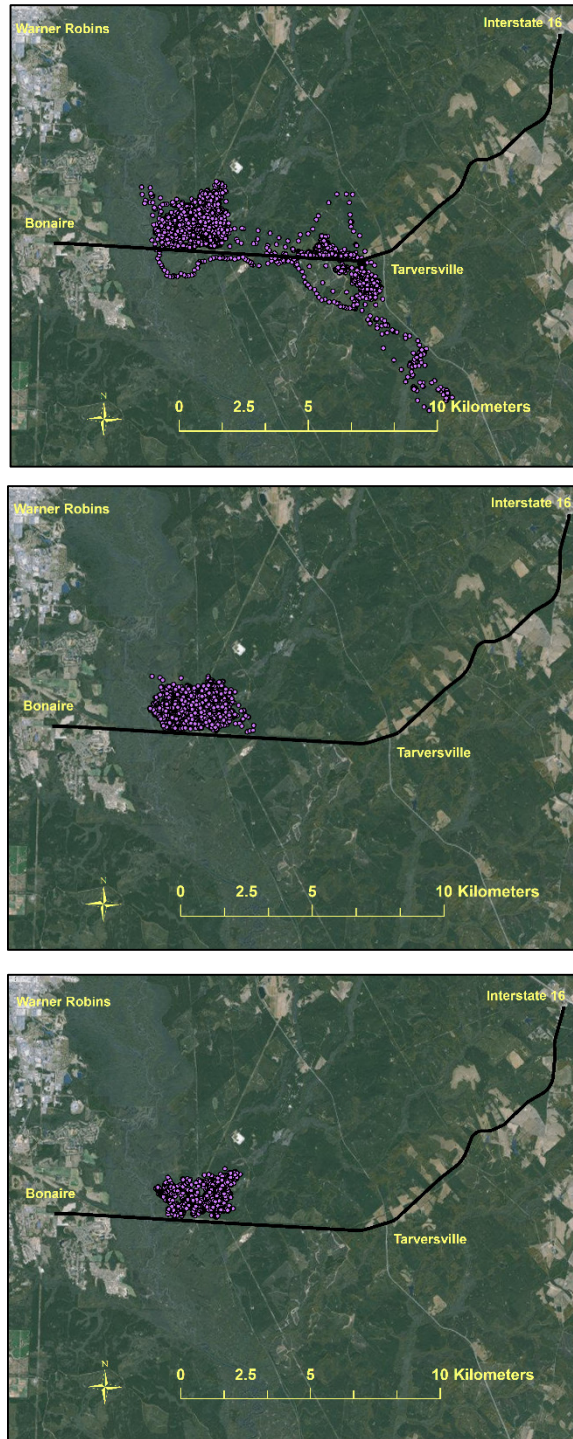


Figure 2.8. Section of Georgia State Route 96 (black line) and location data of female Bear 117 exhibiting crossing of Georgia State Route 96 during 2012 (top), and no crossings of Georgia State Route 96 during 2013 (middle) and 2014 (bottom), Georgia, USA, 2012–2014.

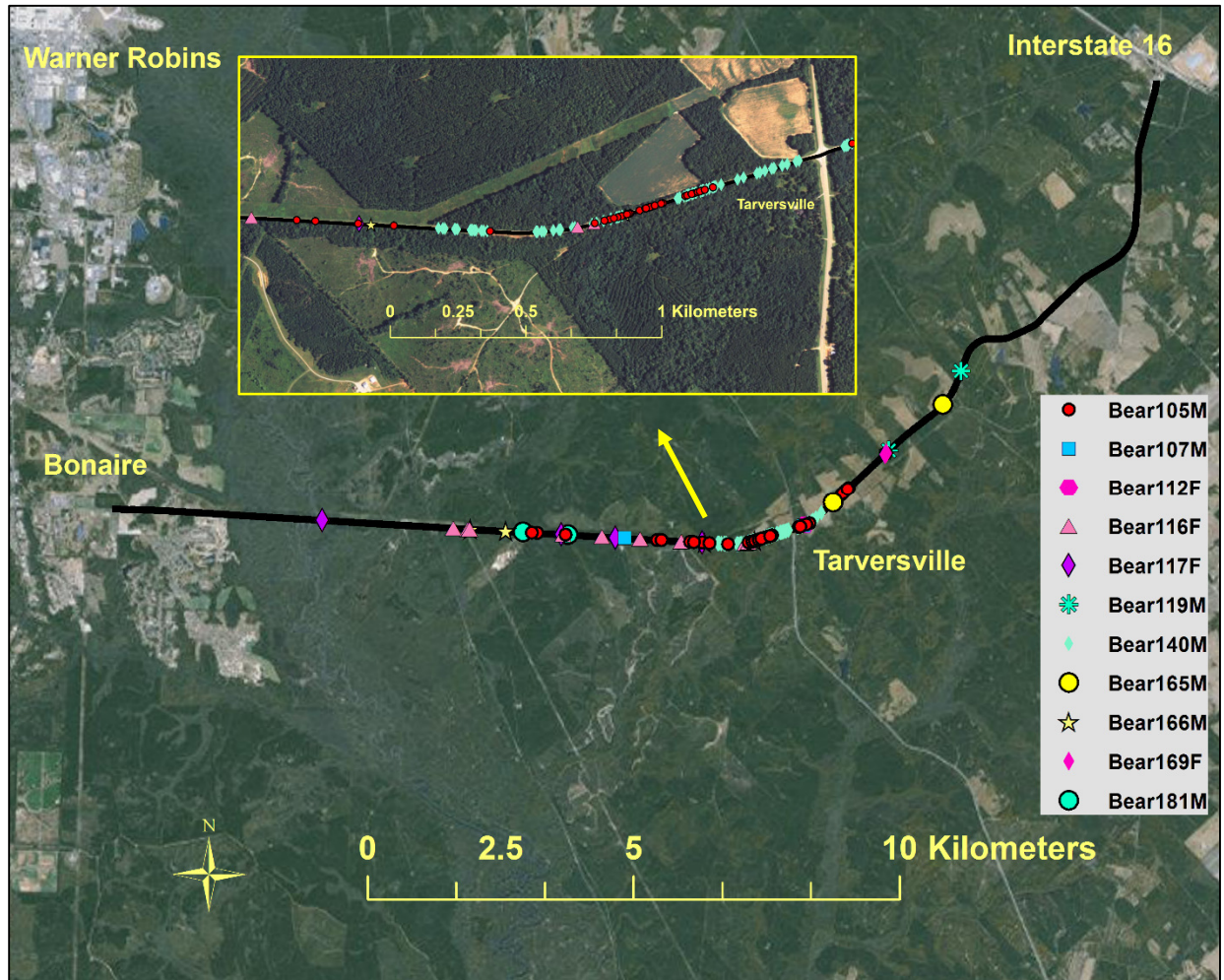


Figure 2.9. Section of Georgia State Route 96 (black line) with crossing locations of 11 GPS-collared black bears, with inset showing concentration of crossings west of Tarversville, Georgia, USA, 2012–2014.

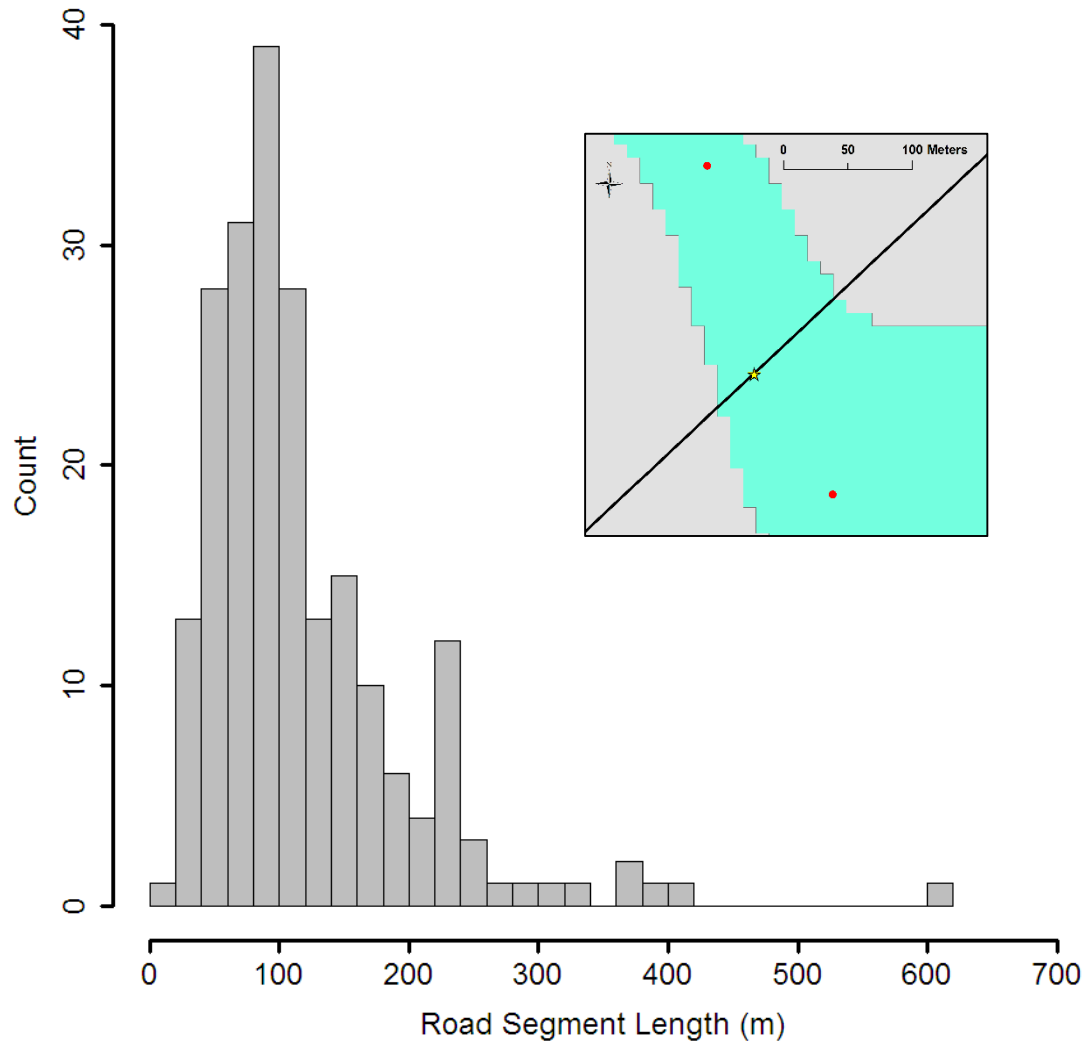


Figure 2.10. Road segment lengths defined by dynamic Brownian Bridge Movement Model, 95 % utilization distributions of bear movement paths that crossed Georgia State Route 96, with inset depicting example including Georgia State Route 96 (black line), bear locations (red dots), utilization distribution (tourmaline area), and random location on Georgia State Route 96 within the utilization distribution (yellow star), Georgia, USA, 2012–2014

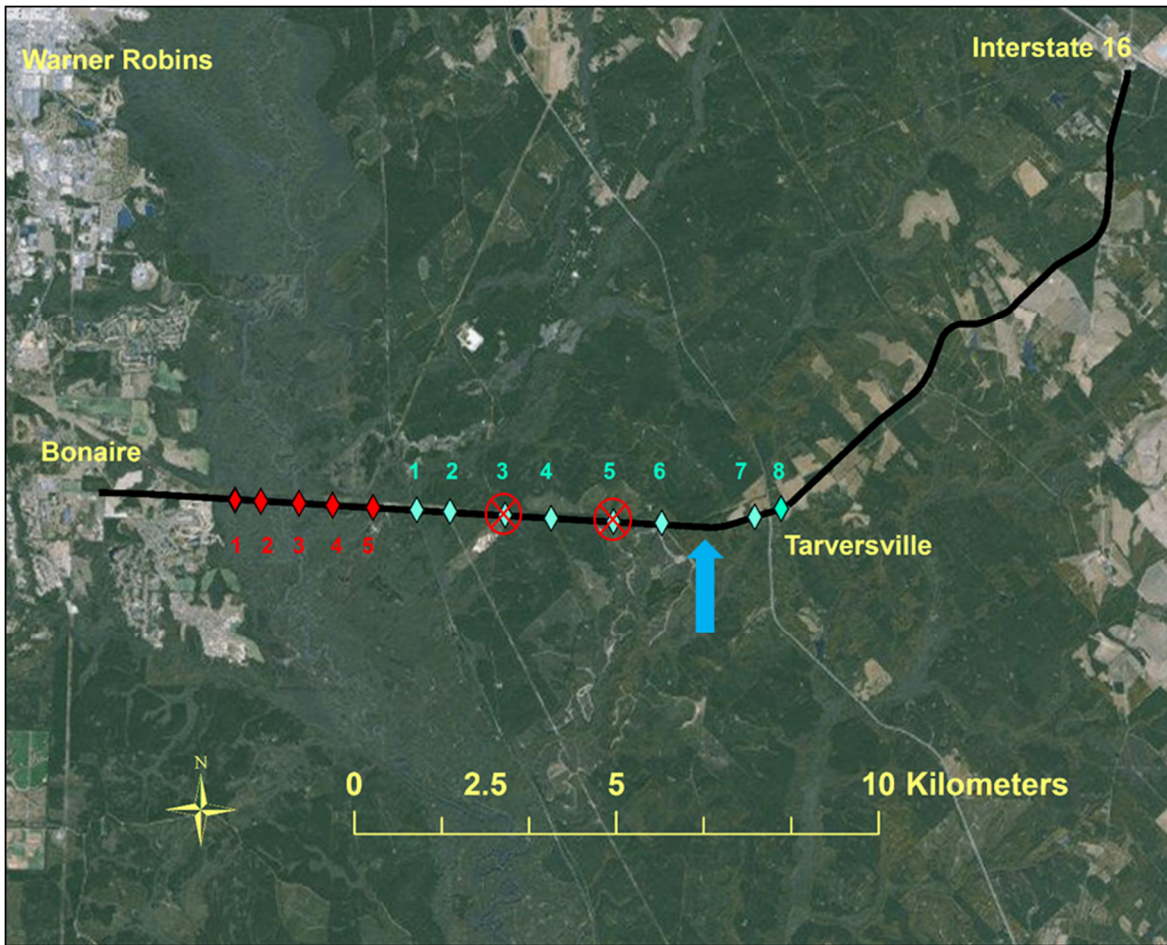


Figure 2.11. Section of Georgia State Route 96 (black line) used to evaluate black bear highway crossings with existing bridges (red diamonds), proposed underpasses (tourmaline diamonds), proposed underpasses which can be dropped from consideration (red, crossed circles), and road section which should be considered for a proposed underpass (blue arrow), Georgia, USA, 2012–2014.

CHAPTER 3
AMERICAN BLACK BEAR (*URSUS AMERICANUS*) POPULATION GENETICS IN
GEORGIA, USA

Hooker, M. J., and M. J. Chamberlain. To be submitted to *Ursus*.

ABSTRACT

There are 3 such bear populations in the state of Georgia. We used multi-locus microsatellite genotypes derived from bear hair and tissue samples collected from the 3 Georgia bear populations to assess levels of genetic diversity within and between populations. We used population assignment clustering to evaluate whether there has been recent immigration into the smallest of the 3 bear populations, the Central Georgia Bear Population. Compared to other United States bear populations, the North Georgia Bear Population and the South Georgia Bear Population have relatively high rates of genetic diversity ($H_o = 0.72 \pm 0.02$, $A = 6.68 \pm 0.32$, and $H_o = 0.72 \pm 0.02$, $A = 6.82 \pm 0.35$, respectively). In contrast, the Central Georgia Bear Population has relatively low rates ($H_o = 0.46 \pm 0.03$, and $A = 3.96 \pm 0.20$). Fixation indices for the pairings between Georgia bear populations indicated that the North Georgia Bear Population was more similar to the South Georgia Bear Population than either was to the Central Georgia Bear Population. Given the juxtaposition of the 3 populations, this finding provides evidence that the Central Georgia Bear population has experienced long-term genetic isolation and genetic drift. Out of a sample of 356 bears in Central Georgia, we only detected 1 immigrant and no admixture. We recommend development and implementation of plans to enhance genetic admixture of the Central Georgia Bear Population.

INDEX WORDS: American black bear, Georgia, genetic structure, microsatellite, *Ursus americanus*

INTRODUCTION

Historically, American black bear (*Ursus americanus*) were widely distributed across forested portions of North America (Pelton 2003). More recently, the range of the black bear receded to <70% of its historic extent (Pelton and van Manen 1994, Scheick and McCown 2014). Overharvest, persecution, and habitat alteration caused a reduction in bear abundance and distribution, especially in the southeastern United States (Pelton 2001). Maehr (1984) estimated that bears inhabited only 10% of their historic range in the Southeast due to habitat loss and historic overexploitation. A 1970 regional estimate of bear numbers across 11 southeastern states totaled < 4,000 animals, with 4 of 11 states reporting <100 bears each (Pelton and Nichols 1972).

Concomitant with reduced bear abundance and range reductions in the Southeast was fragmentation of once contiguous bear populations into numerous smaller populations. These populations were geographically isolated by human development, habitat loss (e.g., conversion of forestland to cropland), and in some cases distance alone. Pelton (1990) reported at least 30 disjunct populations of black bear across 13 southeastern states.

Fragmentation and isolation of populations can cause reduced genetic diversity within populations (Sherwin and Moritz 2000), reduced (or eliminated) gene flow between populations (Vos et al. 2001), and ultimately lead to increased probability of extinction (Saccheri et al. 1998). Fragmentation of habitat and genetic isolation can be especially problematic for large carnivores due to their relative low numbers, slow reproductive rates, and propensity to create conflicts with humans while attempting to move between habitat patches. A classic example is the Florida panther (*Puma concolor coryi*), which was reduced to roughly 30 individuals exhibiting deleterious effects of inbreeding (Roelke et al. 1993). Other notable cases include cryptorchidism in Florida black bears [*Ursus americanus floridanus*, (Dunbar et al. 1996, Dixon et al. 2007)].

Likewise, deleterious effects of inbreeding and reduced genetic diversity are well documented for the gray wolf (*Canis lupus*) population of Isle Royale, Michigan, USA (Wayne et al. 1991, Rääkkönen et al. 2009).

The State of Georgia contains 3 bear populations representing 2 of the southeastern American black bear subspecies described by Hall (1981). The North Georgia Bear Population (NGBP) and the Central Georgia Bear population (CGBP) are considered to be American black bear (*Ursus americanus americanus*), whereas the South Georgia Bear Population (SGBP) is considered to be the Florida black bear. Collectively, these populations contain roughly 5,100 bears with the NGBP being the most abundant population and the CGBP being the least abundant (Georgia Department of Natural Resources 2010, Hooker et al. 2015, Ashley 2016).

Bears in the NGBP occur in the northern counties of Georgia from the Georgia-Tennessee state line southward toward the suburbs north of Atlanta, and the Interstate-85 corridor between Atlanta and Greenville, South Carolina (Fig. 3.1). The CGBP is restricted primarily to 5 counties along the Ocmulgee River in Central Georgia southeast of Macon (i.e., Bibb, Bleckley, Houston, Pulaski, and Twiggs counties). The SGBP is located in the south central counties of Georgia along the Georgia-Florida state line and is associated with the Okefenokee Swamp. Both the NGBP and the SGBP are parts of trans-border populations shared with Georgia's neighboring states: North Carolina, South Carolina, and Tennessee to the north and Florida to the south. The NGBP is contiguous with the bear population in the mountains of southeastern Tennessee and western North and South Carolina. The NGBP is also considered the likely source of bears colonizing northeastern Alabama. The SGBP is contiguous with the Osceola bear population in northern Florida (Dobey et al. 2005). Conversely, the CGBP has been

considered demographically and genetically isolated from other bear populations in the recent past (Miller 1995, Sanderlin et al. 2009).

Jenkins (1953) was the first to report on the CGBP and estimated it to be <40 bears. Later, Grahl (1985) reported an estimate of 64 bears and noted that local residents were mostly unaware of the presence of the CGBP. Recently, the CGBP has been estimated at 430 animals inhabiting about 1,127 km² of forested land along the Ocmulgee River, roughly 150 km southeast of Atlanta (Fig. 3.1; Ashley 2016). This area is almost completely surrounded by human development and fragmented agricultural land. Relatively low abundance and potential isolation from other bear populations makes conservation of the CGBP of special concern. The CGBP is separated from the 2 other Georgia bear populations by distances of ~150 km, resulting in little dispersal and poor connectivity among the populations. Between the CGBP and the NGBP is the city of Atlanta, characterized by considerable urban sprawl and several interstate highways. Between the CGBP and the SGBP is primarily agricultural land cleared of forest. Although bears are occasionally reported in areas between the 3 populations, the level of demographic and genetic separation among these populations is uncertain (Fig. 3.2). Therefore, our objectives were to use microsatellite markers to assess genetic variation within and among all 3 Georgia bear populations and to determine if there was evidence of genetic admixture in the CGBP.

STUDY AREA

We conducted research in all 3 bear population in Georgia. Because some of our samples were collected from hunter harvested bears, especially those from the NGBP and SGBP, we placed emphasis on counties within Georgia's 3 bear hunting zones (Fig. 3.3). These zones were

a combined 49 counties and encompassed most of the area within Georgia known to be occupied by bears.

The North Bear Zone (NBZ, 31,654 km²), the largest of the 3 bear hunt zones, was comprised of Carroll, Fulton, DeKalb, Gwinnett, Walton, Barrow, Jackson, Madison, Hart and all Georgia counties north of these. The South Bear Zone (SBZ, 10,442 km²) included Brantley, Charlton, Clinch, Echols, Lanier, Lowndes and Ware Counties. The smallest zone, the Central Bear Zone (CBZ, 2,555 km²), was comprised of Bibb, Houston, and Twiggs counties. Adjacent to the CBZ were Bleckley and Pulaski counties, which were not within the bear hunt zone but were part of non-invasive sampling activities (see Methods) and location of several road-killed bears used in our analysis.

The NBZ encompassed extremes in terms of terrain, remoteness, and both human and bear densities. Many of the counties in the northeastern portion of the NBZ were mountainous, sparsely populated with humans, and had relatively high bear densities. These counties contained large tracts of federally and state-owned forest land, some of which was roadless wilderness. Conversely, the southwestern portion of the NBZ contained metropolitan Atlanta (pop. 5,710,795 U. S. Census Bureau 2015) and concomitant urban sprawl. The NBZ contained portions of 4 physiographic provinces: Appalachian Plateau, Blue Ridge, Piedmont, and Valley and Ridge (Usery 2016).

The CBZ was in the Ocmulgee River drainage at the Fall Line, the boundary of the Piedmont and Coastal Plain physiographic provinces (Usery 2016). Predominant forest types in the CBZ were bottomland hardwood forests within the Ocmulgee River flood plain and planted pine (*Pinus* spp.), natural pine, and mixed pine-hardwood in the uplands. Most forest land in the CBZ was privately owned and managed for timber production. Within this 3 county zone there

was considerable difference among counties in terms of human density. Bibb County contained the city of Macon (pop. 91,234) and was estimated to contain 153,721 people, whereas neighboring Twiggs County had <9000 residents (U. S. Census Bureau 2015).

The SBZ was in the lower Coastal Plain physiographic province (Usery 2016). This zone was along the Florida-Georgia boundary in the area of Okefenokee Swamp and Okefenokee National Wildlife Refuge. Okefenokee Swamp was one of the largest freshwater swamps in the United States and was typified by bay [e.g., loblolly-bay (*Gordonia lasianthus*), swamp-bay (*Persea palustris*), sweet-bay (*Magnolia virginiana*), black gum (*Nyssa sylvatica*), and cypress (*Taxodium* spp.)] forests. Private lands surrounding Okefenokee Swamp were predominantly managed slash pine (*Pinus elliottii*) forest, with low human population densities.

METHODS

Sample collection

During 2012–2016, we collected a variety of samples from which DNA could be extracted (e.g., hair, tissue, and blood). We obtained samples from bears using non-invasive sampling with barbed wire hair snares (Woods et al. 1999, Sylvest 2014, Hooker et al. 2015, Ashley 2016), live capture of bears using modified Aldrich foot snares (Johnson and Pelton 1980), hunter-harvested bears at check stations, and during investigations of vehicle-bear collisions and other bear mortalities. Samples collected from hair snares were exclusively hair, whereas samples collected from mortalities included hair, tissue, and in 2 cases, when no bear carcass was available, from clotted blood on the road surface at the scene of bear vehicle collisions. Our capture and handling methods were approved by the University of Georgia Institutional Animal Care and Use Committee (Protocol Number A2011 10-004-A1).

All samples collected in central Georgia were placed in #1 paper coin envelopes and stored in a climate-controlled environment at room temperature. Hair snares were checked on a weekly basis and, therefore, samples from hair snares had ≤ 7 days of environmental exposure before collection. Tissue samples or blood swabs (i.e., samples with high moisture content) were held out of storage with other samples until thoroughly desiccated. We collected samples from the NGBP and SGBP using TypiFix™ (IDnostics AG, Schlieren, Switzerland) single-use tissue sample collectors. As above, these samples were inventoried and stored at room temperature. We then forwarded all samples to Wildlife Genetics International (WGI, Nelson, British Columbia, Canada) for DNA extraction and microsatellite genotyping.

DNA was extracted from samples using QIAGEN's DNeasy Tissue kits and specific microsatellite loci were amplified using polymerase chain reaction (PCR). Detailed descriptions of laboratory methods used for our study have been previously described by Paetkau and Strobeck (1994), Paetkau et al. (1998), Paetkau (2003, 2004). All individuals sampled within the NBZ and SBZ were genotyped for 22 microsatellite loci: CPH9, CXX20, CXX110, D1A, D123, G1A, G1D, G10B, G10C, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU23, MU50, MU59, MSUT-2, REN144 A06, and REN145 P07 (Paetkau and Strobeck 1994, Paetkau et al. 1995, Taberlet et al. 1997, Kitahara et al. 2000, Breen et al. 2001) and an amelogenin sex marker (Ennis and Gallagher 1994). Samples from the CBZ were treated the same as above, but only a subset of all CBZ samples were analyzed at all 22 loci. Individual genotypes matching at all but 1 or 2 loci were scrutinized to eliminate error as a possible source of differences. Further error checking and quality control used in our study are described by Paetkau (2003).

Analysis

We tested for deviations from expected values of Hardy-Weinberg equilibrium (HWE) using program Genepop 4.5.1 (Raymond and Rousset 1995). We computed exact P -values using complete enumeration for loci with <4 alleles (Louis and Dempster 1987), otherwise we used the Markov chain method [de-memorization 10,000, batches 20, iterations per batch 5,000, (Guo and Thompson 1992)]. We also tested for linkage disequilibrium and nonrandom associations between alleles at different loci within populations using Markov chain methods (de-memorization 10,000, batches 200, iterations per batch 10,000, (Guo and Thompson 1992)], and again adjusted P -values for multiple comparisons using Bonferroni correction (Rice 1989). As measures of genetic variation within each population, we calculated observed mean heterozygosity (H_o), expected mean heterozygosity (H_e), and mean number of alleles at each locus (A). We calculated genetic distance between all populations (global F_{st}) and between paired populations (pairwise F_{st} ; Weir and Cockerham 1984)

To assess potential inter- and intra-population genetic structure, we initially conducted a factorial correspondence analysis (FCA) implemented in program GENETIX 4.05 (Benzecri 1992, Belkhir 1999). The FCA involves no a priori assumptions regarding sampling location or population of origin for individuals but rather groups like individuals on multiple factorial axes (i.e., in multidimensional space) based on shared alleles (Haroldson et al. 2010). To reduce dimensionality, we plotted the first 2 or 3 dimensions of this data space in 2 or 3-dimension scatterplots and visually inspected the plots for evidence of clustering and whether or not clusters corresponded to sampling location and known population of origin for individuals where this was known.

We used the population assignment test within program STRUCTURE 2.3.4 to determine the likely number of clusters (i.e., populations; K) within our dataset of 22-locus genotypes based on allele frequencies (Pritchard et al. 2000). We used the *admixture model* with the LOCPRIOR option. This option allows sampling location information to aid the clustering algorithm in cases with weak structure signals by assuming that animals sampled from like locations are more likely to share common ancestry (Porrás-Hurtado et al. 2013). In lieu of specific sampling locations, something that was not available for many genotypes in our dataset, we used assignment to one of the 3 Georgia bear populations. Each bear was assigned to the population from within which it was sampled. For the few samples we collected outside of the ranges of any of the 3 bear populations, we assigned samples to the closest population from the area where the sample was collected. Assuming that all 3 Georgia bear populations were historically part of a contiguous bear population, we used the *correlated allele frequency model*. We used a 100,000-step Markov-chain Monte Carlo (MCMC) for 20 runs following a 10,000-step burn-in to considered scenarios in which K ranged from a minimum of 1 to a maximum of 6 [i.e., our assumed number of populations plus 3; (Evanno et al. 2005)]. To mitigate issues of inherent stochasticity among the 20 MCMC runs, [e.g. label-switching or multimodality; (Stephens 2000, Jasra et al. 2005)] we used program CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) implemented through the ‘main pipeline’ of CLUMPAK (Kopelman et al. 2015) to align and find agreement among the results of the 20 runs. To determine the most appropriate value of K for our data, across $K=1-6$, we used CLUMPAK to calculate and plot both the log probability of our data, $\ln \Pr(X | K)$ as suggested by Pritchard et al. (2000) and ΔK , the rate of change of K using the method of Evanno et al. (2005) across $K=2$ to 5.

Because we were specifically interested in detection of immigrants, or offspring of immigrants, within the CGBP, we used the USEPOPINFO model in STRUCTURE 2.3.4 to analyze our dataset including all genotypes regardless of number of loci (Pritchard et al. 2000). Within the USEPOPINFO model it is possible to indicate the number of generations back to consider (GENSBACK) where GENSBACK=0 represents an individual being a migrant and GENSBACK=1 indicates an individual is the offspring of a migrant parent and so on. We limited our analysis to a maximum of GENSBACK=3 due to the decreasing power to detect immigrants as GENSBACK increases (Pritchard et al. 2000). For comparison, we ran models with 2 levels of v (0.05 and 0.10), where v is the probability that an individual is an immigrant to the population from which it was sampled, or has some level of immigrant ancestry, and $1-v$ is the probability the individual is purely from the population from which it was sampled. We used a 100,000-step MCMC for 20 runs following a 10,000-step burn-in and based on the results of the above clustering analysis, limited the number of clusters considered to $K=3$.

RESULTS

From 2012 through 2016, we collected >10,000 samples resulting in 482 individual microsatellite genotypes. Our success rate for deriving a genotype from a sample varied by sample type (e.g. plucked hair vs. tissue) but overall was 87%. The discrepancy between number of samples collected and number of successful genotypes was due in part to a subsampling of hair snare samples from within the CGBP (see Sylvest 2014, Hooker et al. 2015, Ashley 2016). Based on sample collection location, the NGBP, CGBP, and SGBP, yielded 72, 356, and 54 genotypes, respectively. All NGBP, SGPB, and 70 CGBP genotypes were 22-locus genotypes, whereas the remainder of the CGBP genotypes ranged from 11–21 loci (Table 3.1).

After Bonferroni correction, 1 of 22 loci [4.5%, (REN144 A06)] failed to adhere to assumptions of HWE within each of the Georgia bear populations ($P < 0.05$). An additional 4 of 22 [18.0%, (G10B, MU50, G10X, CPH9)] failed within the CGBP. The results of our test for non-random loci pairings indicated that there were no departures from randomness among all pairings within the SGBP. Only 1 of 231 (0.4%) loci pairings within the NGBP failed the linkage disequilibrium test, whereas 5 of 231 (2.2%) failed within the CGBP. The NGBP and the SGBP were similar in mean number of unique alleles per loci and heterozygosity levels, whereas the CGBP was considerably lower than either of those populations (Table 3.2). The degree of genetic separation between the 3 GA bear populations (F_{st}) was greater between the CGBP and either the NGBP or the SGBP, than between the NGBP and the SGBP (Table 3.3).

Plots of the 2 primary factors from the FCA of all individuals genotyped at 22 loci revealed 3 well defined clusters corresponding to the 3 populations sampled and 1 individual that was not within any of the 3 clusters (Fig. 3.3). Similar patterns can be seen in the plot of the full dataset with bears genotyped at a variable number of markers (Fig. 3.4) and a plot of all bears but only using the 10 loci all genotypes had in common (Fig. 3.5). Note that while only considering the 10-loci that all genotypes had in common, there is still clear distinction between the CGBP and the other 2 Georgia bear populations, whereas there is a loss of distinction between the NGBP and the SGBP.

The notable exception within the FCA clustering, Bear RK062715M, was a 3-year-old (aged by cementum annuli; Willey 1974) male bear killed by a vehicle in Central Georgia and assumed to be a member of the CGBP. However, allele frequencies of this male were not consistent with those of the CGBP, nor were they definitively consistent with either the NGBP or SGBP. Subsequent investigation into the possible source population of this individual indicated

that it was likely from the Apalachicola bear population in the panhandle of Florida (D. Paetkau, WGI, personal communication, 8 July 2016).

In estimating the most likely number of clusters (K) within our data, using the algorithm within program STRUCTURE, there was agreement between the method of Pritchard et al. (2000; Fig. 3.7), where the log-likelihood values of K plateau at $K=3$ and beyond $K=4$ variance of the estimates of the log-likelihood expand considerably, and the method of Evanno et al. (2005; Fig. 3.8), where the rate of change of K peaks at $K=3$.

Results of the $K=3$ clustering (Fig. 3.9) indicate that all but 1 individual (the Apalachicola bear mentioned above) clustered with the populations from which they were sampled and had high proportions of ancestry from those populations (i.e., are almost exclusively one color and group with individuals of like color). In the absence of other Apalachicola bears in the data set, Bear RK062715M gave the appearance of having primary ancestry from the SGBP. However, in results of $K=4$ (Fig. 3.10), Bear RK062715 had a high proportion of ancestry in common with a 4th cluster represented, only in part, by several individuals sampled from within the SGBP. The SGBP was contiguous with the Ocala bear population of northeastern Florida, and this population has been used as a destination for bear relocations from elsewhere in Florida (B. Scheick, Florida Fish and Wildlife Conservation Commission, personal communication, 8 July 2016). This likely has resulted in genetic admixture, potentially sourced from more than one of Florida's bear populations, within the SGBP, introducing the possibility of a bear hunter in Georgia (the source of our SGBP samples) harvesting a bear in the SGBP that was not of SGBP origin.

The results of our testing the full dataset for migrants and descendants of migrants flagged Bear RK062715 as being a migrant to the CGBP originating from the Apalachicola bear

population of Florida (Table 3.5). Again, the association of RK062715 with the SGBP is likely an artifact of there being no other bears from the Apalachicola bear population in our dataset and the SGBP, being in close proximity to several Florida bear populations, being more similar to the Apalachicola population than either the NGBP or the CGBP. A second bear sampled from within the CGBP, female bear GA40512101B was flagged as having a 0.24 probability of having full CGBP ancestry and a 0.67 probability of being a 3rd-generation descendant of a NGBP bear (i.e., having a great grandparent from the NGBP). The only other bear in our dataset flagged as having full ancestry from other than the population where he/she was sampled was a NGBP bear, NGA4H500847. This bear had a 0.75 probability of having a great grandparent with CGBP ancestry.

DISCUSSION

Populations are subject to combinations of deterministic (e.g., habitat loss and overexploitation) and stochastic (e.g., demographic and genetic) factors (Shaffer 1981). Small populations, relative to larger populations, tend to have decreased rates of persistence due to stochastic demographic processes (MacArthur and Wilson 1967, Shaffer 1987, Lande 1993). Smaller populations are also more prone to negative impacts of stochastic genetic processes such as fixation of deleterious alleles, genetic drift, and inbreeding depression (Mills 2012). These negative impacts come in 2 forms (Keller and Waller 2002): (1) reduced genetic diversity and inability to adapt to environmental change (e.g., climate change or introduction of a novel disease) and (2) inbreeding and its deleterious effects on individual survival and reproduction (Frankham et al. 2002, Keller and Waller 2002). Additionally, population persistence, or the lack thereof, can be affected by a population's spatial juxtaposition (pattern) and functional

relationship (process) to neighboring populations (Hanski 2005). Hellgren and Vaughan (1994) identified alleviation of negative demographic and genetic consequences caused by habitat loss and fragmentation as conservation and management priorities for Southeastern bear populations.

The patterns of heterozygosity and allelic richness we observed within the CGBP, relative to the NGBP and SGBP, are indicative of the CGBP having experienced a genetic bottleneck and genetic drift as a result of having been reduced to low numbers and remaining in isolation from neighboring bear populations (Frankham et al 2002, Nei et al 1975). Comparing levels of genetic diversity across studies can be problematic due to variability in number of loci used, the specific loci used, and variability in mutation rates for loci (Conner and Hartl 2004). However, previous studies using the same or similar microsatellite makers as those we used observed heterozygosity levels of >0.70 for American black bear populations in areas with large areas of habitat and little impedance of gene flow (Paetkau and Strobeck 1998, Pelletier et al. 2012, Pelletier et al. 2017, Schwartz et al. 2006, Woods et al. 1999). Conversely, similar studies of American black bears from small, isolated populations reported heterozygosities of <0.50 (Boerson et al. 2003, Csiki et al 2003, Brown et al. 2009, Clark et al. 2010, Hooker 2010, Lowe 2011, Troxler 2013, Pelletier et al. 2017). The most extreme case was that of the Chassahowitzka bear population of Florida with an observed heterozygosity of 0.29, allele richness of 2.25 (Table 3.3; Dixon et al. 2007), and higher than expected incidence of cryptorchidism and delayed testicular descent (Dunbar et al. 1995). While inbreeding and low genetic diversity are not exclusive causes of cryptorchidism, the condition was reported to be prevalent in the highly inbred population of Florida panthers prior to a successful genetic rescue of that population (Barone et al. 1994, Mansfield and Land 2002).

While not the main focus of our work, we performed overall health assessments of live-captured bears and post-mortem inspections and/or necropsies of bear mortalities throughout the course of this project. In 80 male bears ≥ 2 years old we detected 6 (7.5%) cases of partial cryptorchidism (i.e., only 1 descended testicle) or ectopic cryptorchidism (i.e., one or both testicles descended from the abdominal cavity but failing to enter the scrotum and migrating elsewhere). A seventh case was suspected but could not be confirmed due to deterioration of the carcass.

Black bears exhibit inbreeding avoidance behavior by which young males disperse from their natal area and young females tend to stay within or near their natal range (Alt 1978, Rogers 1987, Beck 1991, Schwartz and Franzmann 1992, Costello 2010). Male black bears have been documented dispersing distances ranging from <20 km to >200 km (Rogers 1987, Elowe and Dodge 1989, Beck 1991, Lee & Vaughan 2003). Other cases of bears moving considerable distances from their natal ranges, sometimes as a result of being subjected to translocation or other management actions, have been documented. Rogers (1973) reported numerous long-distance bear movements in Arkansas and Missouri after the transplantation of bears into the Ozark and Ouachita National Forest of Arkansas. Maehr et al. (1988) documented the 140 km movement of a male bear across several counties of Florida considered to not be occupied bear range. Likewise, Stratman et al. (2001) documented the ~ 500 km movement of an adult male black bear from Florida to Louisiana. These examples and others demonstrate that black bears, especially males, are capable of long distance movements needed for inter-population exchange among disjunct populations. However, various factors contribute to infrequent and potentially unreliable interchange, and hence, genetic and demographic maintenance of disjunct populations. Low reproductive rates (Bunnell and Tait 1981) combined with dispersal behavior being highly

biased toward sub-adult males means the number of potential dispersers, available on an annual basis, can be quite limited. There is also risk involved in traversing and exploring unfamiliar territory and survival rates are often decreased for dispersing bears (Bunnell and Tait 1981, Schwartz and Franzmann 1992).

In terms of distance alone, both the NGBP and SGBP could be sources of immigrants into the CGBP. However, to the extent that we sampled from within the CGBP, we only detected 1 recent immigrant in the CGBP and no evidence of admixture within the recent past. While the detection of an immigrant is encouraging, this individual was killed crossing an interstate highway, and at 3 years of age was likely a non-breeding sub-adult.

MANAGEMENT IMPLICATIONS

Given the apparent degradation of genetic diversity within the CGBP and continued genetic isolation between the CGBP and surrounding bear populations, primarily the NGBP and SGBP, we encourage the introduction of novel genetic material (i.e., bears from populations other than the CGBP) into the CGBP. This introduction of novel genetic material could be accomplished by corridor development and natural dispersal of bears, by translocation of bears into the CGBP, or a combination. Translocations would likely result in the most rapid genetic admixture into the CGBP. Similar translocations of bears, using the winter soft release method of Eastridge and Clark (2001) have been used to reestablish extirpated bear populations, augment existing populations, and create ‘stepping-stone’ populations between extant but demographically and genetically separate subpopulations in the southeastern US [see Benson and Chamberlain 2007 (Louisiana), Eastridge and Clark 2001 (Kentucky and Tennessee), and Wear et al. 2005 (Arkansas)] and in doing so facilitating genetic connectivity between otherwise

isolated populations (Laufenberg and Clark 2015). We also caution against reduction of the CGBP in the absence of efforts to alleviate the population's isolation. Reducing the population in its current state has potential to further erode its genetic diversity and make long-term conservation less tenable.

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Table 3.1. Number of individual American black bears genotyped at each of 22 microsatellite markers throughout 3 populations of black bears in Georgia, USA. 2012–2016.

Pop.	<u>Microsatellite Marker</u>																					
	G1A	CXX110	CXX20	D123	D1A	G10L	G10M	MU59	G10U	G10X	REN144 A06	REN145 P07	G1D	G10H	MU23	G10B	G10C	MU50	G10P	CPH9	G10J	MSUT-2
NGBP ¹	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72	72
CGBP ²	356	356	356	356	356	356	356	356	356	356	101	187	99	187	101	79	73	78	75	73	72	74
SGBP ³	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54	54
Total	482	482	482	482	482	482	482	482	482	482	227	313	225	313	227	205	199	204	201	199	198	200

¹ North Georgia Bear Population

² Central Georgia Bear Population

³ South Georgia Bear Population

Table 3.2. Measure of genetic variation within 3 populations of American black bears based on 196, 22-locus microsatellite genotypes including the mean number of alleles per locus (A), observed heterozygosity (H_o), expected heterozygosity (H_e), and number of genotypes (n), during 2012–2016, Georgia, USA.

Population	A	H_o	H_e	n
NGBP ¹	6.68±0.32	0.72±0.02	0.73±0.01	72
CGBP ²	3.96±0.20	0.46±0.03	0.47±0.03	70
SGBP ³	6.82±0.35	0.72±0.02	0.71±0.02	54

¹ North Georgia Bear Population

² Central Georgia Bear Population

³ South Georgia Bear Population

Table 3.3. Fixation index (F_{ST}) between pairings of 3 American black bear populations in Georgia USA during 2012–2016.

Population 1	Population 2	F_{ST}
SGBP ¹	NGBP ²	0.077
SGBP	CGBP ³	0.186
NGBP	CGBP	0.164

¹ South Georgia Bear Population

² North Georgia Bear Population

³ Central Georgia Bear Population

Table 3.4. Genetic diversity metrics for American black bear populations in the southeastern United States with observed heterozygosity (H_o), expected heterozygosity (H_e), and mean number of alleles per loci (A).

Population(n)	H_o	H_e	A	Locale	Citation
South Georgia (54)	0.72	0.71	6.82	Georgia	This project
North Georgia (72)	0.72	0.73	6.73	Georgia	This project
Osceola (41)	0.71	0.71	6.67	Florida	Dixon et al. 2007
Apalachicola (40)	0.69	0.71	5.92	Florida	Dixon et al. 2007
St. Johns (40)	0.65	0.66	5.75	Florida	Dixon et al. 2007
Big Cypress (41)	0.64	0.65	5.50	Florida	Dixon et al. 2007
Eglin (40)	0.61	0.54	4.08	Florida	Dixon et al. 2007
Ocala (40)	0.58	0.61	4.75	Florida	Dixon et al. 2007
Aucilla (40)	0.57	0.59	5.00	Florida	Dixon et al. 2007
Central Georgia (70)	0.45	0.45	2.86	Georgia	This project
Highlands/Glades (28)	0.33	0.38	2.75	Florida	Dixon et al. 2007
Southwestern Alabama (19)	0.32	-	2.80	Alabama	Edwards 2002
Chassahowitzka (29)	0.29	0.27	2.25	Florida	Dixon et al. 2007

Table 3.4. Results of testing recent ancestry of 482 American black bear multilocus genotypes from bears sampled within or between 3 Georgia, USA black bear populations. Listed (Bear ID) are 3 bears with probabilities of being from the population from which they were sampled of <1.0 and probabilities of these 3 bears being from, or having ancestry from, 1 of 2 alternative populations. 2012–2016.

No. of generations back	v^1	Bear ID	Assumed pop. of origin	Prob. assumed pop. of origin	Alternative population 1	Prob. bear is a migrant	Prob. 1 st gen descendent	Prob. 2 nd gen descendent	Prob. 3 rd gen descendent	Alternative Population 2	Prob. bear is a migrant	Prob. 1 st gen descendent	Prob. 2 nd gen descendent	Prob. 3 rd gen descendent
2	0.05	GA4RK062715	CGBP ²	0.00	NGBP ³	0.00	0.00	0.00	-	SGBP ⁴	1.00	0.00	0.00	-
		NGA4H500847	NGBP	0.48	CGBP	0.00	0.00	0.52	-	SGBP	0.00	0.00	0.00	-
	0.10	GA4RK062715	CGBP	0.00	NGBP	0.00	0.00	0.00	-	SGBP	1.00	0.00	0.00	-
		GA40512101B	CGBP	0.40	NGBP	0.00	0.00	0.59	-	SGBP	0.00	0.00	0.01	-
3		NGA4H500847	NGBP	0.29	CGBP	0.00	0.00	0.08	0.63	SGBP	0.00	0.00	0.00	0.00
	0.05	GA4RK062715	CGBP	0.00	NGBP	0.00	0.00	0.00	0.00	SGBP	1.00	0.00	0.00	0.00
		GA40512101B	CGBP	0.24	NGBP	0.00	0.00	0.08	0.67	SGBP	0.00	0.00	0.00	0.02
		NGA4H500847	NGBP	0.16	CGBP	0.00	0.00	0.09	0.75	SGBP	0.00	0.00	0.00	0.00
	0.10	GA4RK062715	CGBP	0.00	NGBP	0.00	0.00	0.00	0.00	SGBP	1.00	0.00	0.00	0.00
		GA40512101B	CGBP	0.13	NGBP	0.00	0.00	0.09	0.76	SGBP	0.00	0.00	0.00	0.02

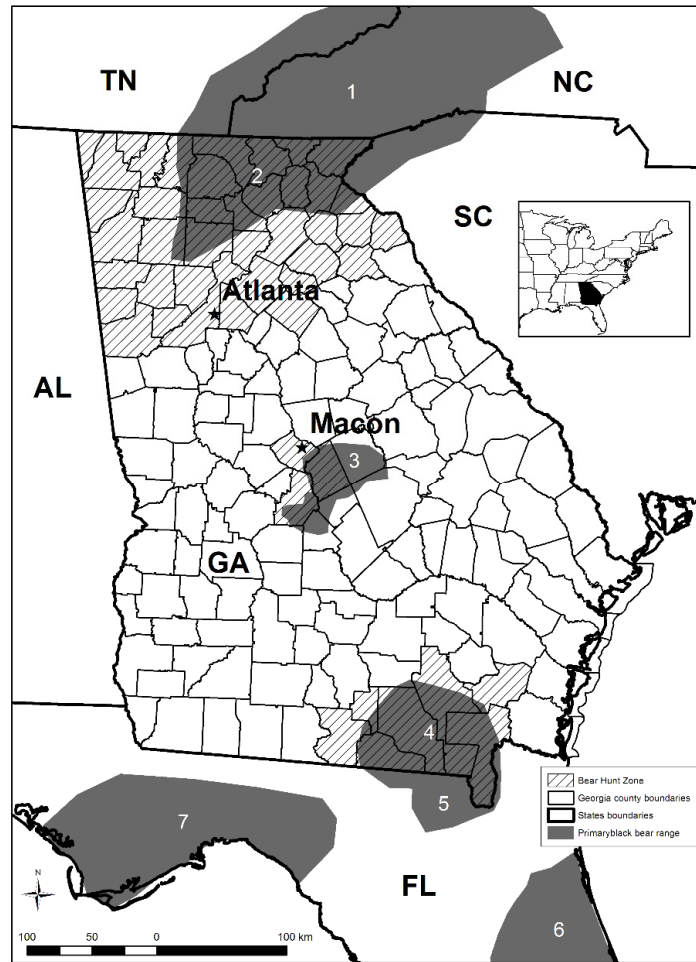


Figure 3.1. Map of the state of Georgia and neighboring states depicting Georgia counties, Georgia black bear hunting zones, and primary black bear ranges including; (1) Great Smoky Mountains black bear population of North Carolina, South Carolina, and Tennessee, (2) The North Georgia black bear population, (3) the Central Georgia black bear population, (4) the South Georgia black bear population, (5) the Ocala black bear population of Florida, (6) the Ocala black bear population of Florida, and (7) the Apalachicola black bear population of Florida during 2012–2016.

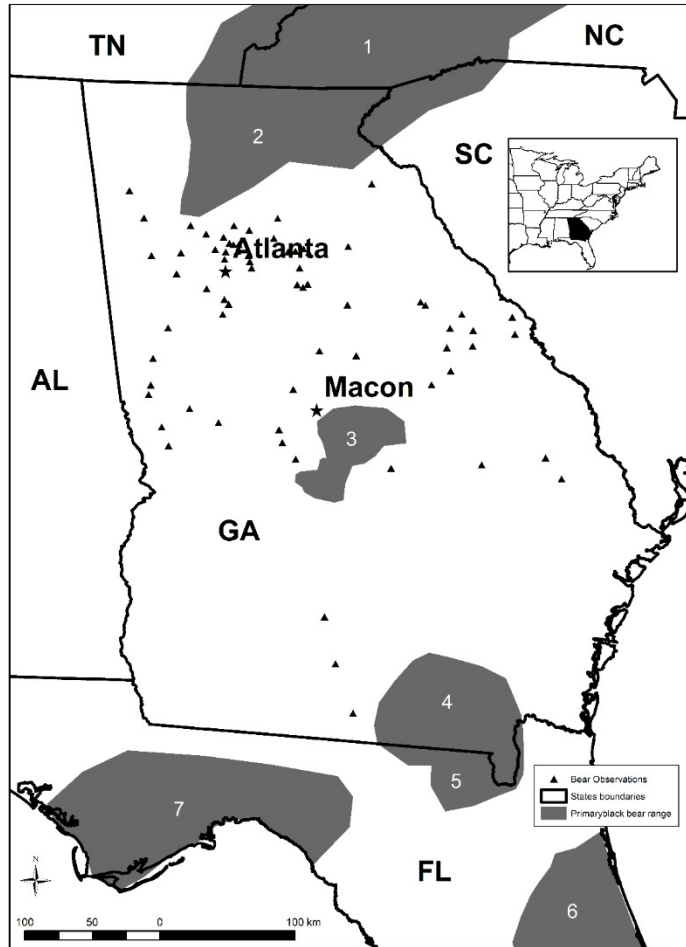


Figure 3.2. Map of the state of Georgia and neighboring states with primary American black bear ranges including; (1) Great Smoky Mountains black bear population of North Carolina, South Carolina, and Tennessee, (2) The North Georgia black bear population, (3) the Central Georgia black bear population, (4) the South Georgia black bear population, (5) the Ocala black bear population of Florida, (6) the Ocala black bear population of Florida, and (7) the Apalachicola black bear population of Florida, and incidental, inter-population American black bear observations in Georgia 2006–2016. Modified and updated from Scheick et al 2011.

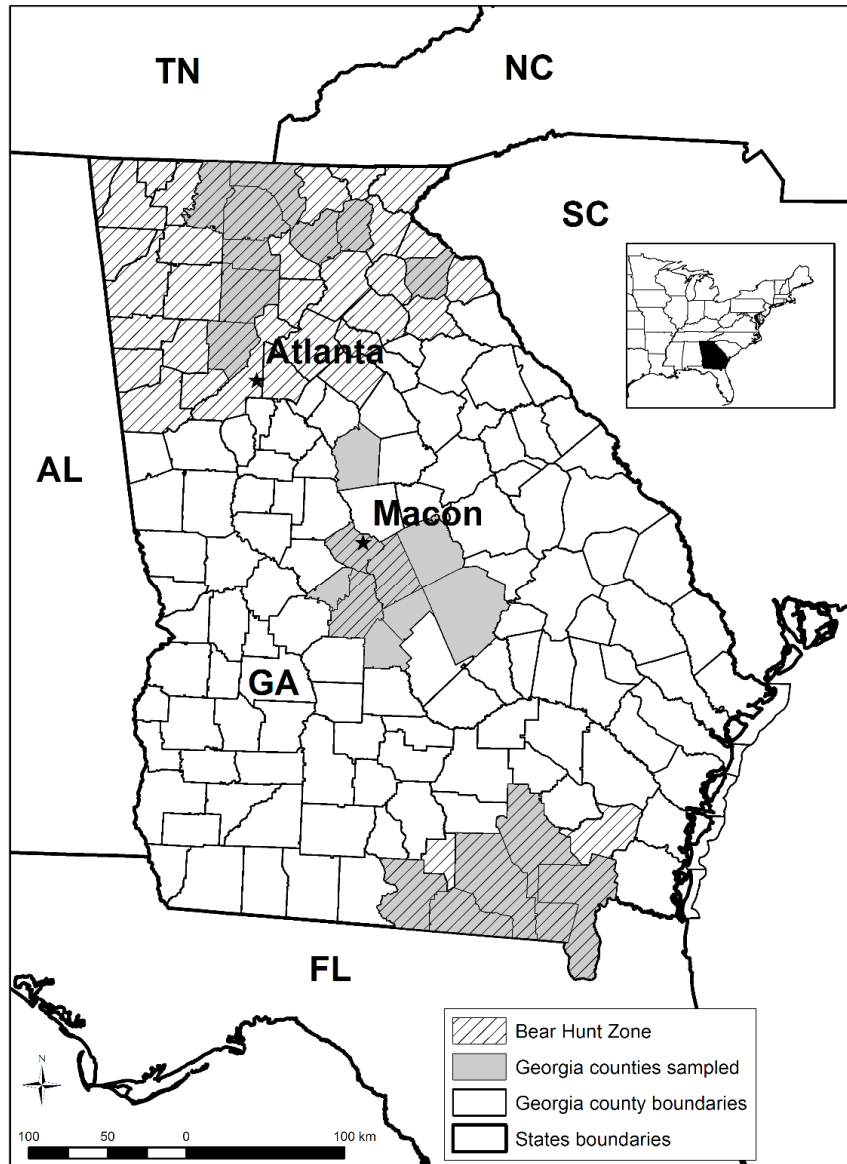


Figure 3.3. Map of the state of Georgia depicting counties, black bear hunting zones, and counties from which black bear samples resulting in genotypes were collected during 2012–2016.

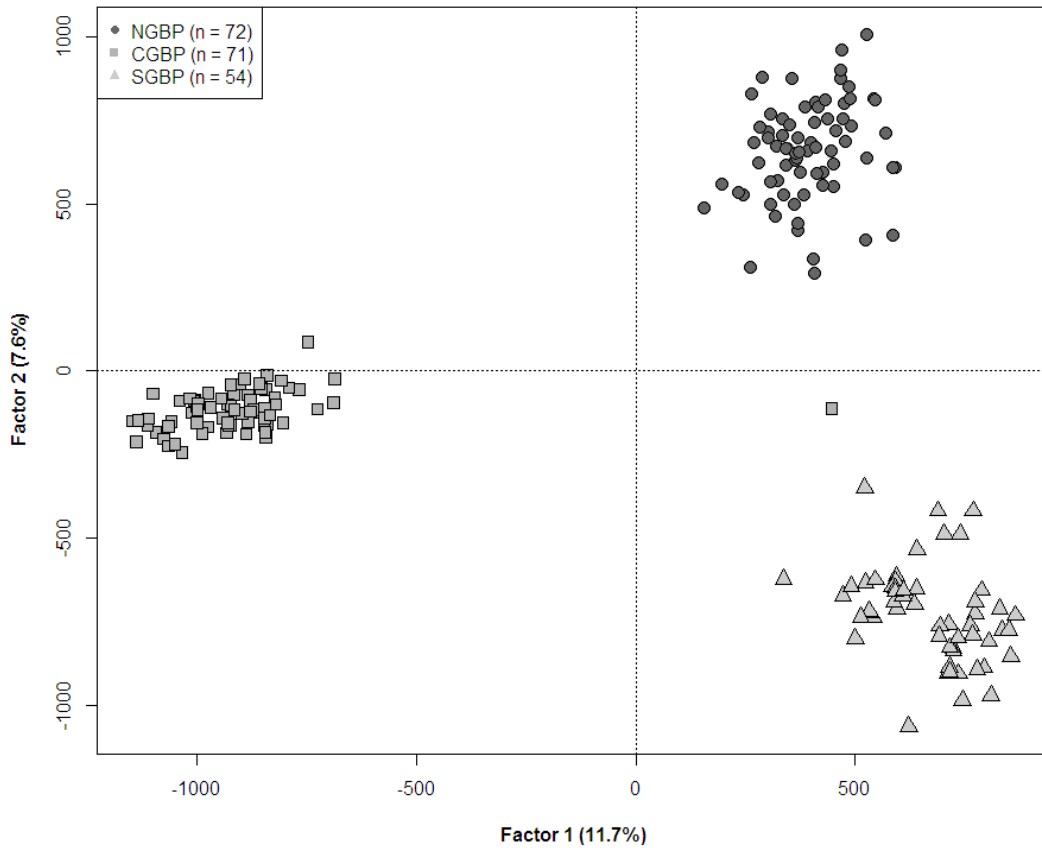


Figure 3.4. Factorial correspondence analysis of 197 American black bear, 22-locus, microsatellite genotypes derived from bears sampled within or between 3 Georgia, USA bear populations: North Georgia Bear Population (NGBP), Central Georgia Bear Population (CGBP), and South Georgia Bear Populations (SGBP), during 2012–2016. Parenthetical percentages are variance accounted for by respective factor.

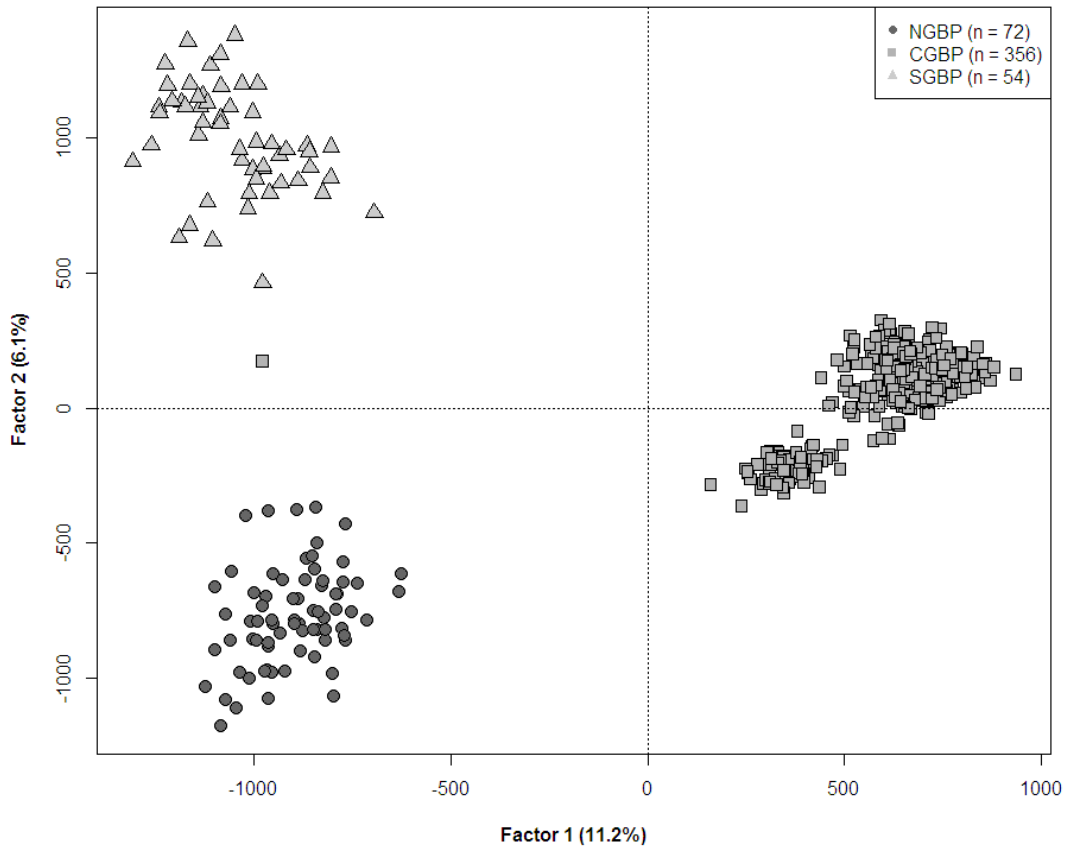


Figure 3.5. Factorial correspondence analysis of 482 American black bear, multi-locus, microsatellite genotypes derived from bears sampled within or between 3 Georgia, USA bear populations: North Georgia Bear Population (NGBP), Central Georgia Bear Population (CGBP), and South Georgia Bear Populations (SGBP) during 2012–2016. Parenthetical percentages are variance accounted for by respective factor.

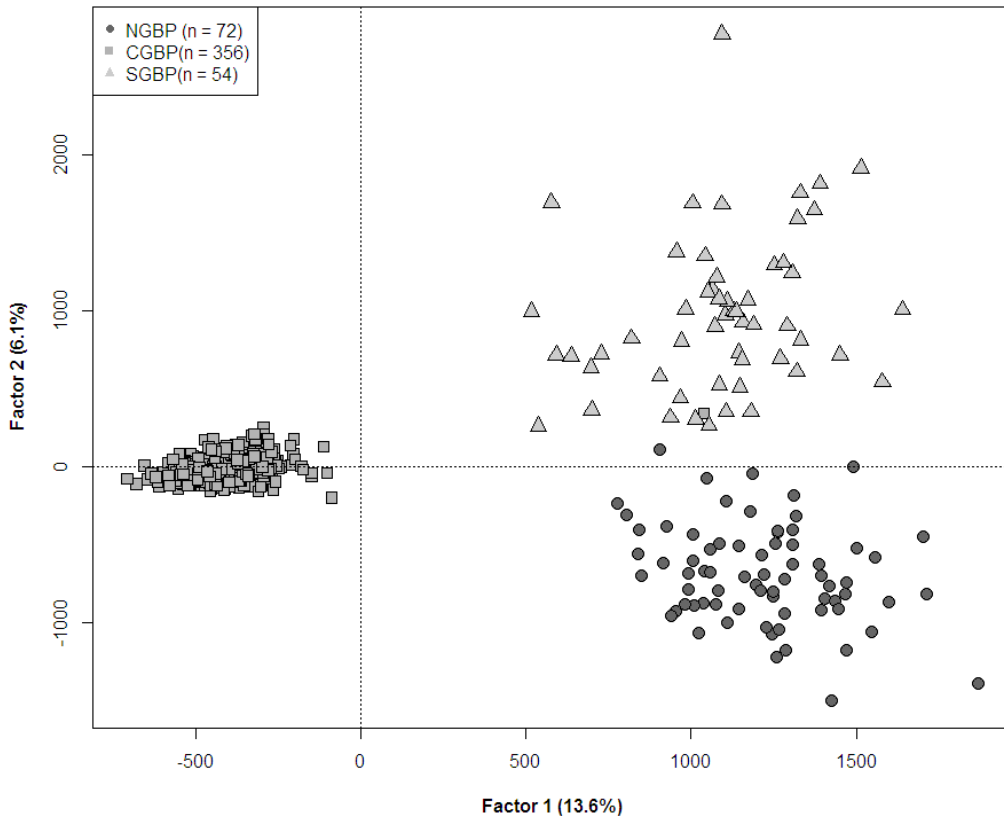


Figure 3.6. Factorial correspondence analysis of 482 American black bear, 10-locus, microsatellite genotypes derived from American black bears sampled within or between 3 Georgia, USA black bear populations: North Georgia Bear Population (NGBP), Central Georgia Bear Population (CGBP), and South Georgia Bear Populations (SGBP) during 2012–2016. Parenthetical percentages are variance accounted for by respective factor.

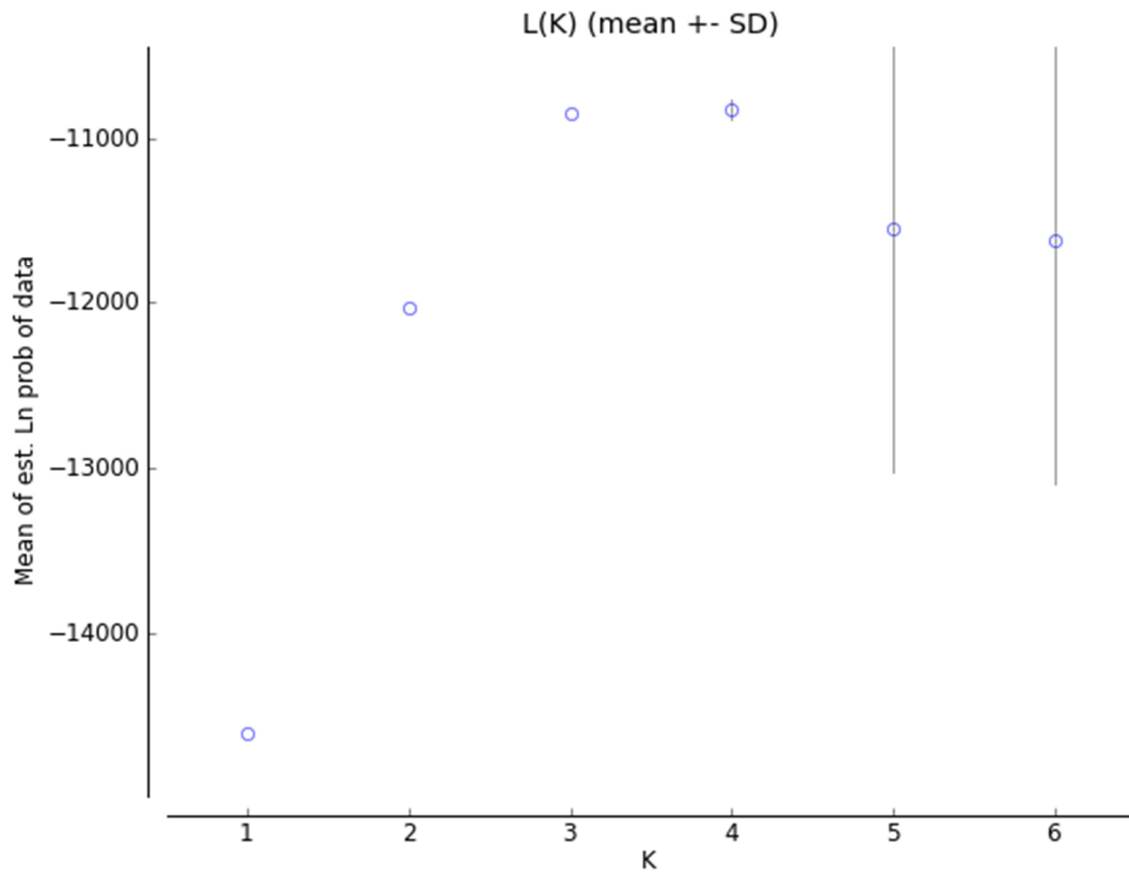


Figure 3.7. Graph depicting log probability [$\ln P(D)$] of 1–6 clusters (K) based on genetic assignment of 482 multilocus, microsatellite genotypes of American black bears sampled from within or between 3 Georgia, USA bear populations during 2012–2016.

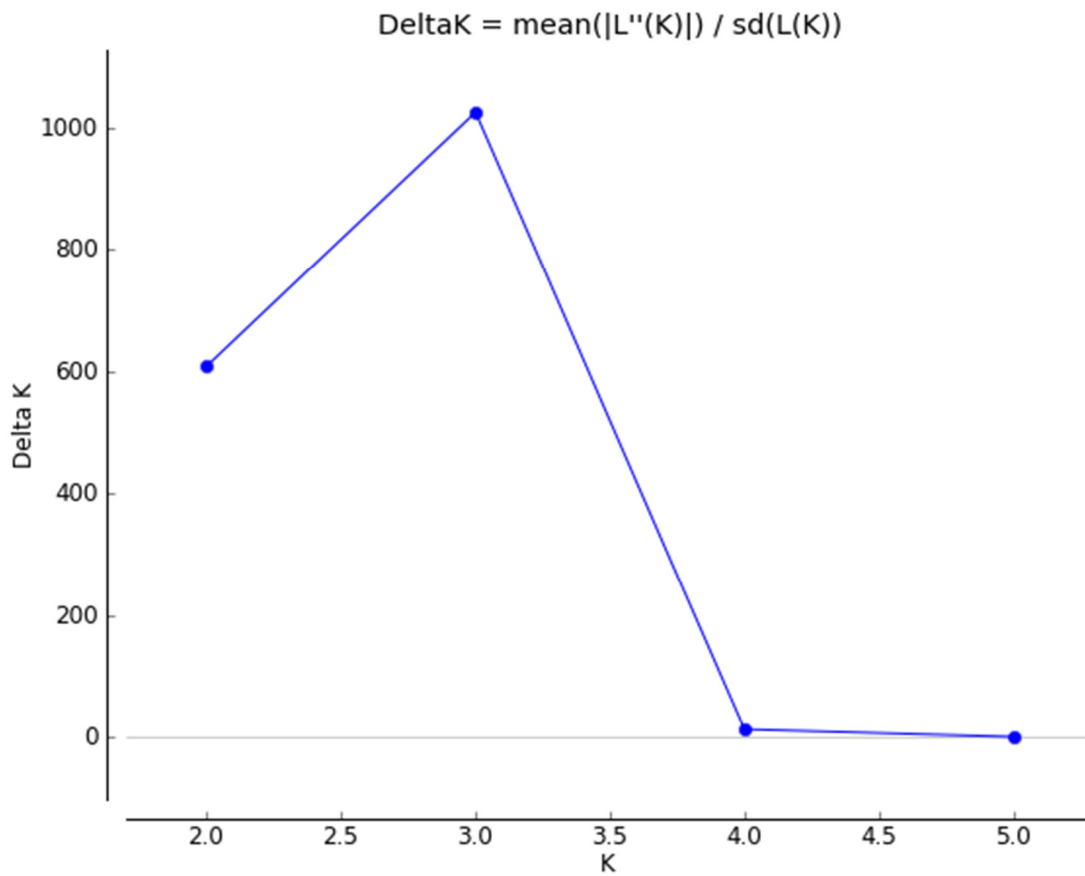


Figure 3.8. Graph depicting Delta K (ΔK) across 2–5 clusters (K) of 482, multilocus microsatellite genotypes of American black bears sampled from within or between 3 bear populations in Georgia, USA. The peak value at $K=3$ indicates the uppermost level of structure among the 4 cluster scenarios during 2012–2016.

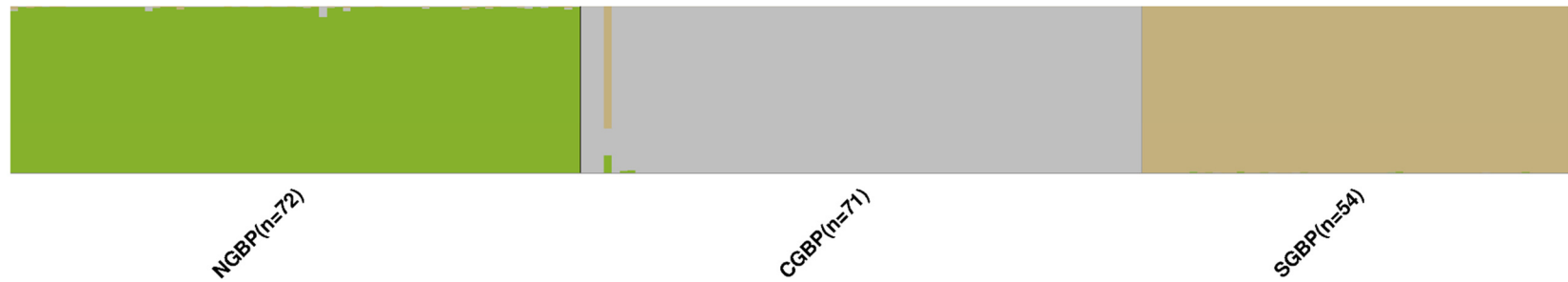


Figure 3.9. Bar graph depicting population assignment clustering ($K=3$) of American black bear 22-locus microsatellite genotypes of 196 bears sampled from within or between 3 Georgia, USA black bear populations and showing little evidence of admixture between populations (individual bars with mixed colors). Each narrow vertical bar represents an individual bear. X-axis labels indicate assumed population of origin, based on sampling location, for individuals with sample size (n) in parenthesis. Y-axis and colors represent each bear's estimated proportion of membership in each of the 3 inferred clusters; North Georgia bear population (green), Central Georgia bear population (gray), South Georgia bear population (tan). 2012–2016.

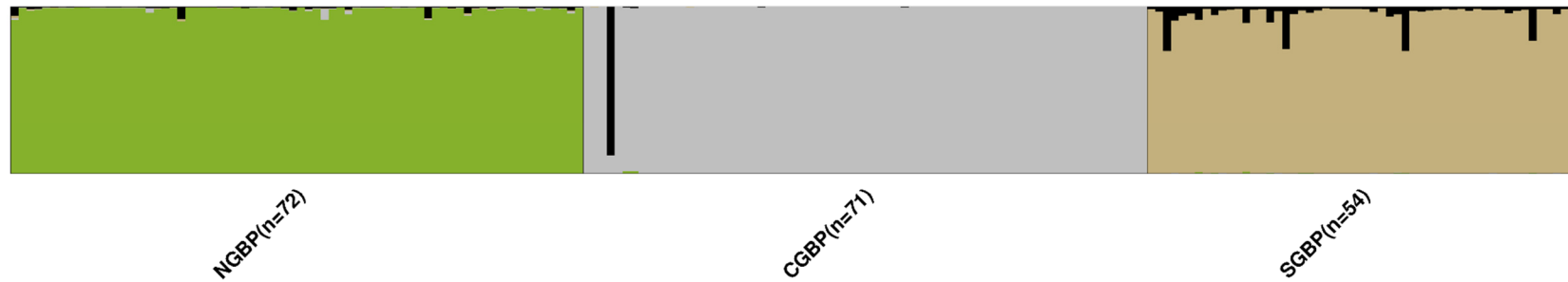


Figure 3.10. Bar graph depicting population assignment clustering ($K=4$) of American black bear 22-locus microsatellite genotypes of 196 bears sampled from within or between 3 Georgia, USA black bear populations. Each narrow vertical bars represent an individual bear. X-axis labels indicate assumed population of origin, based on sampling location, for individuals with sample size (n) in parenthesis. Y-axis and colors represent each bear's estimated proportion of membership in each of the 4 inferred clusters; North Georgia bear population (green), Central Georgia bear population (gray), South Georgia bear population (tan), and other (black). 2012–2016.

CHAPTER 4

EVALUATION OF CONNECTIVITY AMONG AMERICAN BLACK BEAR (*URSUS AMERICANUS*) POPULATIONS IN GEORGIA, USA

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ABSTRACT

Habitat fragmentation and subdivision of wildlife populations are fundamental causes of decline and increased extinction risk for various wildlife species including many large carnivores. The Central Georgia Bear Population, 1 of 3 bear populations in Georgia, USA has a history of isolation and is therefore of conservation concern. We used high-intensity global positioning system location data acquired from male black bears in Central Georgia to develop a step selection function of male bear movement in Georgia. From 2012–2014, we captured, collared, and tracked 33 male bears collecting locations at 20-minute intervals. To characterize connectivity between the Central Georgia Bear Population and surrounding bear populations, we developed a step selection function based on empirical location data. We used a geographic information system to generate a movement cost surface using the regression coefficients of our step selection function, and projected hypothetical bear movement paths across this surface to estimate the suitability of landscape connectivity among Georgia and surrounding bear populations. Our model indicates that connectivity between the Central Georgia Bear Population and surrounding bear populations is poor, and management actions should be taken to improve this connectivity.

INDEX WORDS: American black bear, connectivity, corridor, Georgia, movement, step selection function, *Ursus americanus*

INTRODUCTION

Loss and fragmentation of wildlife habitats, and concomitant subdivision of wildlife populations dependent on these habitats, are common wildlife conservation concerns (Barbault and Sastrapradja 1995). Resultant losses of landscape connectivity among populations can lead to reduced genetic diversity within populations (Sherwin and Moritz 2000), reduced (or eliminated) gene flow between populations (Vos et al. 2002), and ultimately to increased probability of extinction (Saccheri et al. 1998).

Long-term persistence of populations comprised of spatially discrete subpopulations can depend on dispersal of individuals from one subpopulation to another, or on colonization or re-colonization of vacant habitat patches (Hanski 2005). Dispersal events are dependent on many factors including subpopulation demographics (e.g., availability of dispersers), physical capabilities of dispersers, and characteristics of the landscape through which dispersals must occur. Although bears are capable of long-distance movements [80–507 km; (Rogers 1987), (Stratman et al. 2001), (Lee and Vaughan 2003), (Clark et al. 2015)] their dispersals are limited by their relative low numbers, slow reproductive rates, and propensity to create conflicts with humans while attempting to move through human-dominated landscapes.

The American black bear (*Ursus americanus*) is the most common and widely distributed North American member of the family Ursidae (Pelton 2003). However, the current range of the black bear represents only approximately 62% of its historic range (Pelton and van Manen 1994, Scheick and McCown 2014). The conservation status and densities of black bear populations vary widely across this range. In some areas of North America, black bears are abundant, sustain high levels of harvest, and are sometimes considered a pest. Conversely, other regions of North America, including the southeastern United States (hereafter Southeast), maintain only small,

isolated remnant populations of black bears or have experienced black bear extirpation (Pelton 2003).

Maehr (1984) estimated that bears inhabit only 10% of their historic range in the Southeast due to habitat loss and historic overexploitation. However, due to conservation efforts, changes in bear harvest regulations, and protection and/or restoration of bear habitat, many states in the eastern United States have experienced growing bear populations and expansion of bear distribution in recent times (Pelton 2001).

Specific to the Southeast, Wooding et al. (1994) reported at least 13 separate populations of black bear within the Coastal Plain geophysical region. Combined, these populations represent 3 of the 16 black bear subspecies reported by Hall (1981); the eastern black bear (*U. a. americanus*), the Louisiana black bear (*U. a. luteolus*), and the Florida black bear (*U. a. floridanus*). The Florida black bear and the Louisiana black bear are endemic to the Coastal Plain (Wooding et al. 1994). Both the Florida black bear and Louisiana black bear have been the target of intense conservation efforts.

The State of Georgia contains 3 bear populations representing 2 of the southeastern American black bear subspecies described by Hall (1981). The North Georgia Bear Population (NGBP) and the Central Georgia Bear population (CGBP) are considered to be eastern black bear, whereas the South Georgia Bear Population (SGBP) is considered to be the Florida black bear. Collectively, these populations are estimated to contain roughly 5,100 bears with the NGBP being the most abundant population and the CGBP being the least abundant (Georgia Department of Natural Resources 2010, Hooker et al. 2015, Ashley 2016).

Bears in the NGBP can be found in the northern counties of Georgia from the Georgia-Tennessee state line southward toward the suburbs north of Atlanta, and the Interstate-85

corridor between Atlanta and Greenville, South Carolina. The CGBP is restricted primarily to 5 counties along the Ocmulgee River in Central Georgia southeast of Macon (i.e., Bibb, Bleckley, Houston, Pulaski, and Twiggs counties). The SGBP is located in the south-central counties of Georgia along the Georgia-Florida state line and associated with Okefenokee Swamp. Both the NGBP and the SGBP are parts of trans-border populations shared with Georgia's neighboring states: North Carolina, South Carolina, and Tennessee to the north and Florida to the south. The NGBP is contiguous with the bear population in the mountains of south Tennessee and western North and South Carolina. The NGBP is also the likely source of bears colonizing northeastern Alabama. The SGBP is contiguous with the Osceola bear population in northern Florida (Dobey et al. 2005). Conversely, the CGBP has been considered demographically and genetically isolated from other bear populations in the recent past (Miller 1995, Sanderlin et al. 2009).

Jenkins (1953) was the first to report on the CGBP and estimated it to be < 40 bears. Roughly 30 years later, Grahl (1985) reported an estimate of 64 bears and noted that local residents were mostly unaware of the presence of the CGBP. Recently, the CGBP has been estimated at 430 animals inhabiting about 1,127 km² of forested land along the Ocmulgee River, roughly 150 km southeast of Atlanta (Fig. 4.1; Ashley 2016). This area is almost completely surrounded by human development and fragmented agricultural land. Relatively low abundance and potential isolation from other bear populations makes conservation of the CGBP of special concern. The CGBP is separated from the 2 other Georgia bear populations by distances of ~150 km, resulting in frustrated dispersal and poor connectivity among the populations. Between the CGBP and the NGBP is the city of Atlanta, characterized by considerable urban sprawl and several interstate highways. Between the CGBP and the SGBP is primarily agricultural land

cleared of forest. Although bears are occasionally reported in areas between the 3 populations, the level of demographic and genetic separation among these populations is uncertain.

Corridor development and/or maintenance is a common tool that has been used in efforts to conserve or restore a variety of species in fragmented landscapes (Noss et al. 1996, Vos et al. 2002, Nelson et al. 2003, Dixon et al. 2006, Gilbert-Norton et al. 2010). Noss (2003) provided a model for refuge and corridor development meant to facilitate dispersal of animals among subpopulations. Assessment of connectivity and corridor design, sometimes based on expert opinion (Beier et al 2009), can be improved by incorporating empirical data and analytical methods (Clevenger et al. 2002, Pullinger and Johnson 2010). An initial step in corridor establishment should be an evaluation of landscape connectivity among populations of interest, considering not only availability of habitat, but also life history traits and movement capabilities of the focal species.

Advancements in global positioning system (GPS)-based wildlife tracking are making it increasingly possible to acquire accurate and precise high resolution serial location data for many species (Recio et al. 2011). Concomitant with these technological advancements are improved analytical methods for making inference from the resulting data. One such method is the step selection function (SSF; Fortin et al. 2005, Duchesne et al. 2010, Thurfjell et al. 2014). The SSF analysis is a method by which animal steps (i.e., the distance and turning angle between sequential locations) are associated with landscape variables via conditional logistic regression, thus linking the animal's movement to landscape variables in a resource selection manner (Boyce and McDonald 1999).

Our objectives were to (1) characterize bear movement on the landscape, (2) determine habitat types and landscape features influential to bear movement, (3) project bear movement

paths across the inter-population areas of Georgia based on the above information, and (4) estimate the relative rate at which these projected paths (i.e., hypothetical bears dispersing from the NGBP and SGBP) intersect with the CGBP.

STUDY AREA

Data collection was conducted within Houston and Twiggs Counties, Georgia (Fig. 4.2). Predominant forest types were bottomland hardwood forests within the Ocmulgee River flood plain and planted pine (*Pinus* spp.), natural pine, and mixed pine-hardwood in the uplands. Common overstory tree species included loblolly pine (*Pinus taeda*), red and white oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), water tupelo (*Nyssa aquatica*), and bald cypress (*Taxodium distichum*). Clear-cutting, tree thinning, and prescribed burning of the understory were common forestry practices in the study area.

Most forest land in the area was managed for seasonal, recreational hunting. Common large and medium-sized mammals included white-tailed deer (*Odocoileus virginianus*), feral pigs (*Sus scrofa*), black bear (*Ursus americanus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*) opossum (*Didelphis virginianus*) and armadillo (*Dasypus novemcinctus*).

The Ocmulgee River flowed through the study site from north to south and was a defining geographical feature. Nearby human population centers included Macon (pop. 91,234), Warner Robins (pop. 72,531), Bonaire (pop. 13,999), Cochran (pop. 5,150), and Hawkinsville (pop. 4589, U.S. Census Bureau 2010). Much land west of the study area was dominated by human development, whereas land to the south and east was primarily agricultural land. Major

crops included cotton (*Gossypium hirsutum*), corn (*Zea* spp.), peanut (*Arachis hypogaea*), sorghum (*Sorghum* spp.) and other grain crops.

METHODS

GPS Tracking

During summers 2012–2014, we captured bears with modified Aldrich foot snares (Johnson and Pelton 1980) using soured corn and artificial flavoring (Mother Murphy's, Greensboro, North Carolina, USA) to attract bears to the snares. We anesthetized captured bears with Telazol[®] (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) or large animal xylazine (100mg/ml) combined with Telazol[®] (XZT). We reversed bears anesthetized with XZT using atipamazol hydrochloride (Antisedan[®], Orion Pharma, Orion Corporation, Espoo, Finland) and diazepam approximately 45 minutes after initial anesthesia. We monitored rectal temperature throughout the anesthesia event, and bears exhibiting elevated rectal temperatures were cooled by having cold water poured on their extremities. We monitored pulse and blood oxygen saturation levels using pulse-oximeters, and bears with blood oxygen levels below ~90% received supplemental oxygen via nasal cannula.

We ear-tagged all captured bears with paired, numbered button tags (All American[®], Y-Tex Corporation, Cody, Wyoming, USA), and tattooed the inside of the right upper lip with a number corresponding to the ear-tag number. We implanted a passive integrated transponder (PIT) sub-cutaneous along the mid-line of the back between the scapulae. We recorded sex, weight, and a series of standard morphometric measurements, and extracted the first upper premolar (UPM1) using an apical 301 dental elevator. Collected teeth were used for cementum-

annuli aging (Willey 1974). Our capture and handling methods were approved by the University of Georgia Institutional Animal Care and Use Committee (Protocol Number A2011 10-004-A1).

We collared bears with WildCell[®] (Lotek Wireless Inc., Newmarket, Ontario, Canada), GPS/General System for Mobile (GSM) collars (hereafter collar). For bears weighing ~45.4 kg or greater, we used WildCell[®] MG series collars, whereas we used WildCell[®] SG collars on bears in the ~22.7–45.4 kg range. In 2012, all collars were equipped with a timed, mechanized release programmed to release 52 weeks after activation, and a leather break-away (Garshelis and McLaughlin. 1998). After 2012, collars had only a leather break-away.

All collars were pre-programmed so that upon initialization at time of deployment they would begin acquiring 1 GPS-location every hour and after 5 successful locations, the locations would be sent to a desk-top base station via GSM. Once a collar made contact with the base station and location data indicated the bear had recovered from anesthesia and left the capture site, we reprogrammed the collar via GSM to acquire 1 location every 20 minutes.

Analysis

We screened GPS location data using a multi-step approach. Initially, we plotted each bear's location data in ArcMap[®] 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA) visually inspected the data for extreme, nonsensical locations, and removed them. We then removed locations classified as 2 dimensional (2D) with dilution of precision values (PDOP) >5 (Lewis et al. 2007). We used the function *movement.pathmetrics* in Geospatial Modeling Environment (GME) software (Beyer 2012) to calculate step lengths, turning angles, and time intervals between sequential locations for all male bears in our dataset (Beyer 2012). Since our focus was bear movement, we were not interested in sequential locations of stationary

bears (e.g., bedded or denned bears) so we removed sequential locations that were <50 m apart (Latham et al. 2011, Clark et al. 2015).

Because of missed locations, variation in location acquisition time, and other factors, not all locations were precisely 20 minutes apart. We reviewed the distribution of times between sequential locations and determined that most were temporally separated by 17–23 minutes, hence we filtered data to remove locations that fell outside this range. We calculated an angular-linear correlation coefficient for the remaining data to test for correlation between turning angle and step length (Fisher 1995, Agostinelli and Lund 2013).

We grouped observed step lengths arbitrarily into 24 bins ranging from 50 m to 1998 m. We grouped observed turning angles into 18, 20-degree bins. We derived potential bear movements (10 random steps for every observed step for each bear) from the above distributions with each bear being represented by only the empirical data of all other bears in the sample (Thurfjell et al. 2014).

We used a variety of spatial data to characterize landscape attributes we thought could influence bear movement. Our primary source for land cover classification was the 2011 National Land Cover Database (NCLD; U.S. Geological Survey 2014), a 16-class land cover classification scheme. We used ArcMap® 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA) to simplify these 16 classes into broad categories; forest, natural, open water, and agriculture (Table 4.1). Because our empirical data suggested that GPS-collared bears seldom used bottomland hardwoods along the Ocmulgee River, we created a forest category of only this forest type. The water category consisted of any area classified as open water by the NLCD dataset. However, these data under-represented portions of rivers that had forest canopy cover and, therefore, were classified as forest. Hence, we combined the NLCD

open water category with the stream and river data from the National Hydrography Dataset accessed through the National Map (U.S. Geological Survey 2006) to create data which more adequately represented water bodies a bear could encounter while traversing the landscape. We created a hydrologic datasets representing ponds, lakes, reservoirs, and rivers. We created a dataset of primary roads (e.g., paved county roads, state highways, and federal interstates highways) using 2012 TIGER/Line1 data that were based on the redistricting 2010 census (U.S. Bureau of the Census 2010). We created data layers quantifying landscape variables using ArcMap® 10.3.1 (Environmental Systems Research Institute, Redlands, California, USA) to measure Euclidian distance from each raster cell to the nearest cell classified as a given variable (Table 4.2).

Following the creation of the spatial variables, we used the GME tool *Isectlinerst* to combine observed and potential steps with the landscape data. Although 5 summary attributes could be assigned to each landscape variable and step (i.e., the value at the beginning of a step, the end of a step, the maximum value, the minimum value, and the linear weighted mean), the GME tool does not allow attributes to be mixed for evaluating interaction effects, so we used only attributes at the end of each step.

Because our main interest was modeling movement of bears across the landscape between occupied bear ranges, we restricted further analysis to our dataset of male locations. To estimate a step selection function for male bears, we used conditional logistic regression in Program R 2.15.3 (R Core Team 2014) based on a Cox proportional hazards model in the *survival* package (Therneau 2013). First, we performed a correlation analysis and excluded 1 variable of any pair of correlated variables (i.e., Pearson's $r > 0.6$). Remaining variables were used to develop a candidate set of models. We then fit models using the Cox proportional hazard

conditional logistic model in the R-package *survival*. Once fit, we ranked models by Akaike Information Criterion scores (AIC_c; Burnham and Anderson 1998, Mazerolle 2016).

Autocorrelation among sequential location data can produce biased estimates of variance (Nielson et al. 2002), which can lead to model selection errors. Therefore, we estimated robust standard errors for fitted parameters from fixed-effects models based on a sandwich estimator (Fortin et al. 2005, Forester et al. 2009). We used methods described by Forester et al. (2009) whereby we first fit the model with the full data set and calculated the deviance residuals for each stratum (i.e., used vs. random pairings). We then fit an intercept-only mixed effects model and plotted the autocorrelation function of that model to graphically determine the lag of correlation. We then recoded the data by grouping the sequential observations based on the lag into clusters and re-fit the model using the *cluster* option within the *clogit* function of the the R-package *survival* (Therneau 2015).

Lastly, we used the GME function *movement.sfsim1* to simulate bear movement across this cost surface. We created 100 random points within the area of the cost surface representing the range of the NGBP, the SGBP, and the Apalachicola bear population in northern FL. We projected a 26,000 step (i.e., ~1 year assuming 20 min step intervals) movement path using the step selection model we had created from the empirical CGBP movement data.

RESULTS

Between May 2012 and the end of 2014 we GPS-tracked 33 male bears. The median age of 32 collared males for which we received cementum-annuli age data was 4 years and ranged from 1–8 years (Fig. 4.3). The 1 male for which we did not receive a cementum-annuli age was estimated to be a 1 year-old. After filtering and sub-setting data, 92,925 locations remained with

a mean step length of 254.0 m (SD=183.1) and a maximum of 1940.6 m. We found a mean of 2734.1 (SD=2008.1) steps per male bear with a range of 77–9646 steps.

Step lengths were skewed toward shorter distances with few steps >750 m (Fig. 4.4). Turning angles ranged from -179.9–179.9 degrees with 0 representing no change in direction from the previous location. There was skew in the distribution of turning angles favoring values closer to 0 indicating forward movement (Fig. 4.5). We found no correlation between step lengths and turning angles ($R^2 < 0.001$).

We removed distance to forest due to correlation with distance to natural, but we observed no appreciable correlation in pairings of the remaining variables. With the remaining 5 Euclidean distance variables, we developed and fit 11 models with various combinations of the variables and 3 interaction terms (Table 4.3). Model selection favored the global model containing all parameters and interaction terms.

The probability of a step being taken increased as distance between the endpoint of the step and natural habitat, agriculture fields, woody wetlands, or the interaction between natural and agriculture decreased (Table 4.4). Conversely, the probability of a step being taken decreased as the endpoint of the step neared roads, open water, or the interaction terms of natural and roads and natural and woody wetland. All variable coefficient values were relatively weak with Euclidean distance to natural being the strongest.

Of the 100 simulated 6-month-long bear movement paths emanating from the NGBP, SGBP, and Apalachicola, FL bear population, none intersected with the range of the CGBP (Fig. 4.6). Paths from the NGBP intersected with no other bear population. No paths emanating from the SGBP and the Apalachicola population intersected other populations; however, one path emanating from the SGBP intersected a path emanating from the Apalachicola population in an

area midway between the 2 populations. Two additional paths, one from each of these populations were also in this area. It should be noted that the SGBP and the Apalachicola bear population of FL are the 2 closest populations to one another of the populations we considered.

DISCUSSION

We found that male black bears in Central Georgia exhibited selectivity in making steps (i.e., relocations from one position to another) relative to landscape variables at the temporal and spatial scale we considered. Based on the regression coefficients of the landscape variables in our SSF model, selection was relatively weak for most variables indicating variation in the step-selection process for which we did not account. However, we believe that our model captured the essence of black bear movement across the Georgia landscape and allowed us to make inference regarding the level of connectivity among the 3 Georgia bear populations and the bear populations of Northern FL.

Connectivity (e.g. corridor design) often uses basic habitat requirements of the focal species and expert opinion to determine the existence of, or development of, wildlife corridors (see Kennedy 2014). However, connectivity should be measured in terms of function and not just form [i.e., the spatial pattern of habitat patches (Tishendorf and Fahrig 2000)]. Movement characteristics of the focal species as they relate to resource selection should also be considered (Forester et al. 2009). We used empirical data and a SSF to evaluate functional connectivity between bear populations by simulating bear movement and the step-by-step decision making process bears use relative to landscape variables. Our focus was the landscape between populations and not necessarily in demographic realism. We modeled 100 bears leaving each of the 3 source populations and moving continuously for the equivalent of 1 year. We acknowledge

that this is far from reality both in terms of the actual number of dispersing males the source populations could be expected to produce in a given year, and the amount of time a bear would actually spend in motion. However, this approach did ensure that we sampled the landscape adequately by having a large number of bears in constant motion exploring the cost surface. For a similar reason, we did not factor in mortality which is usually inflated for dispersing bears (Bunnell and Tate 1981, Elowe and Dodge 1989, Schwartz and Fransmann 1992, Lee and Vaughan 2003). It should also be noted that while we refer to our simulated bears as dispersers, none of the bears from which we collected movement data dispersed from the CGBP while data collection was taking place. However, several males made forays up to 80 km away from the CGBP through the landscapes of interest before returning to the CGBP.

None of our simulated bear paths reached the CGBP, but we recognize that this does not mean that bears originating outside the CGBP are incapable of reaching the CGBP. In 2015, a 3-year-old male bear with a microsatellite genotype consistent with bears from the Apalachicola bear population in Florida was killed by a vehicle in Central Georgia, roughly 20 km from habitat known to be occupied by Central Georgia bears (see Chapter 3). It is likely that had we run our simulations for longer durations, eventually simulated paths would intersect the CGBP. Clark et al. (2015) suggested that in addition to landscape variables that influence bear movement (e.g., roads), Euclidian distance between populations was also an important factor affecting exchange between bear populations. The distances between the populations considered Clark et al. (2015) ranged from 22.8 to 91.3 km. Distances between the CGBP and any other bear population exceed 100 km. We suggest our model demonstrates that the rate at which bears from outside the CGBP could be expected to reach the CGBP is far lower than what would be necessary to constitute demographic or genetic connectivity between the CGBP and other

regional bear populations. We offer that distance between the CGBP and surrounding bear populations and the lack of corridors between these populations currently prevent such connectivity.

MANAGEMENT IMPLICATIONS

Managers should consider the CGBP demographically closed and genetically isolated from other bear populations, and therefore use caution in managing the CGBP. Combined with low levels of genetic diversity within the CGBP (see Chapter 3) our results suggest that neither demographic closure or genetic isolation are likely to abate without management action. We advise against extensive reduction of the CGBP without also taking action to facilitate demographic and genetic support of the CGBP from outside populations. These actions could include the direct introduction of novel genetic material via translocation of bears to the CGBP, or development of corridors to facilitate bear movement toward the CGBP. Likewise, managers could consider development of, via translocation, additional population(s) that would not only have a direct influence on the CGBP, but would also function as a stepping stone for bears moving among bear populations and effectively reduce distances between the CGBP and other populations and thus enhancing connectivity. The SSF model we developed could be used to design and test the effectiveness of various corridor designs or to select areas within which bear populations could be established to facilitate exchange among regional bear populations.

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Table 4.1. Landscape variables used to develop step selection function for male American black bears in Georgia, USA with data source and land cover categories included in each variable, 2012–2014.

Variable	Data Source	Categories Included
Forest	2011 National Land Cover Database	deciduous forest evergreen forest mixed forest woody wetland
Natural	2011 National Land Cover Database	barren deciduous forest evergreen forest grassland herbaceous wetland mixed forest shrub woody wetland
Woody Wetland	2011 National Land Cover Database	woody wetland
Agriculture	2011 National Land Cover Database	crop
Road	2012 TIGER/line data	primary roads
Open Water	2011 National Land Cover Database and National Hydrography Data	open water and rivers

Table 4.2. Landscape variables used to develop step selection function for male American black bears in Georgia, USA with data source and procedure used to develop raster data layer for variable, 2012–2014.

Variable (units)	Source	Procedure
Distance to Forest (m)	2011 National Land Cover Database	Calculated minimum Euclidean distance to nearest Forest
Distance to Natural (m)	2011 National Land Cover Database	Calculated minimum Euclidean distance to nearest area classified as Natural
Distance to Agriculture (m)	2011 National Land Cover Database	Calculated minimum Euclidean distance to nearest Agriculture
Distance to Roads (m)	2012 TIGER/line data	Calculated minimum Euclidean distance to nearest Road
Distance to Woody Wetland (m)	2011 National Land Cover Database	Calculated minimum Euclidean distance to Woody Wetland
Distance to Open Water (m)	2011 National Land Cover Database, National Hydrography Data	Calculated minimum Euclidean distance to Open Water

Table 4.3. Models used to develop a step selection function for male American black bears in Georgia, USA, with log likelihood ($\text{Log}(L)$), number of model parameters (K), Akaike Information Criterion adjusted for small sample (AIC_c), and model weight (w), 2012–2014.

Model	$\text{Log}(L)$	K	AIC_c	Δ	w
$\text{DistRD}^1 + \text{DistNAT}^2 + \text{DistAG}^3 + \text{DistOW}^4 + \text{DistWW}^5 + \text{DistRD}^6 * \text{DistNAT}^6 + \text{DistAG}^7 * \text{DistNAT}^7 + \text{DistWW}^8 * \text{DistNAT}^8$	-221973.1	8	443962.1	0.0	1
$\text{DistRD} + \text{DistNAT} + \text{DistAG} + \text{DistRD} * \text{DistNAT} + \text{DistNAT} * \text{DistAG}$	-221997.7	5	444005.5	43.3	0
$\text{DistRD} + \text{DistNAT} + \text{DistRD} * \text{DistNAT}$	-222018.2	3	444042.4	80.2	0
$\text{DistAG} + \text{DistNAT} + \text{DistAG} * \text{DistNAT}$	-222070.7	3	444147.4	185.2	0
$\text{DistWW} + \text{DistNAT} + \text{DistWW} * \text{DistNAT}$	-222070.9	3	444147.9	185.8	0
$\text{DistRD} + \text{DistNAT} + \text{DistCROP} + \text{DistOW} + \text{DistWW}$	-222103.0	5	444216.0	253.9	0
$\text{DistRD} + \text{DistNAT} + \text{DistCROP}$	-222107.7	3	444221.5	259.4	0
DistNAT	-222116.1	1	444234.2	272.1	0
DistAG	-222818.4	1	445638.7	1676.6	0
DistWW	-222810.1	1	445622.2	1660.1	0
DistRD	-222805.9	1	445613.7	1651.6	0

¹ Distance to road

² Distance to natural

³ Distance to agriculture

⁴ Distance to open water

⁵ Distance to woody wetland

⁶ Interaction of distance to road and distance to natural

⁷ Interaction of distance to agriculture and distance to natural

⁸ Interaction of distance to woody wetland and distance to natural

Table 4.4. Landscape variables used in development of a step selection function for male American black bears in Georgia, USA, with conditional logistic regression results including regression coefficients (β), standard error (se), robust standard error (robust se), z-scores (z) and p values (p), 2012–2014.

Variable	β	se	robust se	z	p
DistRD ¹	5.626E-05	1.808E-05	1.722E-05	3.267	0.00109
DistNAT ²	-1.449E-02	5.903E-04	2.128E-04	-68.075	< 2E-16
DistAG ³	-2.178E-05	2.032E-05	6.981E-06	-3.120	0.00181
DistOW ⁴	1.407E-05	1.817E-05	8.282E-06	1.699	0.08939
DistWW ⁵	-8.870E-05	2.674E-05	2.752E-06	-32.232	< 2E-16
DistRD*DistNAT ⁶	9.072E-07	9.548E-08	8.035E-08	11.291	< 2E-16
DistAG*DistNAT ⁷	-4.081E-06	6.623E-07	3.585E-07	-11.383	< 2E-16
DistWW*DistNAT ⁸	5.893E-06	9.072E-07	5.591E-07	10.540	< 2E-16

¹ Distance to Road

² Distance to Natural

³ Distance to Agriculture

⁴ Distance to Open Water

⁵ Distance to Woody Wetland

⁶ Interaction of Distance to Road and Distance to Natural

⁷ Interaction of Distance to Agriculture and Distance to Natural

⁸ Interaction of Distance to Woody Wetland and Distance to Natural

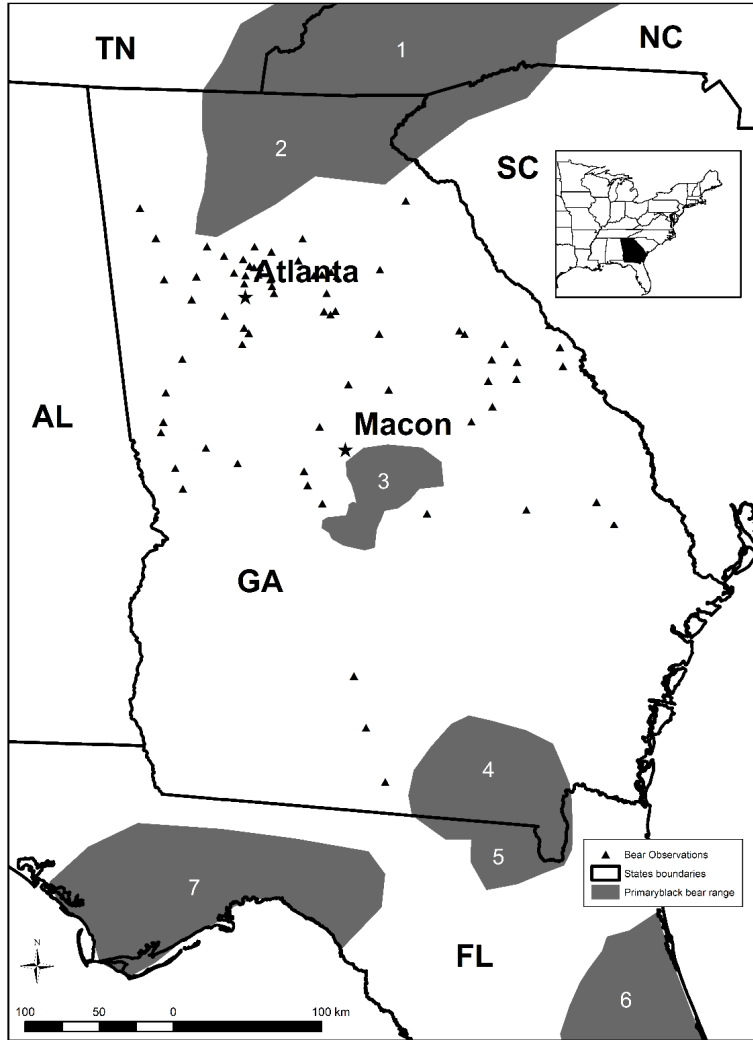


Figure 4.1. Map of the state of Georgia and neighboring states with primary American black bear ranges including; (1) Great Smoky Mountains black bear population of North Carolina, South Carolina, and Tennessee, (2) The North Georgia black bear population, (3) the Central Georgia black bear population, (4) the South Georgia black bear population, (5) the Ocala black bear population of Florida, (6) the Ocala black bear population of Florida, and (7) the Apalachicola black bear population of Florida, and incidental, inter-population American black bear observations in Georgia 2006–2016. Modified and updated from Scheick et al 2011.

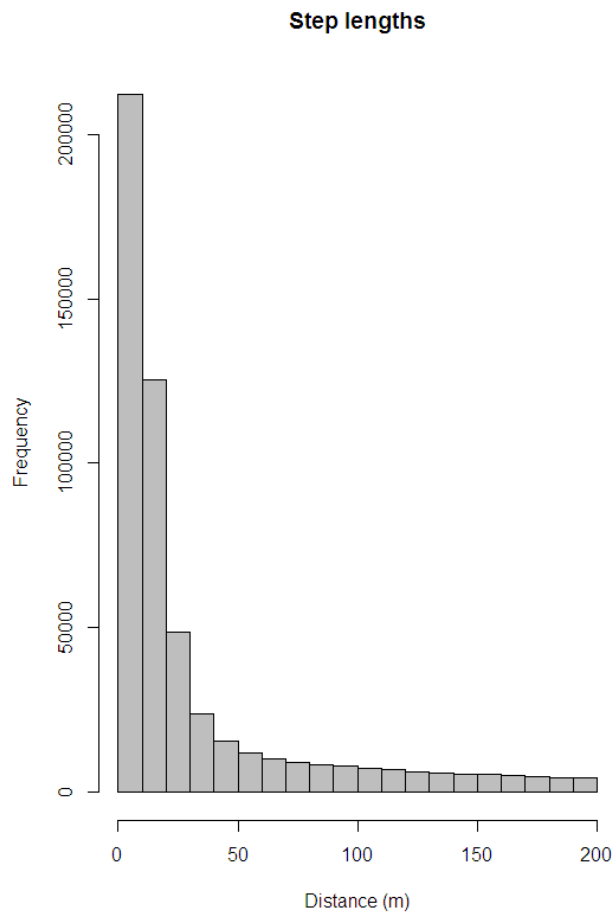


Figure 4.2. Step lengths <200 m for American black bears based on global positioning system collar data collected in Central Georgia, USA from 2012–2014.



Figure 4.3. Histogram of cementum-annuli ages rounded down to whole year and binned by 2 years for 32 male black bears tracked in Central Georgia, USA from 2012–2014.

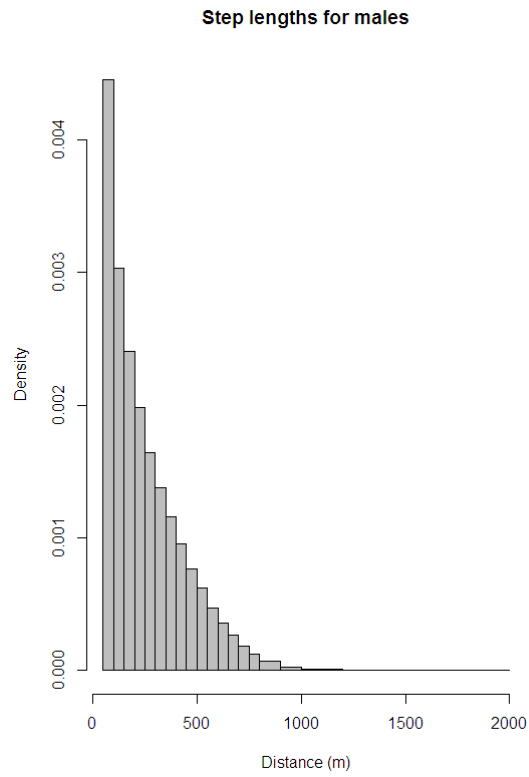


Figure 4.4. Step lengths for male American black bears based on global positioning system collar data collected in Central Georgia, USA from 2012–2014.

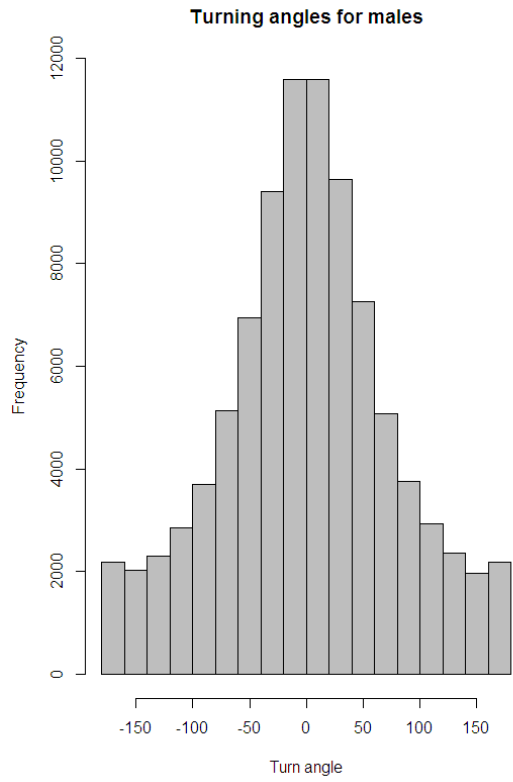


Figure 4.5. Turning angles for male American black bears based on global positioning system collar data collected in Central Georgia, USA from 2012–2014.

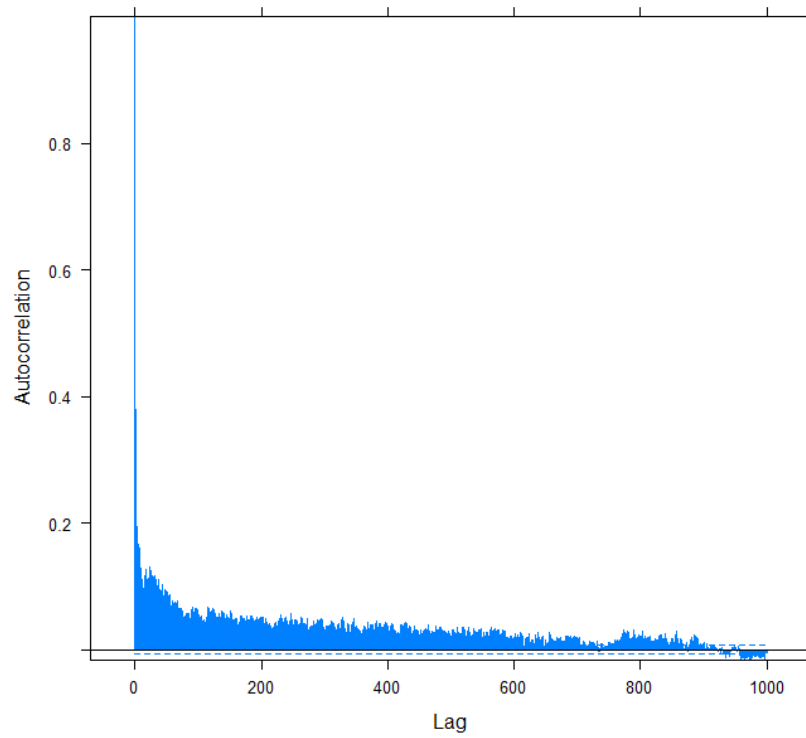


Figure 4.6. Level of serial autocorrelation among male American black bear global positioning system locations used to develop a step selection function for bears in Georgia, USA, 2012–2014.

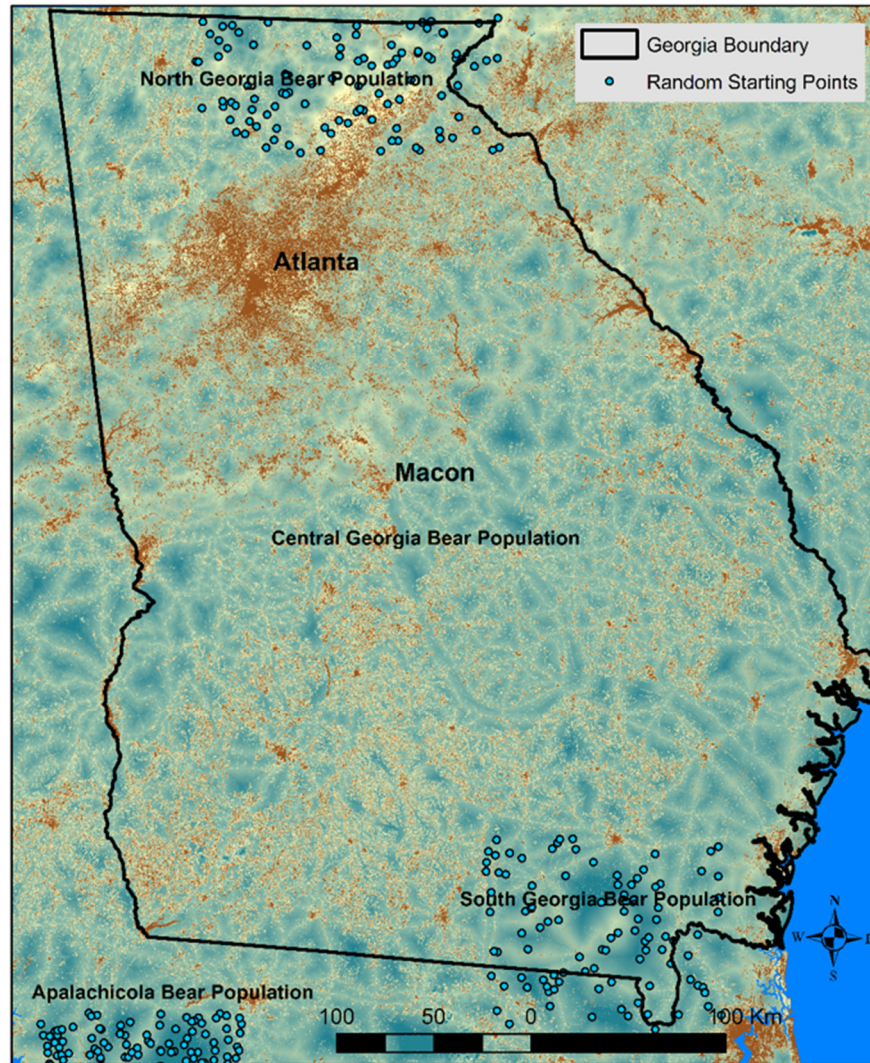


Figure 4.7. Bear movement cost surface derived from male American black bear step selection function and 300 random locations used as starting points for bear movement simulations. Map coloration indicates resistance to bear movement with green indicating less resistance and brown indicating higher resistance. Georgia, USA, 2012–2014.

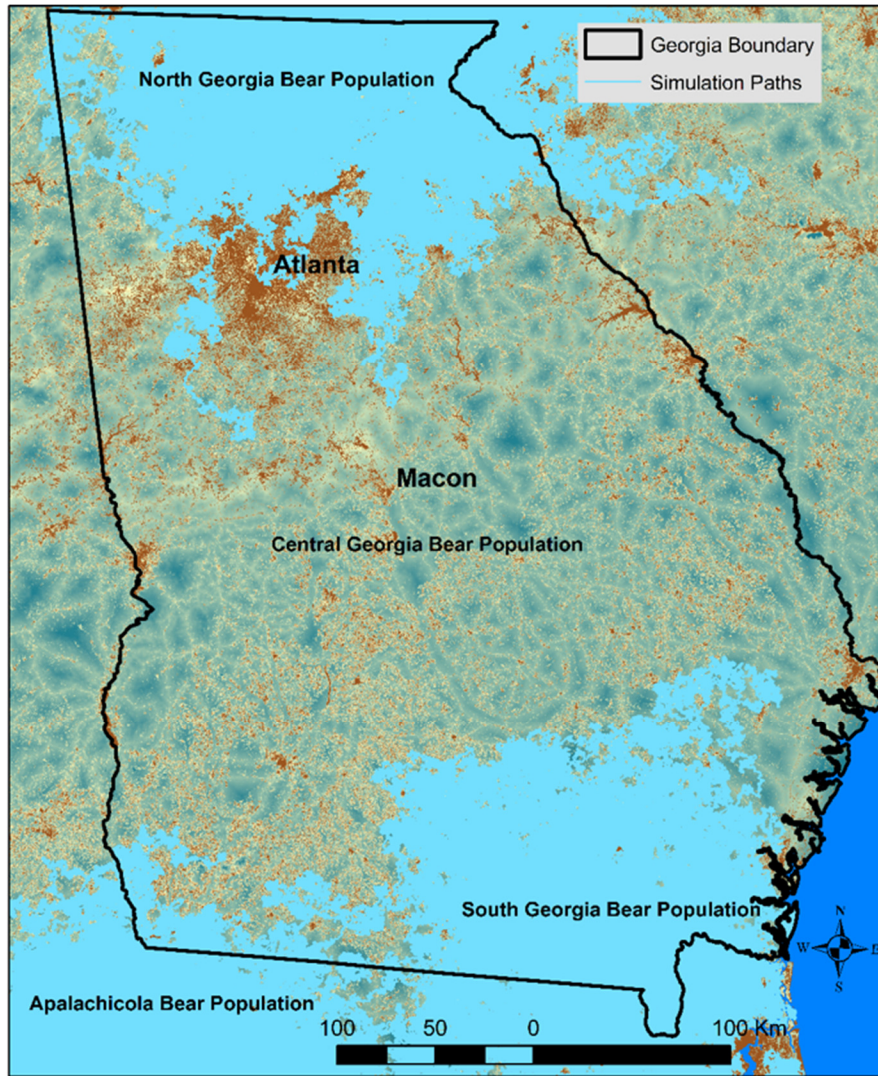


Figure 4.8. Bear movement cost surface derived from male American black bear step selection function and 300 simulated 26,000-step bear movements emanating from 1 of 3 bear populations. Map coloration indicates resistance to bear movement with green indicating less resistance and brown indicating higher resistance. Georgia, USA, 2012–2014.

CHAPTER 5

CONCLUSIONS

For many wildlife populations, the greatest threat to long-term persistence is continued isolation as the result of lost connectivity between populations, and fragmentation of habitat which subdivides already isolated populations (Hilty et al. 2006). Isolation and fragmentation can have both negative demographic and genetic consequences, and can ultimately lead to population decline and loss. This is especially true for many large carnivore species, such as bears, that tend to have large home ranges (i.e., require large areas with which to meet their needs), and are required to make extensive seasonal movements for breeding or to find seasonably available food sources (Beckman and Hilty 2010).

I studied the Central Georgia Bear Population (CGBP), which has history of isolation after having been reduced to ≤ 40 bears during the 1950s (Jenkins 1953). Despite increased abundance of the CGPB since the 1950s (Sanderlin 2009, Hooker et al. 2015, Ashley 2016), the CGPB still faces the threats of isolation from other bear populations and potential subdivision from the widening of a highway which bisects the area inhabited by the CGBP, Georgia State Route (SR) 96.

I GPS-tracked 63 bears near SR 96 and found bear home ranges defined, in part, by the highway. Most bears I tracked did not cross SR 96 although many had home ranges adjacent to the highway. Of bears that did cross the highway most only crossed a few times. Crossings were concentrated in a 2 km section of SR 96 and several bears that crossed did so after traveling away from their apparent home ranges. Our resource selection analysis of bear crossing

locations indicated that distance between the road and forest edge was influential in determining where bears chose to cross SR 96. I used this information to make recommendations regarding the location and design of highway underpasses. Future research should be conducted after SR 96 is widened to determine if the rates or locations of bear crossings differ from what I observed, whether or not bears are using the SR 96 underpasses, and effects the expanded highway might have on demography and genetics of the CGBP.

As a result of isolation and having experienced a genetic bottleneck, I found the CGBP to have low levels genetic diversity compared to larger outbreeding bear populations. Comparing 355 multi-loci microsatellite genotypes of Central Georgia bears to genotypes of bears from the populations in North and South Georgia, I found no evidence of admixture. The levels of diversity I observed combined with continued isolation should be taken into account when managing the CGBP. Reduction of the CGBP without demographic or genetic support from other bear populations risks further loss of diversity within the CGBP. A population viability analysis (PVA), possibly incorporating genetic data, should be conducted to determine demographic parameters of the CGBP.

To assess landscape connectivity between the CGBP and other regional bear populations, I developed a step selection function (SSF) linking empirical bear movement data to landscape attributes. I then simulated bear movement using the SSF to determine landscape connectivity among bear populations. Our results indicate that connectivity between the CGBP and other bear populations is limited by a lack of landscapes conducive to bear travel and (likely the larger issue) distances too great for there to be consistent reliable movement of bears into the CGBP. The SSF I developed could be used to identify potential corridors, and also test corridor design that would facilitate bear movement into the CGBP.

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