

**POPULATION DEMOGRAPHICS AND GENETIC
STRUCTURE OF BLACK BEARS IN COASTAL
LOUISIANA**

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Degree
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ABSTRACT

The range and abundance of the Louisiana black bear (*Ursus americanus luteolus*) were greatly diminished during the 20th century. This subspecies was reduced to 3 small, isolated subpopulations in Louisiana as bottomland hardwood habitat was converted to agriculture. These bears were listed as threatened by the U.S. Fish and Wildlife Service in 1992 and a recovery plan was published in 1995. Recovery requires estimates of population parameters to evaluate current population status and future viability. I conducted a mark-recapture study from 2010 to 2012 to estimate demographic parameters of the coastal population of Louisiana black bears. Because inbreeding is a concern for small, isolated populations, I analyzed 23 microsatellite loci to investigate genetic structure and migration rates within the coastal population and between the coastal and other regional populations. Using non-invasive methods, I collected 3,698 hair samples during 3 summers and used DNA to identify 190 individuals. I analyzed encounter histories using Robust Design, a combination of open and closed mark-recapture models, with the full closed captures with heterogeneity model in Program MARK. I estimated density using spatially explicit capture-recapture. I used Akaike's Information Criterion (AIC) to rank models and averaged across years according to AIC weight. The model-averaged abundance estimate for females was 77 (95% CI = 66–89) and for males was 61 (95% CI = 53–69). Population growth rate was negative from 2010 to 2011, positive from 2011 to 2012, and averaged 1.08. Apparent survival ranged from 0.83 to 0.89 depending on sex and year. Population density was 0.35 bears/km² (95% CI = 0.30–0.41). Principal Coordinate Analysis and assignment tests revealed 2 genetic clusters within the population. Migration rates were male biased and higher than

expected based on genetic structure. The population appears to be recovering from past fragmentation but evidence for a bottleneck was inconclusive. I conclude that genetic isolation and inbreeding within the coastal population pose less danger than isolation and demographic threats. My results will ultimately be used as part of a population viability analysis to estimate the sustainability of the Louisiana black bear population.

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CHAPTER I

INTRODUCTION

The Louisiana black bear (*Ursus americanus luteolus*), 1 of 16 subspecies of the American black bear (*Ursus americanus*), was historically distributed across all of Louisiana, eastern Texas, southern Arkansas, and southern Mississippi (Hall 1981, Figure 1). Within their historic range, Louisiana black bears were thought to reach greatest densities in the bottomland hardwood forests of the Mississippi River and Atchafalaya River alluvial plains (St. Amant 1959). Habitat requirements of the Louisiana black bear include relatively large areas of contiguous bottomland and upland forest and forested wetland with trees of diverse age and size classes. These forests provided den sites, escape cover, and hard and soft mast (Boggs 2008).

The Louisiana black bear's status in the early 20th century was summarized by Theodore Roosevelt, who wrote “which, until within a very few years, was extraordinarily plentiful in the swamps and canebrakes on both sides of the lower Mississippi, and which is still found here and there, although in greatly diminished numbers” (Roosevelt 1908:50). In his narrative, Roosevelt revealed that his guide Holt Collier had killed or assisted in killing >3,000 bears. He also foresaw flood control and predicted that “the whole land will be cultivated and densely peopled”. This process would eventually fragment bear habitat, isolating small subpopulations in the Tensas River Basin (TRB), the Upper Atchafalaya River Basin (UARB), and the Lower ARB (hereinafter, coastal population or coast; Figure 1). Cypress timber cutting dominated the economy of southern Louisiana from 1880 until the mid-1920s resulting in complete harvest of many swamps (Davis 2010). During this period, the sugarcane industry rapidly expanded as levee building, wetland drainage, and channelization allowed agriculture to extend into marshes and swamps (Davis 2010). The 1959 Louisiana wildlife inventory estimated

the statewide black bear population at 80–120 individuals in 6 parishes, declining from 17 parishes in 1890 (St. Amant 1959). This inventory also indicated that up until 1920, crop damage and predation by bears were common. Conversion of bottomland hardwood forests accelerated again between the 1950s and 1970s due to government flood control and the growth of agriculture in the region due to increased commodity prices (King et al. 2006). Between settlement and 1980, bottomland hardwood habitat was reduced by >80% from 25 million acres (97,000 km²) to <5 million acres (20,000 km²) in the Lower Mississippi Alluvial Valley, with the remaining habitat reduced in quality by fragmentation (Neal 1992). By 1981, the coastal bear population was thought to number <30 (Nowak 1986).

Coordinated efforts to conserve and restore the bear population have been initiated in the past 25 years. In 1987, the U.S. Fish and Wildlife Service (USFWS) was petitioned to protect the Louisiana black bear under the Endangered Species Act of 1973. In 1992, the bear was listed as “Threatened” because of past habitat loss and vulnerability to continued habitat loss and illegal killing (Neal 1992). A significant portion of habitat in the LARB was protected in 2001 when the Bayou Teche National Wildlife Refuge was established in St. Mary Parish with the primary purpose of conserving and managing habitat for the coastal bear population (USFWS 2009a). In 2009, the USFWS designated critical habitat including 541 km² within the LARB (USFWS 2009b).

Human–related mortality continues to be a primary threat to recovery of the Louisiana black bear (USFWS 1995). Although hunting was suspended in 1988, illegal kills and vehicle collisions have been significant sources of mortality with the majority of confirmed deaths coming from the LARB (Pace et al. 2000). Another obstacle to the viability of the coastal population is nuisance behavior, which frequently results in problem bears being euthanized or

relocated from the LARB to a repatriation area located between the Tensas and UARB populations (Figure 1).

A milestone in the Louisiana black bear conservation effort was reached in 1995 when a recovery plan prepared by the Black Bear Conservation Committee and USFWS was approved. The recovery plan requires that 3 criteria be met for a successful recovery:

- (1) At least 2 viable subpopulations, 1 each in the Tensas and Atchafalaya River basins (Figure 2),
- (2) Establishment of immigration and emigration corridors between the 2 subpopulations, and
- (3) Protection of the habitat and interconnecting corridors that support each of the 2 viable subpopulations used as justification for delisting (USFWS 1995).

The recovery plan defines viability as a $\geq 95\%$ probability of survival over 100 years (USFWS 1995). Additionally, the plan prescribes the following actions needed to meet the delisting criteria:

- (1) Restore and protect bear habitat,
- (2) Develop and implement information and education programs,
- (3) Protect and manage bear populations, and
- (4) Conduct research on population viability and bear biology (USFWS 1995).

Previous research on the coastal bear population has included work on habitat relationships (Nyland 1995), movement extent and pattern (Wagner 1995, Wagner et al. 2001), denning ecology (Hightower et al. 2002), fine-scale movement and habitat use (Hightower 2003), genetics (Triant 2001, Csiki et al. 2003, Triant et al. 2004), mortality (Pace et al. 2000), aversive conditioning (Leigh 2007), and habitat assessment (Nyland and Pace 1997, Wagner

2003, Murrow and Clark 2012). Previous work on population dynamics of the coastal population was limited to a population estimate (Triant 2001, Triant et al. 2004). That research was limited to 1 year and restricted to only a portion of the coastal population thought to exist today.

Data for the other 2 remnant subpopulations are being evaluated in several completed or ongoing studies (J. Clark, U.S. Geological Survey, unpublished data). To evaluate recovery and estimate future viability of the coastal population, estimates of population abundance and other demographic parameters and their variances are necessary. Initial demographic studies were conducted using closed capture-mark-recapture (CMR) models in the TRB (Beausoleil 1999, Boersen 2001, Boersen et al. 2003), and the UARB and LARB (Triant 2001, Triant et al. 2004). Recently, Robust Design CMR studies by Hooker (2010) and Lowe (2011) provided more current and comprehensive estimates for the Tensas and UARB subpopulations, respectively. Updated abundance estimates for the TRB and UARB were 294 (SE = 31.0) and 56 (SE = 4.5), respectively. Apparent annual survival was 0.91 (95% CI = 0.62–0.98) at TRB (Hooker 2010) as it was also at UARB (95% CI = 0.79–1.0, Lowe 2011). The TRB had a relatively high density (0.66 bears/km², SE = 0.07) and positive mean annual growth rate ($\lambda = 1.04$, SE = 0.18) whereas the UARB population had a lower density (0.15 bears/km²) and positive growth rate ($\lambda = 1.32$, SE = 0.07).

The landscape of south Louisiana creates particular challenges for bear managers. The relatively dry areas in the region such as salt domes and natural levees as well as converted former wetlands are occupied by humans, with bears being relegated to the remainder. In more mesic areas, bears and humans come into frequent contact and nuisance incidents and vehicle

collisions are common, especially in the eastern half of St. Mary Parish. Bears are also vulnerable to illegal kills, accidents, and other anthropogenic mortality.

Despite the challenges involved in managing bears on the coast, this population may warrant special conservation consideration because it may be the population most genetically representative of the native Louisiana bear (Triant et al. 2004). Previous studies have concluded that bears of the UARB and TRB share some genetic similarity with the population of Cook County, MN, the source of a restocking effort from 1964 to 1967, whereas bears of the LARB are relatively unique (Csiki et al. 2003, Triant et al. 2004). Regardless, habitat fragmentation may increase the isolation of this population and reduce its size. When populations are reduced, rare alleles are lost and inbreeding and genetic drift can increase, further diminishing genetic diversity (Masel 2011). When that reduction is rapid, genetic “bottlenecks” may occur as alleles are lost from the population (Allendorf 1986). Inbreeding and reduced genetic diversity may result in expression of harmful recessive alleles leaving individuals less capable of survival, reproduction, and adaptation. When population abundance stabilizes, recovery occurs as new alleles are generated through mutation. Such mutations can create any new allele randomly (i.e., the Infinite Alleles Model; Kimura and Crow 1964) or the mutation may gain or lose one repeat at a time (i.e., the Stepwise Mutation Model; Ohta and Kimura 1973). Most microsatellite data better fit the 2-phased mutation model which is intermediate between the 2 previously mentioned models (Di Rienzo et al. 1994).

Additionally, disjunct populations are subject to genetic drift, which may cause discrete groups or “population structure” to form. Population structure may indicate genetic isolation and barriers to dispersal. Severe fragmentation inhibits natural dispersal which can prevent inbreeding. Consequently, establishment of movement corridors is a priority for Louisiana black

bear recovery. Although the Atchafalaya Basin contains extensive forests, seasonal flooding may discourage habitation and natural dispersal by bears. Consequently, it is thought that the coastal population is isolated from bear populations further inland.

In accordance with the Louisiana black bear recovery plan, parameter estimates from bear populations in Louisiana are needed to perform a population viability analysis. Data are being collected and analyzed with that objective in mind for the TRB and UARB bear populations. My objectives were to determine the current status of the coastal population and provide data to evaluate future viability, a prerequisite to delisting. Data from my study will ultimately be combined with data from the other 2 bear populations in the state to determine the overall persistence of the Louisiana black bear metapopulation. More specifically, my objectives are to apply CMR techniques to estimate abundance, density, apparent survival, and population growth for the coastal bear population. An additional objective is to use an extended set of microsatellites to determine genetic structure and migration rates within the coastal population. Although genetic differentiation is expected to increase with geographic distance in many species, relative dissimilarity between neighboring subpopulations indicates fragmentation. My final study objective was to compare my sample collected from 2010 to 2012 with a sample collected from 1992 to 2000 for evidence of a genetic bottleneck. These data will help inform managers of current status and provide a baseline for future monitoring and population projection.

CHAPTER II

STUDY AREA

My study area encompassed the core of black bear habitat in the Lower Atchafalaya River Basin. It consisted of approximately 406 km² of forest and forested wetlands in St. Mary and Iberia parishes (Figure 2). Natural land cover in the study area was interspersed with agricultural, industrial, and residential development, most notably the towns of Franklin, Patterson, Bayou Vista, and Berwick (Figure 3). The study area extended approximately 75 km from Avery Island to the west to Morgan City to the east. Most sampling took place south of U.S. Highway 90 (future Interstate 49) and north of the Gulf Intracoastal Waterway. The study area was within the Mississippi Alluvial Plain Ecoregion and primarily contained Inland Swamps bordered by Southern Holocene Meander Belts to the north and Deltaic Coastal Marshes to the south (EPA 2011). Soils were Quaternary (Holocene) alluvial, deltaic, and lacustrine deposits and sediments (EPA 2011). Mean minimum and maximum temperatures for January were 5° and 17° C, respectively, and for July were 22° and 32° C, respectively, with annual precipitation ranging from 158 to 178 cm (EPA 2011). Elevation of most of the study area was between 0 and 1 m above or below sea level. Three salt dome formations within the study area had maximum elevations between 25 and 52 m (U.S. Geological Survey; USGS; 2009).

The coastal Atchafalaya River Basin included a diversity of habitats that generally became more hydric and saline along a northeast to southwest gradient (Figure 4). Urban and agricultural zones occupied high ground protected by a network of levees and drainage canals. Row crops, predominantly sugarcane but also soybeans, were a major land use in south Louisiana. Also within the levee system were bottomland hardwood forests characterized by bald cypress (*Taxodium distichum*), water oak (*Quercus nigra*), and red maple (*Acer rubrum*).

Beyond the levees, bottomlands gave way to swamps of cypress and water tupelo (*Nyssa aquatica*). Moving toward the Gulf, swamps transitioned to brackish marshes of scrub/shrub. Common species included dwarf palmetto (*Sabal minor*), wax myrtle (*Myrica cerifera*), and eastern baccharis (*Baccharis halimifolia*). The marshes were traversed by canals flanked with spoil banks occupied by deciduous species: water and Virginia live oak (*Quercus virginiana*), black willow (*Salix nigra*), southern hackberry (*Celtis laevigata*), honey locust (*Gleditsia triacanthos*), wax myrtle, redbay (*Persea borbonia*), and invasive Chinese tallow (*Sapium sebiferum*). Further south lay salt marshes of sedges (*Cyperus* spp.), needlegrass (*Juncus roemerianus*), big cordgrass (*Spartina cynosuroides*), and broadleaf cattail (*Typha latifolia*). Surrounded by marsh, several salt dome “islands” provided rolling upland habitat of live and water oak, sweetgum (*Liquidambar styraciflua*), and southern magnolia (*Magnolia grandiflora*). Palmetto and yaupon (*Ilex vomitoria*) were ubiquitous in all habitats, except salt marsh, and created a dense undergrowth on nearly all spoil banks, bottomlands, and uplands. Common water hyacinth (*Eichhornia crassipes*), an invasive species, formed dense floating mats that covered many canals and lakes.

The diverse habitats of coastal Louisiana were extremely productive. Aquatic life such as channel catfish (*Ictalurus punctatus*), white shrimp (*Litopenaeus setiferus*), crawfish (*Procambarus* spp.), Atlantic blue crab (*Callinectes sapidus*), and gar (*Lepistosteidae* spp.) were important food sources for wildlife and humans. The area provided refuge for wading birds such as great egret (*Ardea alba*) and black-crowned night heron (*Nycticorax nycticorax*) and raptors such as swallow-tailed kite (*Elanoides forficatus*), and barred owl (*Strix varia*). The Gulf Coast also provided important stopover and wintering habitat for a variety of neotropical migrants and waterfowl. Commonly encountered reptiles and amphibians included pond slider (*Trachemys*

scripta), American alligator (*Alligator mississippiensis*), garter snake (*Thamnophis* spp.), and American green tree frog (*Hyla cinerea*). Mammals included armadillo (*Dasypus novemcinctus*), raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), Virginia opossum (*Didelphis virginiana*), white-tailed deer (*Odocoileus virginianus*), feral hog (*Sus scrofa*), coyote (*Canis latrans*), nutria (*Myocastor coypus*), and muskrat (*Ondatra zibethicus*).

Coastal Louisiana is vulnerable to hurricanes and land loss due to subsidence, coastal erosion, and sea level rise. Computer modeling of various scenarios indicated that dramatic losses of swamps, fresh marshes, and tidal marshes is likely by 2100 as each of these respective ecosystems migrate inland (USFWS 2009a).

CHAPTER III

METHODS

Robust Design Capture-Mark-Recapture

Management of wildlife populations frequently requires knowledge of demographic parameters. These include abundance (N), the number of individuals in the population; density (D), the number of individuals per km²; apparent survival (ϕ), the proportion of animals that survive and do not permanently emigrate between sampling sessions and are thus available for recapture; and population growth (λ), the ratio of N in a session to N in the previous session. Estimation of additional parameters is necessary to achieve unbiased estimates of N , D , ϕ , and λ ; these include probability of capture (p), the proportion of the population that is encountered on a given occasion; and probability of recapture (c), the proportion of the population that has been encountered on a previous occasion and reencountered on a given occasion. To achieve precise estimates of ϕ , mortality must be distinguished from temporary emigration, γ , the probability of being away from the study area given that the animal was (γ'') or was not (γ') present during the preceding capture session.

Many species, including black bears, are difficult to find and observe. Because of this imperfect detection, exact counts of animals are usually impractical or impossible and managers must rely on estimation. The most common estimation method is capture-mark-recapture which involves sampling on 2 or more occasions, marking all animals captured, and comparing the ratio of marked to unmarked animals in subsequent occasions. Capture and marking may involve physical handling and marking, or observation of natural identifying markings or DNA. The most basic estimator for this method is $N=M/p$ where N is the number of individuals in the population, M is the number of individuals marked, and p is the average probability of capture.

This is a closed model which requires these 4 fundamental assumptions according to Otis et al. (1978):

- (1) The population is closed both demographically and geographically,
- (2) Animals do not lose their marks during the experiment,
- (3) All marks are correctly noted and recorded at each trapping occasion, and
- (4) Each animal has a constant and equal probability of capture on each trapping occasion.

Assumption 1 can be relaxed by using open models which allow changes to the population between sampling occasions (Jolly 1965, Seber 1965). White et al. (1982) classify these changes as either demographic (birth and death) or geographic (immigration and emigration). These geographic and demographic closure assumptions can be relaxed with so-called open mark-recapture models, which can provide session-specific estimates of population change over an extended period, and allow estimation of parameters such as ϕ , p , recruitment (f), and λ . The disadvantage of open models is sampling must take place over multiple time periods (generally >3) and abundance estimates are generally less precise and may be biased by unequal catchability (Gilbert 1973).

Assumption 2 can be violated if animals lose their identifying marks which results in an overestimate of N because previously encountered animals appear unmarked. Violations of Assumption 3 can occur if animals are misidentified, causing positive or negative biases depending whether an individual was erroneously “created” or mistaken for another individual and which sample the error applies to.

Finally, an important assumption of mark-recapture studies is that each animal has an equal and constant probability of capture on each trapping occasion (assumption 4). According

to Otis et al. (1978), p may vary by time, individual heterogeneity, and behavioral response. Individual heterogeneity, e.g., differences in p by age, size, sex, or other individual characteristic, is perhaps the most difficult of these variations to account for. When animals have intrinsically different capture probabilities which are not accounted for, estimates of N will be biased low (Pledger 2000). A behavioral response occurs when the capture of an individual animal affects the subsequent probability of capture for that animal. Typical behavioral responses are “trap happy” and “trap shy”. Finally, a time response is a change in p between capture occasions caused by events like weather, migration, or changes in food availability. Equal catchability assumptions are commonly violated in wildlife studies and a myriad of methods have been developed to account for such biases (Williams et al. 2002).

To address Assumption 1, my closed population estimates were conducted during 8 consecutive weeklong “sampling occasions” during June and July, a period when no cubs were born and death, emigration, and immigration were likely negligible. I assumed the study area to be geographically closed because it consisted of a thin linear series of forest fragments surrounded by tidal marsh to the south and west and agriculture and urban development to the north and east. I was able to sample most of the core habitat although some bears do live outside this area. I addressed Assumptions 2 and 3 by using DNA, a unique and permanent identifying mark and by using error-checking protocols such as reanalyzing mismatching markers in similar pairs of genotypes to ensure correct identification of individuals. Using such protocols, the chances of sample misidentification are dramatically reduced if not nearly eliminated (Paetkau 2003). To address Assumption 4, I used methods to account for time, sex, and behavioral responses. I modeled individual heterogeneity biases with mixture models (Pledger 2000). These models partition the population in a closed capture experiment into any number of

segments or “finite mixtures” according to catchability and estimate the proportion of the population and unique capture probabilities within each segment (Pledger 2000). I partitioned the population into 2 mixtures and estimated π_a , the probability of belonging to the first mixture. Probability of belonging to the second mixture π_b is $1-\pi_a$.

Although parameter estimates for closed populations may be precise, they are not realistic over an extended period because populations experience demographic and or geographic changes. Therefore, in addition to closed estimates of abundance, I estimated demographic changes between sampling occasions using an open model. A mixture of open and closed models is known as Robust Design (Pollock 1982). The Robust Design works by sampling a population at 2 temporal scales. An open model is used to estimate population change parameters ϕ , γ' , γ'' , and λ during intervals known as primary periods between sampling sessions. Gains and losses to the population are allowed during these intervals. Between intervals, multiple samples are taken over a short duration termed the secondary sampling period. Within each secondary period the population is assumed to be unchanging and closed population estimators are used to estimate parameters p , c , π , and N . My primary periods lasted 1 year and my secondary periods consisted of 8 consecutive weekly “sampling occasions”. I tested models that allowed p and c to vary by primary session, sex, and finite mixture and models that fit a behavioral effect by allowing p to differ from c . I used Laufenberg’s method (2013) to evaluate accuracy (i.e., the probability of obtaining an estimated N that is within 20% of true N), coverage (i.e., the probability that the 95% confidence interval includes the true N), and precision (i.e., the probability of obtaining a coefficient of variation $\leq 20\%$) of estimates using logistic regression.

DNA Sampling

I marked and recaptured black bears by collecting hair samples and identifying individuals by genotyping DNA from the roots of sampled hair. Samples were collected using a network of baited barbed wire enclosures. This technique was pioneered by Woods et al. (1999) for estimating bear populations and has been successfully used on Louisiana black bears (Boersen 2001, Triant 2001, Hooker 2010, Lowe 2011). DNA is a useful marker for identifying animals because it cannot be altered and is unique to each individual. It is capable of distinguishing individual, sex, species, and genetic structure. Non-invasive sampling is safer than live capture for animals and researchers and should minimize the chance of a negative behavioral response, i.e., animals becoming trap shy (Woods et al. 1999). A final advantage of this technique is greater efficiency; it requires less money (Woods et al. 1999), time, and effort (Mowat and Strobeck 2000) per individual identified than live capture.

To meet the assumption of equal probability of capture, I followed the recommendation by Otis et al. (1978) of 4 traps per home range. Telemetry-based home ranges of females in the coastal population averaged 11.8 km² (Murrow and Clark 2012). I divided this area by 4 to create a grid of 2.95-km² cells which I plotted on the study area using ArcMap 9.3 GIS (Environmental Systems Research Institute, Inc., Redlands, CA). In each cell that contained >50% forest cover I attempted to establish 1 hair collection site while maintaining approximately 1.7 km between adjacent sites. In some areas, even spacing was prohibited by landowners or field conditions that prevented access; consequently, my sampling locations were not strictly uniform. Only forested areas were considered Louisiana black bear habitat by the USFWS although marshes and agricultural lands were also used by bears (Neal 1992); therefore, I delineated forest cover by combining 4 GAP cover types (Table 1; USGS 2011) where I

established 118 hair sampling sites. One-hundred ten of the sites were between Highway 90 (future I-49) and the Intracoastal Waterway, 6 were located north of the highway, and 2 were located on Cote Blanche Island, south of the Intracoastal Waterway.

Hair collection sites consisted of 4-point, 15.5-gauge barbed wire tightly stretched around 3–5 trees and fastened with fencing staples (Woods et al. 1999). Previous researchers in Louisiana used a single wire which may have enabled some bears to step over or crawl under the wire (Hooker 2010, Lowe 2011). To reduce such potential capture heterogeneity, I stretched 2 wires at heights of 35 and 70 cm, respectively (Lowe 2011). I flagged hair collection sites with fluorescent tape for visibility and human safety and maintained wire tension by cinching corners together with size 21 nylon twine (Figure 5). I baited hair sites with approximately 100 g of sweet baked goods which were placed inside a biodegradable bag (BioBag[®], BIOgroupUSA, Palm Harbor, Florida) and suspended approximately 1.8 m above the ground in the center of the hair site. I also suspended a tampon soaked in approximately 50 ml of raspberry- or honey-flavored extract (Mother Murphy's Laboratories, Greensboro, NC) as a scent lure. Bait and scent lures were replaced or refreshed weekly. Sites were baited 7 days prior to the first collection.

I collected hair samples during primary and secondary sampling sessions as required by Robust Design. Primary sessions were the summer months of 2010, 2011, and 2012. The population was assumed to be open demographically and geographically in the 10-month intervals between primary sessions. Within each primary sampling session, hair samples were collected at each site on 8 secondary sampling occasions. Secondary sampling occasions for each site lasted approximately 1 week from baiting to sample collection and were continuous for the 8 weeks of the secondary period. I treated hair from a single barb as an individual sample. I

culled samples with <1 guard hair or <5 underfur hairs to reduce genotyping failure as advised by D. Paetkau (Wildlife Genetics International, personal communication). I used forceps to transfer hair samples from a single barb into a single coin envelope. To prevent cross contamination, I sterilized forceps and all barbs with a propane torch after collecting each sample. I labeled hair samples, stored them in coin envelopes, sealed them in airtight bags, and kept them in a climate-controlled environment. I recorded capture session, date, location, and sample number on each sample envelope and entered this information into a database. Additional samples for genetic analysis were collected by LDWF employees from bears that were killed on highways or otherwise died or were relocated outside the study area from November, 2009 to November, 2012.

Subsampling

Bears that are detected more than once at the same site during a particular secondary sampling occasion add nothing to their capture histories. Consequently, analyzing multiple samples from the same bear during a single site-week combination would result in inefficiency and unnecessary expense. Therefore, I designed a subsampling protocol to minimize this scenario. Subsampling intensities must be sufficient to achieve adequate capture probabilities ($p \geq 0.2$) to reliably estimate population abundance (Laufenberg et al. 2013). To achieve this capture probability while maintaining cost efficiency, I selected 533 samples for extraction from each primary session. I selected samples by assigning a random number to each site-week combination and to each sample within a site-week combination. I selected samples based on an optimal quality threshold of 5 guard hairs or 20 underfur, if available, or a lenient threshold of 1 guard hair or 5 underfur if otherwise. In 2010, I selected 1 sample from each site-week combination in their randomized order, taking the first sample to meet the optimal threshold if

available or the lenient threshold otherwise. Multiple rounds of selection through all site-week combinations were required to reach the target of 533 samples. For 2011 and 2012, I subsampled by randomly selecting 1 sample at the optimal threshold from each site-week combination where any were available, then randomly sampling at the lenient threshold until all possible site-week combinations were represented. Once all site-week combinations were represented, I made additional passes exhausting the optimal then lenient threshold within each pass until 533 samples were selected. I used this subsampling protocol to distribute my sample across sites and weeks, attempting to maximize individuals detected while minimizing redundant samples from a single site visit by a bear.

Microsatellite Analyses

Microsatellites are short (<100 bp) runs of tandemly repeated DNA sequences with repeat lengths of 6 bp or less, that contain highly variable numbers of repeats. Microsatellites can be efficiently analyzed using Polymerase Chain Reaction methods (PCR, Beckmann and Weber 1992). PCR is an enzymatic amplification of target sequences in DNA resulting in the exponential increase of target DNA (Saiki et al. 1985). Because of their high variability, microsatellites are a useful tool for studying bear populations which often have low levels of genetic variation (Paetkau et al. 1995). Bears have 2 matching sets of 37 chromosomes for a total of 74. Each homologous chromosome contains an allele which is an alternative form of a particular gene (Guttmacher and Collins 2002). If alleles on both chromosomes at a locus are identical, the organism is homozygous for the trait. If they are different, the organism is heterozygous for that trait (Guttmacher and Collins 2002).

Subsampling and genotyping were performed at Wildlife Genetics International (WGI; Nelson, British Columbia, Canada). PCR was used to amplify DNA material and electrophoresis

was used to distinguish genotypes (Paetkau 2003). Marker selection began with an initial set of 45 samples drawn from different site-week combinations. These were examined at 23 markers (*G10P*, *MU23*, *MU59*, *G10U*, *CXX110*, *D123*, *G10J*, *MU50*, *G10C*, *REN144A06*, *CPH9*, *REN145P07*, *MU26*, *G1D*, *G10L*, *MSUT2*, *G10M*, *G10B*, *G10H*, *CXX20*, *G10X*, *D1A*, *G1A*, and *MU51*) to determine which microsatellite markers had the highest variability. The 8 most variable markers (*G10P*, *MU23*, *MU59*, *G10U*, *CXX110*, *D123*, *G10J*, *MU50*) and an amelogenin marker to determine sex (Ennis and Gallagher 1994) were used to distinguish identity for the rest of the samples (D. Paetkau, Wildlife Genetics International, personal communication). To investigate my population genetics objective, 23 markers were genotyped for all individuals captured in 2010 and 2011 as well as all dead or relocated animals handled by LDWF.

The analysis of individual identity started with a first pass of all 8 selected microsatellite markers plus sex. Next, samples that produced very weak or mixed data were culled. Finally, remaining samples that were weak or difficult to read were reanalyzed. Similar genotypes were selectively re-analyzed to further reduce error (Paetkau 2003).

Genotyping Assumptions and Error Checking

To achieve unbiased parameter estimates, all marks must be correctly noted and recorded (Otis et al. 1978). Two types of error are possible when identifying individuals from genotypes. The first is the creation of “false” individuals by misinterpreting a DNA signature as that of a newly captured individual when in reality it is a recapture of a previously captured animal. This artificially increases the detected population (M), decreases p , and inflates N . The second type of identification error is failure to distinguish individuals with similar genotypes (Mills et al. 2000). This “shadow effect” results in artificially high p and reduced M , causing N to be biased low

even as precision increases (Mills et al. 2000). To check for errors, individuals with matching genotypes at all but 1 or 2 markers were re-analyzed to detect false matches and if necessary, analyzed at 5 additional markers (D. Paetkau, personal communication). The shadow effect can also be prevented by analyzing a sufficient number of loci and by selecting alleles with high variability (Mills et al. 2000).

If individuals within a population are closely related, the probability of similar genotypes and thus misidentification is greater. Previous analysis of the coastal population revealed low genetic variability (Triant et al. 2004) which is common in small, isolated, and low density populations (Paetkau and Strobeck 1994). To estimate the probability that 2 individuals from a population will share identical genotypes at multiple loci, I calculated probability of

identity, $PI_{\text{single locus}} = \sum_i x_i^4 + \sum_i \sum_{j>i} 2x_i x_j^2$, where x_i and x_j are the frequencies of the i th and j th alleles

(Paetkau and Strobeck 1994). PI over all loci can be calculated as $PI_{\text{overall}} = \prod PI_{\text{single locus}}$

(Taberlet and Luikart 1999). PI_{overall} calculated with this formula will be biased low for many wild populations because it does not account for subdivision within populations or philopatry of relatives (Taberlet and Luikart 1999). Waits et al. (2001) discovered that observed PI may be higher than theoretical PI when populations contain related individuals; they developed the PI among siblings (PI_{sib}) as a conservative alternative to PI_{overall} , $PI_{\text{sib}} = 0.25 + (0.5 \sum PI_{\text{sib}} = 0.25 + (0.5 \sum p_i^2) + [0.5 \sum p_i^2]^2 - (0.5 \sum p_i^4))$, where p_i is the frequency of the i th allele. Given the limited habitat and small black bear population in coastal Louisiana, non-random mating and collection of samples from closely related individuals are likely. Consequently, I calculated PI and PI_{sib} for the 8- and 23-locus data sets using Program GenALEX (Program GenALEX Version 6.5, www.biology.anu.edu.au/GenALEX/, accessed 28 May 2013; Peakall and Smouse 2012). I used

Taberlet and Luikart's (1999) suggested threshold of $PI_{sib} \leq 0.01$ to evaluate the risk of encountering individuals with identical genotypes for all analyzed loci.

Demographic Parameter Estimation

I used genotyping results to compile capture histories for all individuals encountered. Capture histories consisted of an indicator of detection or non-detection during each of the 24 secondary occasions. I analyzed capture histories in Program MARK (MARK Version 7.1, www.phidot.org/software/mark/downloads/, accessed 2 Mar 2013; White and Burnham 1999) using maximum likelihood to fit Robust Design models to data in the full closed captures with heterogeneity data type. Full likelihood models include N in the likelihood, $f_0 = N - M_{(t+1)}$, where f_0 is the number of animals never captured and $M_{(t+1)}$ is the number captured at the conclusion of the final capture occasion (t).

I created a candidate set of 23 competing models. I created models allowing ϕ to vary by sex and year or remain constant. I tested models allowing "random movement" where $\gamma'' = \gamma'$, representing the hypothesis that the probability of being off the study area is independent of location in a previous primary sampling session. I tested "no movement" models where animals do not enter or leave the study area; $\gamma'' = \gamma' = 0$. I also tested "even-flow" models where emigration and immigration ($1-\gamma'$) are equal. I allowed π to vary by sex, year, or remain constant. For p and c , I fit invariant models and others that included variation by sex, year, or both. I also modeled behavioral response by fitting models where c differed from p . Finally, I tested for capture heterogeneity by comparing models with and without mixtures for p and c .

I ranked models using the Akaike Information Criterion corrected for small samples (AICc) (Burnham and Anderson 2002). AICc ranks are based on empirical support and model simplicity. Models are assigned an AICc score which is penalized in AICc units with more

severe penalties as number of parameters increases and sample size decreases. Thus, only parameters with significant explanatory power improve score. I considered models well supported if their AICc scores were within 2 units of the top model. An AICc weight can be calculated based on the proportion of support for each model in the model set. I derived parameter estimates by averaging supported models according to weight to account for model uncertainty (Burnham and Anderson 2002). When averaging parameters across sexes, years, or mixtures, I derived estimates of standard error and confidence intervals using the delta method (Powell 2007).

Density Estimation

Density (individuals/km²) was calculated using spatially explicit capture recapture (SECR; Efford et al. 2004, Borchers and Efford 2008). This method is based on a maximum likelihood estimator and incorporates the locations of hair-sampling sites and the capture locations and capture history of each individual to estimate density. Program SECR (SECR Version 2.6.0, www.otago.ac.nz/density/SECRinR.html, accessed 21 June 2013; Efford 2013) is a program in the R programming language (R Version 2.15.1, www.cran.r-project.org/bin/windows/base/, accessed 15 Nov 2012; R Core Team 2012), that can be used to fit models that include density (D) and parameters for the detection process in the likelihood (Williams et al. 2002). The detection process is represented by a mathematical function which includes 2 submodels to describe an animal's declining probability of being detected as its home range center gets further from a detector (Williams et al. 2002). The parameters that define the detection function are the probability of detection if an individual's activity center is at a detector (g_0) and spatial scale (σ), analogous to an individual's home range radius (Efford et al. 2004). Several types of detection functions are available. I tested models that included half-normal, gamma, and hazard functions.

I built models allowing D , g_0 , and σ to remain constant or to differ by year, sex, or both. I also tested for behavioral responses following initial capture. I used a buffer suggestion routine in Program SECR to determine a suitable buffer width for the integration mask. Within this buffer, I further refined the analysis area by using ArcMap 10.1 GIS to exclude less suitable bear habitat from density calculation by creating a habitat mask. I used forest cover to define my habitat mask. Beginning with GAP Landcover data (USGS 2011), I reclassified cells from 30 m in size to cells 180 m in size based on majority coverage. This allowed faster processing without significantly sacrificing detail. I reclassified 4 forested habitat types (Table 1) as bear habitat and excluded area outside the suggested buffer. Program SECR allows the use of spatial covariates as predictors of density. I used this feature to estimate location-specific bear densities for St. Mary and Iberia parishes. I tested 8 landcover classes and percent forest canopy (USGS 2001) for correlation with density. I used a circular moving window the size of an average female home range (11.8 km^2) to calculate the percentage of the 8 covariates and mean percent canopy surrounding every GIS cell in the integration buffer suggested by SECR. Next I modeled D using covariates with constant g_0 , and σ . As with my other parameters, I used AICc and model-averaging to select models and derive density estimates. I used β -values of supported covariates, measures of how strongly each covariate influenced the dependent variable (D), to construct a linear model to predict density for my study area. Finally, I adjusted the density estimate to exclude non-forest cover by dividing estimates by the ratio of forest to non-forest within the buffer.

Population Genetics

My final objectives were to assess genetic signatures of population structure and a population bottleneck in past generations of the coastal population and migration to or from other regional

populations. I evaluated a subset of 127 individuals at additional loci to better distinguish individuals and increase statistical power. The full set of markers used for the population genetic analysis contained sex and 23 markers.

I performed a correspondence analysis with Program GENETIX (GENETIX Version 4.05, www.genetix.univ-montp2.fr, accessed 1 Dec 2012; Belkhir et al. 1996) to investigate the prospect of dispersal and gene interchange between the coastal population and other local populations. This software can be used to group individuals along various axes based on genetic similarity at multiple loci. In addition to the UARB and TRB, I also compared the coastal population with a genetically similar population at White River in southern Arkansas (Warrillow et al. 2001, Csiki et al. 2003). I performed 3 analyses comparing the 8 markers used to identify bears at UARB, TRB, and White River with the 23-locus set from the coastal bears, which contained each of those 8-locus subsets. I compared my sample of 127 individuals with all genotyped individuals from each area; 109 from Upper ARB, 498 from Tensas, and 105 from White River.

I also used Program GENETIX to investigate genetic structure within the study area using the full set of 23 loci for the coastal population. To test for genetic structure at 2 scales and compare genetic effects of possible movement barriers, I divided the study area into 6 zones. Zones 1 and 2 were divided by LA 83, a 2-lane highway. Zones 2 and 3 were divided by the same highway and an agricultural area approximately 3 km wide. Zones 3 and 4 were separated by the 100-m wide Charenton Canal. Zones 4 and 5 were divided by LA 317, another 2-lane highway and approximately 1.6 km of agriculture. Zones 5 and 6 were separated by the 200-m wide Wax Lake Outlet Canal. In addition, I combined the 4 western zones and the 2 eastern zones to create 2 larger zones. Using minimum convex polygons and home range centers

derived from hair site encounters, I assigned individuals to a large zone (west or east) and 1 of 6 small geographic zones. For bears that were detected in >1 zone, I assigned a geographic origin based on quantity and date of detections. I performed correspondence analyses on these subpopulations and analyzed the results to detect genetic similarity based on locations of detection.

Further analyses of genetic stratification within the population involved the use of Program STRUCTURE (STRUCTURE 2.3.4, <http://pritch.bsd.uchicago.edu/structure.html>, accessed 2 Apr 2013; Pritchard et al. 2000) to assign individuals to a population based on competing hypotheses of the number of population clusters (k). Program STRUCTURE uses a Bayesian algorithm to assign individuals to populations based on inferred ancestry. It uses the mean value of the log likelihood as evidence for the most likely k . Because estimation of the true k may be incorrect when patterns of dispersal among populations are not homogeneous, I used Evanno's delta method (Evanno et al. 2005) in the STRUCTURE HARVESTER (Program STRUCTURE HARVESTER Version 0.6.9, www.taylor0.biology.ucla.edu/structureHarvester/, accessed 30 Jun 2013; Dent and vonHoldt 2012) to select the most likely k based on the rate of change in the log probability of data between successive k values. I tested values of k ranging from 1 to 6 using a burn-in of 1,000,000 repetitions followed by 1,000,000 Markov Chain Monte Carlo repetitions under the admixture model. Evanno's delta method requires >1 replicate; therefore, I repeated this test until 4 iterations were complete.

I categorized individuals based on their assigned genetic population and used ArcMap 10.1 GIS to map geographic correlations between genetic assignments. This technique has been used to identify possible migrants and quantify sex-specific dispersal rates within the population (Proctor et al. 2012). Based on percent assignment in Program STRUCTURE, I allocated the

population into genetically similar groups. Using home range centers calculated in ArcMap 10.1 GIS based on the hair site encounters, I plotted the location and genetic assignment of each individual.

To test for genetic signatures of potential barriers to dispersal, I examined the possibility of substructure using the fixation index F_{ST} (Wright 1951) and the genetic distance measurement Nei's D (Nei 1972) with Program GenALEX (Peakall and Smouse 2012). F_{ST} measures the proportion of the total genetic diversity (heterozygosity) that is distributed among the subpopulations relative to the total (Peakall and Smouse 2009). Using my 6 designated geographic zones, I performed pairwise comparisons of Nei's D and F_{ST} and graphed Nei's D against geographic distance based on averaged UTM coordinates of detections for each individual. A common rule of thumb holds that one migrant per generation into a subpopulation is sufficient to minimize the loss of polymorphism and heterozygosity within subpopulations (Mills and Allendorf 1996). I calculated the approximate number of successfully breeding

migrants per generation (Nm) as $F_{ST} = \frac{1}{4Nm + 1}$ (Wright 1969).

I used Program BOTTLENECK (BOTTLENECK Version 1.2.02, <http://www1.montpellier.inra.fr/URLB/bottleneck/bottleneck.html>, accessed 1 June 2013; (Cornuet and Luikart 1996) to test for past bottlenecks by measuring for excess heterozygosity relative to observed allele diversity. To evaluate allelic diversity in the coastal population, I performed 3 tests for evidence of a past bottleneck. First, I obtained genetic data from Triant's (2001) sample which consisted of 57 genotypes from individuals sampled at hair snares in 1999 and 41 archived 8-locus genotypes from other individuals sampled from 1992 to 2000. I randomly selected 98 individuals from my own sample to equalize sample size and tested both samples using Triant's 8 markers; $G10P$, $G10M$, $G10B$, $G10L$, $G10C$, $G10X$, $G1D$, and $G1A$. I

compared results of the Wilcoxon test under the 2-phased model of mutation using the 90% Stepwise Mutation Model to evaluate evidence of a historic bottleneck in both samples (Cornuet and Luikart 1996). I tested my full set of individuals at all 23 markers to increase power. Finally, I separately evaluated the eastern and western coastal subpopulations at 23 markers to compare heterozygosity. Differences in heterozygosity between geographic areas could be evidence of population structure.

CHAPTER IV

RESULTS

DNA Sampling

My sampling grid included 118 hair collection sites and covered most of the 541 km² designated by the USFWS (2009b) as critical habitat for the Louisiana black bear in the Lower Atchafalaya River Basin. Five-hundred ninety-two km² of terrestrial habitat were located within 1,938 m (an average female home range radius) of a sampling site (Figure 6). This 592 km² included 316 km² of forest cover, which is considered primary habitat (Neal 1992).

I collected hair samples at weekly intervals for 8 weeks each summer. Collection dates for the 3 primary sessions were 14 June, 2010 through 7 August, 2010, 6 June, 2011 through 29 July, 2011, and 4 June, 2012 through 27 July, 2012. I collected 672 samples from 90 sites, 1,416 samples from 100 sites, and 1,610 samples from 104 sites in 2010, 2011, and 2012, respectively. Sites visited by bears (i.e., leaving a hair sample) increased annually from 76%, to 85% to 88% and I collected hair samples from an average of 38, 59, and 64 sites each week in 2010, 2011, and 2012, respectively (Figure 7). The number of samples varied greatly by site (0–123) and week (53–281). Eleven sites never produced hair samples. Within years, I collected more samples and recorded more bear detections in occasions 1 through 5 than in 6 through 8 when samples declined from 2,662 to 1,035 and detections declined from 849 to 440 (Figure 7). The number of individuals detected at each site over the 24 secondary sampling sessions ranged from 0 (12 sites) to 11 (3 sites) with a mean of 4.8. Areas where greater numbers of individuals were detected were Weeks Island, the Franklin unit of Bayou Teche NWR, the areas west of Glencoe, east of Hwy 317, and the area south of Patterson. No hair was collected from the Centerville unit of Bayou Teche National Wildlife Refuge and only a single sample was collected on Cote

Blanche Island. Video from a motion-activated game camera (Reconyx, Holmen, WI) revealed cubs of the year passing under the 35-cm wire; therefore, my parameter estimates only apply to bears >1 year of age.

I collected additional hair or tissue samples from 19 vehicle kills and 1 illegal kill, 8 of which had been previously detected at hair sites. I also collected hair from 8 individuals live captured by LDWF for nuisance behavior, 6 of which were detected at a hair site. Four bears were captured for GPS collaring, 1 of which was detected at a hair site. Two of the nuisance animals were euthanized; 2 were relocated, dispersed, and were subsequently shot; 2 were relocated, returned to the coast, and were recaptured (1 of these twice); and 2 were not encountered after relocation. All bears captured for GPS collaring were killed, 2 by illegal shooting, 1 by accidental asphyxiation under anesthesia, and 1 was caught and killed in a hog-snare.

Microsatellite Analyses

I received 1,415 genotyped samples from WGI which were assigned to 190 individuals (93 males and 97 females). Ninety different individuals were encountered in 2010, 101 in 2011, and 123 in 2012 (Figure 8). The 2012 sample contained 80 recaptures (65%) from previous sessions and 43 previously uncaptured individuals. Seventy-one of 101 (70%) individuals from 2011 and 56 of 90 (62%) from 2010 were recaptured in 2012. Sixty of 90 (66%) from 2010 were encountered in 2011. Individual males were encountered up to 41 times with an average of 8.07 encounters at 4.3 sites and females up to 22 times with an average of 5.56 encounters at 2.3 sites (Figure 9).

Observed heterozygosity ranged from 0.32 at locus *GIA* to 0.73 at *G10P* (Table 2).

Following the initial investigation of 45 individuals at 22 markers, *MU5I* was determined to be

fixed and was dropped from analysis. Marker *D123* was discovered to be highly variable in the coastal population and was added to the 10-locus set. *RENN144A06* and *G10C* were subsequently dropped from the 10-locus set, leaving 8 loci plus sex for individual identification. Finally, *DIA* was added to the marker set for the genetic structuring analysis, bringing the total to 23 markers plus sex.

Observed and expected heterozygosity for the 8-locus set averaged 0.66 each, with mean variability of 4.1 alleles per locus (Table 2). For the full set of 23 loci, observed and expected heterozygosity averaged 0.56 each with a mean of 4.1 alleles per locus (Table 2). PI and PI_{sib} in the full genetic data set were 1.0×10^{-14} and 4.7×10^{-7} respectively (Table 2). For the 63 individuals not included in the genetic sample, PI for 8 loci was 1.3×10^{-6} and PI_{sib} was 2.4×10^{-3} , meeting the suggested threshold of Taberlet and Luikart (1999). Prior to the addition of *D123*, a pair of individuals matched at all markers. The addition of *D123* successfully distinguished this pair, increasing the apparent number of individuals from 189 to 190.

Demographic Parameter Estimation

My final model set included 23 models (Table 3). The 5 highest-ranked models were within 2 $\Delta AICc$ units and made up 71% of the model weight. All of the top 5 models included 2 finite mixtures, no behavioral effects, and year effects on capture and recapture probabilities. The highest ranked model included an interaction between sex and year in p and c . Allowing p and c to vary by sex greatly improved model fit whereas varying ϕ by year lowered $AICc$ only slightly. Thirteen models had $\Delta AICc$ values <10 and $AICc$ weight $\geq 1\%$ indicating some support.

Model-averaged estimates of ϕ for females were 0.83 (SE = 0.04, 95% CI = 0.71–0.91) between 2010 and 2011 and 0.89 (SE = 0.06, 95% CI = 0.60–0.98) between 2011 and 2012. For males, estimates of ϕ were 0.83 (SE = 0.04, 95% CI = 0.72–0.90) between 2010 and 2011 and

0.88 (SE = 0.06, 95% CI = 0.59–0.97) between 2011 and 2012. Survival estimates were slightly higher for females but this effect was not significant as β values overlapped 0 ($\beta = 0.58$, 95% CI = -0.51–1.68). Mean survival for both sexes and years was 0.86 (SE = 0.03, 95% CI = 0.79–0.93). Because of sparse data, temporary emigration was not estimable by year, sex, or by any models that did not include a behavioral effect. Setting immigration equal to emigration also resulted in both parameters being inestimable. For models where capture and recapture probabilities differed, invariant movement rates were estimated as 0.07 (SE = 0.07, 95% CI = 0.01–0.36) for both γ' and γ'' . Models where emigration was constrained to 0 and models without finite mixtures were not supported. Probability of belonging to mixture π_a was 0.62 (SE = 0.04, 95% CI = 0.52–0.72) and π_b was 0.38, and these proportions did not vary by sex or year. Weekly capture and recapture probabilities were highest in 2011, and were consistently higher for males than females (Table 4). Average weekly capture probabilities calculated as $\bar{p} = (\pi_a \bar{p}_a) + (\pi_b \bar{p}_b)$ averaged across all years and mixtures were 0.25 (SE = 0.02, 95% CI = 0.20–0.30) for females and 0.28 for males (SE = 0.02, 95% CI = 0.24–0.32). Weekly p averaged across sexes and mixtures were 0.19 for 2010 (SE = 0.03, 95% CI = 0.15–0.25), 0.32 for 2011 (SE = 0.03, 95% CI = 0.26–0.38), and 0.27 for 2012 (SE = 0.03, 95% CI = 0.22–0.33). Models without behavioral effects received more support than those with behavioral effects.

Model-averaged abundance estimates of females were 80.0 (SE = 12.8, 95% CI = 54.9–105.2), 66.3 (SE = 11.3, 95% CI = 54.7–78.0), and 85.2 (SE = 5.0, 95% CI = 63.0–107.5) and for males were 56.4 (SE = 5.9, 95% CI = 41.4–71.4), 54.2 (SE = 7.7, 95% CI = 44.3–64.0), and 73.2 (SE = 7.0, 95% CI = 59.4–87.0) during 2010, 2011, and 2012, respectively (Figure 10). My estimate of N averaged across all years for both sexes was 138.4 (SE = 9.9, 95% CI = 118.9–157.9). Annual population growth rates for males were 0.96 (SE = 0.13, 95% CI = 0.54–1.11)

and 1.35, (SE = 0.16, 95% CI = 0.89–1.68) and for females were 0.83 (SE = 0.15, 95% CI = 0.70–1.22) and 1.29, (SE = 0.20, 95% CI = 1.03–1.67) from 2010 to 2011 and 2011 to 2012, respectively. Pooled population growth over all years for both sexes was 1.08 (SE = 0.04, 95% CI = 1.02–1.18).

Laufenberg's logistic regression equation (2013) for evaluating accuracy estimated a 91% probability that my estimate of N was within 20% of the true N . Using the same method to estimate coverage yielded an 83% probability that my 95% confidence interval included the true N . The probability of obtaining a coefficient of variation $\leq 20\%$ of estimates was 81% using Laufenberg's method (2013).

Density Estimation

The buffer suggestion routine in Program SECR resulted in a recommended buffer of 4,000 m. Within this buffer, 406 km² consisted of forest cover types and were included in the integration mask (Figure 6). My model set included 25 models but only 4 received AICc weights > 0 (Table 5). Variation by sex proved to be an important factor in estimating population density. The top 4 models all included sex effects on all parameters as well as year effects on σ . Behavioral effect on g_0 was also well supported and appeared in the top 2 models. The hazard rate function was well supported but was abandoned in favor of the half-normal estimates because of the unreasonably large buffer required for stable density estimates (Efford 2012).

Estimates of density were 0.22/km² (SE = 0.02, 95% CI = 0.19–0.26) for females and 0.14/km² (SE = 0.01, 95% CI = 0.11–0.16) for males across all years. Overall density was 0.35/km² (SE = 0.02, 95% CI = 0.30–0.41). Mean g_0 was 0.19 (SE = 0.02, 95% CI = 0.15–0.29) for females, 0.09 (SE = 0.01, 95% CI = 0.07–0.14) for males and remained essentially the same across sessions. Mean σ was 970.9 (SE = 18.5, 95% CI = 934.8–1,007.1) for females, 2,287.1

(SE = 40.3, 95% CI = 2,208.1–2,366.2) for males, and followed a similar pattern to estimates of p , lowest in 2010, increasing in 2011, then decreasing in 2012. A spatially explicit estimate of N derived as D multiplied by mask area was 143.8 (SE = 12.1, 95% CI = 120.2–167.5).

Among the suite of 9 covariates, percent canopy was positively correlated with D ($\beta = 0.009$, 95% CI = 0.003–0.015), explained variation in D better than any other covariate, and was associated with 68% of AICc weight (Table 6). Percent marsh was negatively correlated ($\beta = -0.09$, SE = 0.37, 95% CI = -1.57–0.13) and percent swamp positively correlated ($\beta = 0.65$, SE = 0.27, 95% CI = 0.12–1.17) with D . I included them in the predictive model because each had >10% of model weight, and $\Delta\text{AICc} < 4$. The 6 remaining covariates were not included because their 95% confidence intervals encompassed 0. Based on the predictive model ($\text{logit}D = -7.84 + 0.009$ (percent canopy) - 0.85 (percent marsh) + 0.64 (percent swamp)), predicted bear density ranged from 0.02 to 0.15/km² and was greatest in the interior of large blocks of forest cover. After adjusting to exclude non-forest cover, the estimate ranged from 0.05–0.47/km².

Population Genetics

Correspondence analysis revealed that no bears sampled in this project clustered with individuals sampled at White River, TRB, or UARB (Figures 11–13) indicating that none of my sample were immigrants from those areas. A single female sampled at the TRB study area clustered with the coastal population (Figure 12). I detected a genetic subdivision within the coastal population, roughly dividing the population into 2 clusters (Figure 14). Categorizing individuals in the analysis according to capture location revealed that the 2 clusters were separated by longitude with little admixture. Based on the method of Evanno et al. (2005) for determining the number of clusters from Program STRUCTURE, 2 genetic groups were present within the population. Based on inferred ancestry in Program STRUCTURE, when the population was

divided into 2 genetic groups, 69 and 47 individuals had >75% assignment to clusters K_1 and K_2 respectively (Figure 15). Eleven individuals did not assign to either group based on assignment between thresholds of 25% and 75%. Mapping individuals according to these assignments revealed that individuals detected west of UTM zone 15N E 649500 primarily assigned to K_1 whereas individuals detected east of this longitude primarily assigned to K_2 (Figure 16). Twenty-seven of 33 males and 35 of 36 females from K_1 were located primarily in the western zone of the study area. Sixteen of 21 males and 25 of 26 females from K_2 were located primarily in the eastern zone. Both females flagged as possible migrants had range centers located approximately 1 km from the border with their assigned population. Based on movement between populations, sex-specific migration rates for the overall population were 20% for males and 3% for females.

Tests of genetic variation between subpopulations provided evidence of greater genetic isolation between eastern and western bears than between other neighboring populations. Although pairwise F_{ST} was positively correlated with distance between populations, F_{ST} in the eastern portion of the study area compared with the west was consistently higher than F_{ST} between eastern or western pairings (Figure 17). The greatest F_{ST} between neighboring areas was 0.046 between areas 4 in the western zone and 5 in the eastern zone (Figure 17). Mean F_{ST} between all other neighboring pairs was 0.025 (Table 7). Estimated migration rates were lowest between areas 4 and 5 ($Nm = 5.2$) and highest between areas 1 and 2 ($Nm = 16.6$; Table 7). Nei's genetic distance followed the same pattern as F_{ST} (Table 8; Figure 18). Greatest distance was between zones 4 and 5 (0.046) and greatest genetic similarity between zones 1 and 2 (0.015; Figure 19).

Replication of the bottleneck test using the 8 markers from Triant (2001) revealed weak evidence of a heterozygosity deficiency in both samples (Table 9). Five of 8 loci in Triant's (2001) sample from 1999 to 2000 showed heterozygosity deficiency (P -value for deficiency = 0.12) as did 4 of 8 loci in my sample (P -value for deficiency = 0.42). Using all 127 individuals and 23 loci to increase power, 16 loci showed heterozygosity excess (P -value for excess = 0.06). When eastern and western geographic groups from my sample were separately analyzed, 13 of 23 loci in the western group showed evidence of heterozygosity excess (P -value for excess = 0.29) as did 17 of 23 loci in the eastern group (P -value for excess = 0.01).

CHAPTER V

DISCUSSION

My model-averaged abundance estimate from 2010-2012 was 138 (95% CI = 119–158), a substantial difference from the 1999 estimate of 77 (95% CI = 68–86) reported by Triant (2001). Caution should be used when comparing these numbers, however, as our methods and study areas differed. Triant (2001) used 2 sets of samples collected over sessions of 15 days and estimated abundance with Chapman's modified Lincoln-Peterson estimator (Seber 1982). This simple model may underestimate N because it does not account for capture heterogeneity (Pollock 1990). Collection sites for Triant (2001) consisted of a single strand of barbed wire, 45 cm high; therefore, small or large bears may have avoided detection. Finally, the Triant (2001) study sampled a grid of 208 km² with 60, then 120 sites for site densities of 0.29 then 0.58/km², respectively. I maintained 118 sites over a grid of 348 km² for a site density of 0.34/km². If the estimates of Triant (2001) are unbiased, my estimates represent a substantial increase in the 11- to 13- year interval between our sampling sessions. Given that Triant (2001) used a single strand of wire, a simplified estimator, and a smaller coverage area, it seems likely that the 1999 population estimate was biased low relative to my study, although the magnitude of this bias is unknown and therefore population growth since 1999 is also unknown.

The final 9-locus mismatch distribution included 20 pairs of individuals that matched at all but 2 markers and 3 pairs with only a single mismatch. Extrapolation from this predicts about a 50% chance that the data set would include a 0MM-pair although more are possible (D. Paetkau, personal communication). If this was the case, I incorrectly reported data from >190 individuals in 190 individual records. However, the implications of including a small number of

extra individuals in my estimates are insignificant in light of demographic changes that constantly alter the coastal population.

Estimates of precision and bias improve dramatically for $p > 0.2$ (Boulanger et al. 2004, Laufenberg et al. 2013). My average weekly capture probabilities, 0.25 for females and 0.28 for males, indicated that I encountered 90% of females and 93% of males in the area each year. Capture probabilities were higher for males compared with females, possibly an artifact of locating sampling sites along spoil banks which bears used to traverse their home ranges (J. Clark, USGS, unpublished data). Males have larger home ranges and I sampled during the season when males are searching for estrous females. By concentrating sampling sites along travel corridors, I potentially exposed males to a disproportionate risk of capture.

Capture probabilities were highest in 2011 and estimates of abundance and density were lowest at this time. In the same year, I visually observed more bears than in either of the other sessions. These observations seem contradictory but 2 events occurred in 2011 that are worth noting. First, a severe drought struck the southern U.S. beginning in late 2010 and peaking in July 2011 (NOAA 2011). I observed failure of soft mast crops, possibly causing bears to become more active with some emigrating from the study area. Spatially explicit capture recapture analysis indicated that σ was highest for both sexes in 2011. Confirmed losses were higher and survival estimates were lower in the first interval than the second. These losses and movements likely resulted in increased p for those bears that remained, owing to our subsampling procedure. Consistent with this hypothesis, the number of samples collected more than doubled from 2010 to 2011 with only a 12% increase in individuals encountered.

The second event which affected my study area was record spring rainfall in the Ohio Valley which caused historic flooding of the Mississippi River (NOAA 2011). The U.S. Army

Corps of Engineers diverted water through the Atchafalaya River Basin and its distributaries, raising water levels north, south, and east of my sampling sites. Although flooding adjacent to the study area had the potential to cause immigration, neither an increase in N nor a decrease in p was observed. I conclude that the increase in bear visibility was due to increased movement and not immigration.

My secondary sampling periods were scheduled for 8 weeks in the summer to meet the assumption of demographic closure. Because my study area consisted of an isolated fragment of suitable bear habitat, it likely met the geographic closure assumption as well. The habitat in St. Mary and Iberia parishes is surrounded by marsh, agriculture, development, and seasonally flooded swamp (Figure 4). One parcel of possible habitat bordering the study area to the southeast was not sampled. It contained approximately 70 km² of cypress/tupelo swamp, south of the Intracoastal Waterway. My parameter estimates do not indicate significant immigration or emigration but it is possible that some animals inhabiting this area may have avoided detection or that animals emigrated to this bayou-rich area during the drought.

My average survival rate of 0.86 (SE = 0.01) was lower than the 0.91 reported for the Tensas and Pointe Coupee populations (Hooker 2010, Lowe 2011). This is not surprising given the higher human density in my study area. Although the coastal population is legally protected, illegal kills, vehicle collisions, and relocations add up to losses comparable to those in hunted populations, where mortality rates can average 16.6% for females and 21.6% for males (Bunnell and Tait 1981). Published estimates of maximum sustainable harvest include 14% (Miller 1990) and 20% (Neal 1992). Research on natality and recruitment is needed to determine whether estimated mortality rates are sustainable. Review of known mortalities and relocations (USGS BearTRAK 2013) indicated 17 losses in the first sampling interval, 12 losses in the second, and

an average of 14 losses per year from January 2010 to December 2012 (Table 10). This represents approximately 10–12% of the coastal population based on my estimates of N , and was consistent with my estimates of ϕ given that undocumented losses would increase this proportion.

My average λ estimate of 1.1 (95% CI = 1.01–1.17) indicates that the mortality rate did not prevent population growth; however, population fluctuations were evident as λ was 0.88 (95% CI = 0.75–1.02) in the first interval, then rebounded to 1.31 (95% CI = 1.14–1.49) in the second. Average annual per capita recruitment (f) estimated as $\lambda - \phi$ was 0.22 (SE = 0.02, 95% CI = 0.18–0.26). Because these estimates apply to a relatively short period, they may not reflect long-term trends. Additional monitoring of the coastal population would allow for more certainty in dynamic parameters estimated between sessions.

Density estimates for the coastal population were 0.35/km², a moderate density compared with other Southeastern populations (Table 11). Density estimates were consistent with estimates of N ; for example, multiplying my density estimate of 0.35/km² by my habitat mask of 406 km² produced a spatially explicit estimate of $N = 142$, only 4 more than my estimate using Program MARK. Parameter g_0 remained constant across years whereas σ for both sexes increased during 2011, supporting the hypothesis that bears increased their movements, possibly in response to the drought. My linear model to predict site specific density performed poorly, estimating greater density within forested areas and predicting highest densities in areas that were inconsistent with my sampling results. This may be a result of the size of my analysis window relative to the size of habitat fragments; the model predicted high bear density in the center of large blocks of forest regardless of cover type. Lack of data on flooding regime also made it difficult to model the coastal habitat. Quality bear habitat such as bottomland hardwood

forests exists in a matrix of lower quality swamps and depressions. Because canopy cover may be similar between hardwood forests and swamps, it did not predict density accurately despite being the most supported covariate.

Correspondence analyses revealed only a single individual moving between the coast and other regional populations (Figure 12). This was a female that assigned to the coast but was sampled at the southern end of the Tensas study area. Given that females are philopatric it seems unlikely that this bear naturally dispersed from the coast to Tensas. It is more likely that she was relocated to the repatriation area (Figure 1), then dispersed to Tensas. Relocated bears frequently travel great distances from release sites (Clark and Eastridge 2001).

Results of correspondence analyses, assignment tests, F_{ST} and genetic distance analyses all indicate 2 genetic groups divided into eastern and western subpopulations on either side of Highway 317 south of Centerville. One possible explanation is that the highway, adjacent agriculture, a metal floodwall, and marginal habitat west of the highway (Figure 16) discourage movement through this area, causing separation and genetic drift. A similar highway flanked by agriculture also had high F_{ST} (Figure 17) and genetic distance (Figure 19) indicating that large gaps between natural cover present some resistance to bear movement. Despite being larger, the agricultural area surrounding Hwy 83 seems to be less of a barrier than Hwy 317. Seven males and 1 female were detected on both sides of Hwy 317 during my 3-year study, and radio collared bears were observed moving across the highway and floodwall (J. Clark, USGS, unpublished data). This mixture is consistent with estimates of Nm although the cause of the genetic difference observed between east and west remains uncertain. A second hypothesis is that historic population fragmentation resulting from low abundance resulted in small, geographically disjunct populations; a reduction in N combined with genetic drift, ultimately resulted in 2

distinguishable groups. This hypothesis seems likely given that the coastal population was possibly reduced to as few as 30 individuals in the 1980s (Nowak 1986). Quantity of samples collected and number of individuals captured indicate higher bear density on Weeks Island in western Iberia Parish and the Patterson/Calumet area in eastern St. Mary Parish. It seems likely that these areas may have been historic refuges for small populations and sources for recolonization of the surrounding habitat. Heavy losses along Highways 317 and 90 (Figure 20) are another possible factor shaping genetic structure in the coastal population. Bears moving through this area are frequently killed or relocated, preventing genetic exchange between eastern and western subpopulations.

The combined effects of illegal kills, management removals, and vehicle collisions create a loss rate comparable to a hunted population in the coastal population. Pace et al. (2000) reported a mark-recapture estimated survival rate of 76% for adult females in the coastal population from 1992-2000. In this same period, they report that 65% (49 of 75) of deaths or removals from the statewide population came from the coast. In comparison, I counted 10 relocations and 31 confirmed mortalities during my 3 sampling years (USGS BearTRAK 2013). Losses during 2010–2012 were heaviest from November–January including all confirmed illegal kills and 17 of 22 fatal collisions (Figure 21). Consistent with Pace et al. (2000), approximately 25% of losses occurred in November alone, primarily due to excessive roadkill (Figure 21). In coastal Louisiana, many bears use sugar cane fields in fall (Nyland 1995), which places them near roads more often (Pace et al. 2000). Mapping of mortalities and management removals revealed that a disproportionate number of vehicle mortalities (11 of 22) and relocations (4 of 10) occurred along Highways 90 and 317 south of Centerville (Figure 20). This

seems to indicate a source-sink pattern between the productive habitat east of Highway 317 and the surrounding developed areas.

Tests for a past genetic bottleneck revealed a heterozygosity deficiency in the sample collected by Triant (2001). Unlike heterozygosity excess which indicates a bottleneck, heterozygote deficiency can be a result of population structure (Rousset and Raymond 1995). This deficiency was not strong and I suspect it was an artifact of the small number of loci tested. My own 8-locus sample was very close to equilibrium but adding all loci and increasing sample size resulted in a heterozygosity excess, the signal of a bottleneck. Evidence for a bottleneck was strong in the eastern subpopulation but weak in the larger western subpopulation. This is a further indicator of genetic structure.

CHAPTER VI

MANAGEMENT IMPLICATIONS

My survival and population growth estimates indicate that the coastal population of Louisiana black bears is increasing at a moderate rate but subject to fluctuations and declines in some years. Apparent survival rates are lower than those observed in other unharvested populations in the Southeast (Dobey et al. 2005, Clark et al. 2010, Hooker 2010, Lowe 2011). It is important to remember that these estimates are based on only 2 intervals and longer term data is needed to reach any definitive conclusions about population trend. If a viable population or sustainable harvest are management goals, I recommend focusing efforts on preventing mortality along the 25 km of Highways 90 and 317 connecting Patterson and Bayou Sale (Figure 20). Management efforts in this area will almost certainly give the greatest return on investment. Without addressing losses from this population sink, the additional mortality of harvest may cause the coastal bear population to decline. The conversion of Hwy 90 to I-49 has the potential to either alleviate or increase roadkills. Landscape-level planning, fencing, and underpasses are tools currently available to reduce the frequency and costs of wildlife/vehicle collisions (McCollister and van Manen 2010).

My abundance and density estimates created a baseline for future monitoring of population trends. Taken alone, these data are only a snapshot of a dynamic population. I recommend continued monitoring with population indices such as bait-station surveys which can be a relatively inexpensive tool compared with population estimation and are robust to biases that affect estimation of abundance and density (Boulanger 2004). This is especially vital if harvest is a management goal for this population. Any future take should be conservative and seek to balance net mortality with recruitment.

Genetic analyses showed no exchange between bear populations in the UARB and LARB. The coast appears to be isolated with little or no function from a metapopulation standpoint. Genetic analyses indicate a genetic bottleneck within the eastern portion of the coastal population; currently however, demographic factors are a greater threat than genetic ones. Although the coastal population appears to be increasing, little suitable habitat is available for future expansion. Isolated from other populations and confined to a narrow area, the coastal population is vulnerable to decline and extinction from unpredictable or stochastic events such as disease, development, hurricanes, land subsidence, or sea-level rise. Although dispersing males frequently move north from the coast, the UARB and LARB populations are separated by approximately 70 to 100 km and numerous obstacles, including areas that are permanently or seasonally flooded, highways, and development. Natural landcover north of the coastal population primarily consists of swamp and although natural ridges exist, a scarcity of mast producing trees and lack of female bears discourages males from establishing home ranges or reaching the inland populations. Finally, although male dispersal can alleviate genetic threats, exchange of females is necessary for there to be a demographic effect. Suitable habitat corridors or translocation of females between the coastal and inland populations may be necessary to allow rescue or recolonization of the coastal population in the event of a future decline.

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APPENDICES

APPENDIX A: TABLES

Table 1. GIS layers and ecological systems used to delineate habitat for predict density of Louisiana black bears in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012.

Layer	Value	Classified as bear habitat
USGS Gap Landcover	Mississippi Delta Maritime Forest	Yes
USGS Gap Landcover	Mississippi River Floodplain and Riparian Forest	Yes
USGS Gap Landcover	Mississippi River Bottomland Depression	Yes
USGS Gap Landcover	Gulf and Atlantic Coastal Plain Swamp Systems	Yes
USGS Gap Landcover	Agriculture, Reclassified from Cultivated Cropland and Hay/Pasture	No
USGS Gap Landcover	Gulf and Atlantic Coastal Plain Tidal Marsh Systems	No
USGS Gap Landcover	Developed, Reclassified from Developed Low, Medium, and High Intensity	No
USGS Gap Landcover	Open Water	No
USGS NCLD 2001	Percent Canopy	NA

Table 2. Heterozygosity and Probability of Identity for 23 microsatellite markers used for identification and genetic structure analyses of Louisiana black bears in coastal Louisiana, USA 2010–2012.

Locus	N ^a	A ^b	H _E ^c	H _O ^d	PI ₈ ^e	PI _{sib 8} ^f	PI ₂₃	PI _{sib 23}
<i>G10P</i>	190	5	0.73	0.73	0.12	0.41	0.12	0.42
<i>MU59</i>	190	4	0.69	0.66	0.17	0.45	0.17	0.45
<i>MU23</i>	190	5	0.69	0.68	0.16	0.45	0.16	0.45
<i>G10U</i>	190	4	0.66	0.65	0.18	0.47	0.18	0.47
<i>CXX110</i>	190	3	0.65	0.65	0.20	0.47	0.20	0.47
<i>G10J</i>	190	5	0.63	0.66	0.22	0.50	0.22	0.50
<i>D123</i>	190	3	0.63	0.64	0.22	0.49	0.22	0.49
<i>MU50</i>	190	4	0.58	0.59	0.25	0.53	0.25	0.50
8-Locus Mean	190	4.1	0.66	0.66				
8-Locus Combined PI, PI _{sib}					1.3x10 ⁻⁶	2.4x10 ⁻³		
<i>A06</i>	143	7	0.73	0.58			0.12	0.41
<i>D1A</i>	127	3	0.65	0.67			0.20	0.48
<i>P07</i>	143	3	0.62	0.62			0.22	0.50
<i>CPH9</i>	143	4	0.62	0.62			0.24	0.51
<i>G10C</i>	143	4	0.61	0.61			0.23	0.51
<i>G10L</i>	127	4	0.57	0.58			0.23	0.53
<i>MU26</i>	143	5	0.53	0.53			0.27	0.55
<i>CXX20</i>	127	4	0.5	0.47			0.30	0.58
<i>G10B</i>	127	6	0.47	0.45			0.32	0.60
<i>MSUT2</i>	127	3	0.45	0.41			0.34	0.61
<i>G1D</i>	127	3	0.42	0.44			0.42	0.64
<i>G10M</i>	127	4	0.41	0.42			0.38	0.64
<i>G10H</i>	127	4	0.41	0.41			0.39	0.64
<i>G10X</i>	127	4	0.39	0.35			0.41	0.66
<i>G1A</i>	127	3	0.3	0.32			0.52	0.73
23-Locus Mean	152	4.1	0.56	0.55				
23-Locus Combined PI, PI _{sib}							1.0x10 ⁻¹⁴	4.7x10 ⁻⁷

^a Number of bears identified using a given locus.

^b Number of alleles.

^c Expected heterozygosity.

^d Observed heterozygosity.

^e Probability of Identity.

^f Probability of Identity among siblings.

Table 3. Robust Design model rankings based on AICc to estimate demographic parameters for the Louisiana black bear population of St. Mary and Iberia parishes, Louisiana, USA, 2010–2012. Competing models included constant (\cdot), sex, year, additive, and interactive (sex * year) effects on apparent survival (ϕ), probability of belonging to 1 of 2 mixtures (π), probability of capture (p), and probability of recapture (c). I fit models without a behavioral effect ($p = c$), with a behavioral effect ($p + c$), and with a behavioral effect where p and c were estimated independently ($p + c \text{ int}$). I also modeled probability of being off the study area given that an individual was (γ') or was not (γ'') available for capture in the previous primary session. I modeled random movement $\gamma' = \gamma'' = (\cdot)$ and no movement $\gamma' = 0, \gamma'' = 1$. Parameters were averaged based on model AICc weight.

Rank	Model	AICc	Δ AICc	AICc Weight	Parameters	Deviance
1	{ ϕ (year), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex * year, mix) = c }	1448.35	0.00	0.19	16	1828.14
2	{ ϕ (year), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, year, mix) = c }	1448.77	0.42	0.16	14	1832.71
3	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, year, mix) = c }	1448.85	0.50	0.15	13	1834.87
4	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (year, mix) = c }	1449.51	1.16	0.11	12	1837.58
5	{ ϕ (sex), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, year, mix) = c }	1449.72	1.37	0.10	14	1833.67
6	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (year, mix) + $c \text{ int.}$ (year, mix) }	1450.73	2.38	0.06	15	1832.60
7	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (year, mix) + c (year, mix) }	1450.79	2.44	0.06	13	1836.80
8	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (year, mix) + $c \text{ int.}$ (sex, year, mix) }	1451.19	2.85	0.05	16	1830.99
9	{ ϕ (\cdot), γ' (0), γ'' (1), $\pi(\cdot)$, p (year, mix) + $c \text{ int.}$ (year, mix) }	1451.80	3.45	0.03	15	1833.67
10	{ ϕ (\cdot), γ' (0), γ'' (1), $\pi(\cdot)$, p (year, mix) + $c \text{ int.}$ (sex, year, mix) }	1452.27	3.92	0.03	16	1832.07
11	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, year, mix) + $c \text{ int.}$ (sex, year, mix) }	1452.45	4.10	0.03	17	1830.16
12	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, year, mix) + $c \text{ int.}$ (year, mix) }	1452.59	4.24	0.02	16	1832.38
13	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (year, mix) + $c \text{ int.}$ (mix) }	1454.14	5.79	0.01	15	1836.01
14	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (mix) = c }	1458.85	10.50	0.00	10	1851.03
15	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, mix) = c }	1459.01	10.66	0.00	11	1849.14
16	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\text{sex})$, p (sex, mix) = c }	1459.34	10.99	0.00	12	1847.42
17	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (mix) + $c \text{ int.}$ (year, mix) }	1460.02	11.67	0.00	15	1841.89
18	{ ϕ (year), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (mix) = c }	1460.35	12.00	0.00	11	1850.48
19	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (mix) + c (mix) }	1460.39	12.04	0.00	11	1850.53
20	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (sex, mix) + c (sex, mix) }	1460.48	12.13	0.00	12	1848.55
21	{ ϕ (sex), γ' (\cdot), γ'' (\cdot), $\pi(\cdot)$, p (mix) = c }	1460.56	12.21	0.00	11	1850.69
22	{ ϕ (\cdot), γ' (\cdot), γ'' (\cdot), $\pi(\text{year})$, p (year, mix) + c (year, mix) }	1468.68	20.33	0.00	16	1848.47
23	{ ϕ (year), γ' (\cdot), γ'' (\cdot), $\pi(\text{year})$, p (sex, year) = c }	1572.98	124.63	0.00	13	1958.99

Table 4. Weekly probabilities of capture (p) and recapture (c) for Louisiana black bears sampled in 2010–2012 in a capture-mark-recapture study in coastal Louisiana, USA.

		p 2010	p 2011	p 2012	c 2010	c 2011	c 2012
Female	π_a	0.07	0.15	0.11	0.06	0.13	0.10
Female	π_b	0.37	0.57	0.49	0.37	0.58	0.49
Male	π_a	0.09	0.16	0.14	0.08	0.14	0.12
Male	π_b	0.42	0.59	0.54	0.43	0.60	0.55

Table 5. Spatially explicit capture-recapture model rankings based on AICc to estimate density (D) for the Louisiana black bear population of St. Mary and Iberia parishes, Louisiana, USA, 2010–2012. The parameters that define the detection function are the probability of detection if an individual’s activity center is at a detector (g_0), spatial scale (σ), and shape (z). Competing models included constant (\cdot), sex, year, and additive effects on D , g_0 , and σ as well as behavioral effects on g_0 and σ .

Rank	Model	Detection Function	Parameters	AIC	AICc	Δ AICc	AICc weight
1	{ D (sex), g_0 (sex + behavior), σ (sex + year) }	Half-normal	9	9063.43	9064.03	0.00	0.86
2	{ D (sex), g_0 (sex + behavior + year), σ (sex + year) }	Half-normal	11	9066.96	9067.83	3.81	0.13
3	{ D (sex + year), g_0 (sex), σ (sex + year) }	Half-normal	10	9072.73	9073.46	9.43	0.01
4	{ D (sex), g_0 (sex), σ (sex + year) }	Half-normal	8	9073.43	9073.91	9.88	0.01

Table 6. Spatially explicit capture recapture model rankings based on AICc to predict Louisiana black bear density as a function of landcover covariates. Beta values from supported covariates were included in a linear model to predict bear density in St Mary and Iberia parishes, Louisiana, USA, 2010–2012. The parameters that define the detection function are the probability of detection if an individual’s activity center is at a detector (g_0), spatial scale (σ), and shape (z). Competing models included percentage of 8 cover classes and canopy within 1,938 m, equal to the radius of the mean home range for female bears.

Model	DF ^a	P ^b	AIC	AICc	Δ AICc	Weight. ^c	β^d	SE	LCL ^e	UCL ^f
{ D (% canopy), g_0 (.), σ (.), z (.) }	Hazard rate	5	9172.97	9173.16	0.00	0.68	0.01	0.00	0.00	0.02
{ D (% marsh), g_0 (.), σ (.), z (.) }	Hazard rate	5	9176.30	9176.50	3.33	0.13	-0.09	0.37	-1.57	-0.13
{ D (% swamp), g_0 (.), σ (.), z (.) }	Hazard rate	5	9176.58	9176.77	3.61	0.11	0.65	0.27	0.12	1.17
{ D (% maritime forest), g_0 (.), σ (.), z (.) }	Hazard rate	5	9179.97	9180.16	7.00	0.02	1.35	0.82	-0.26	2.96
{ D (% depression), g_0 (.), σ (.), z (.) }	Hazard rate	5	9180.21	9180.40	7.24	0.02	3.40	2.26	-1.02	7.82
{ D (% agriculture), g_0 (.), σ (.), z (.) }	Hazard rate	5	9181.40	9181.60	8.43	0.01	-0.31	0.34	-0.98	0.36
{ D (% water), g_0 (.), σ (.), z (.) }	Hazard rate	5	9181.62	9181.82	8.65	0.01	0.39	0.46	-0.50	1.29
{ D (% developed), g_0 (.), σ (.), z (.) }	Hazard rate	5	9181.79	9181.99	8.82	0.01	-0.76	1.13	-2.97	1.46
{ D (% bottomland hardwood), g_0 (.), σ (.), z (.) }	Hazard rate	5	9182.09	9182.29	9.12	0.01	0.60	1.38	-2.10	3.30

^aDetection function.

^bNumber of Parameters.

^cAICc weight.

^dSlope parameter; correlation with density.

^eLower confidence limit.

^fUpper confidence limit.

Table 7. Fixation index (F_{ST}) and estimated migrants per generation (Nm) between geographic groupings of Louisiana black bears sampled in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012. Based on capture locations, bears were assigned to the eastern or western area and 1 of 6 geographic groups defined by possible barriers such as agriculture, highways, and canals.

Pairwise Genetic Distance (F_{ST})						
	Pop1 West	Pop2 West	Pop3 West	Pop4 West	Pop5 East	Pop6 East
Pop1 West	0.000				East vs. West	0.035
Pop2 West	0.015	0.000				
Pop3 West	0.024	0.033	0.000			
Pop4 West	0.018	0.026	0.022	0.000		
Pop5 East	0.049	0.045	0.059	0.046	0.000	
Pop6 East	0.048	0.048	0.059	0.054	0.029	0.000
Successfully breeding migrants per generation (Nm)						
Pop1 West	0.0				East vs. West	6.9
Pop2 West	16.6	0.0				
Pop3 West	10.0	7.4	0.0			
Pop4 West	13.4	9.4	11.1	0.0		
Pop5 East	4.9	5.2	4.0	5.2	0.0	
Pop6 East	4.9	5.0	4.0	4.4	8.4	0.0

Table 8. Genetic and linear distances between geographic groupings of Louisiana black bears sampled in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012. Genetic distance was measured by Nei’s *D* and linear distance was measured in km. Based on capture locations, bears were assigned to the eastern or western area and to 1 of 6 geographic groups defined by possible barriers such as agriculture, highways, and canals.

Pairwise Genetic Distance (Nei’s <i>D</i>)						
	Pop1 West	Pop2 West	Pop3 West	Pop4 West	Pop5 East	Pop6 East
Pop1 West	0.000					
Pop2 West	0.015	0.000				
Pop3 West	0.024	0.033	0.000			
Pop4 West	0.018	0.026	0.022	0.000		
Pop5 East	0.049	0.045	0.059	0.046	0.000	
Pop6 East	0.048	0.048	0.059	0.054	0.029	0.000
Pairwise Linear Distance (km)						
Pop1 West	0.00					
Pop2 West	7.78	0.00				
Pop3 West	15.02	7.53	0.00			
Pop4 West	30.47	22.83	15.45	0.00		
Pop5 East	39.37	31.62	24.50	9.38	0.00	
Pop6 East	49.54	41.80	34.62	19.28	10.18	0.00

Table 9. *P*-values of Wilcoxon tests for a genetic bottleneck within the Louisiana black bear population of St. Mary and Iberia parishes, Louisiana, USA 1992–2000 and 2010–2012. Models were tested under the 2-phase mutation model which assumes that mutation may gain or lose one repeat at a time (the Stepwise Mutation Model; Infinite SMM) but may also create any new allele randomly (the Alleles Model; IAM). Triant (2001) used 8 markers from samples collected from 1992–2000. Using samples collected from 2010–2012, I replicated the test of Triant (2001) and used a 23-marker set to test for a bottleneck in the overall population and compare eastern and western subgroups.

Test	Triant et		23-loci	23-loci	23-loci
	al. (2001)	8-loci		West	East
Number of loci with heterozygosity > expected	3/8	4/8	16/23	13/23	17/23
Wilcoxon test <i>P</i> -value for heterozygosity excess	0.90	0.62	0.05	0.29	0.12
Number of loci with heterozygosity < expected	5/8	4/8	7/23	10/23	6/23
Wilcoxon test <i>P</i> -value for heterozygosity deficiency	0.12	0.42	0.95	0.72	0.98

Table 10. Mortalities and relocations of Louisiana black bears from St. Mary and Iberia parishes, Louisiana, USA, 1 November, 2009 to 31 December, 2012.

LDWF ID	UT ID	Sex	Date	Notes	Age Class	DNA sampled
NA	CMORT2010-3	F	11/1/2009	Roadkill	Old adult	No
NA	NA	F	1/10/2010	Nuisance; euthanized	Unknown	No
NA	CMORT2010-1	M	1/27/2010	Roadkill	Young adult	No
630	NA	M	4/24/2010	Relocated to Monroe Zoo	Middle aged	No
NA	NA	F	5/5/2010	Roadkill	Unknown	No
769	769-2011	F	6/1/2010	Relocated to Red River WMA	Sub adult	Yes
NA	CMORT2010-2	F	8/20/2010	Roadkill	Unknown	No
803	NA	M	9/2/2010	Relocated to Red River WMA	Sub adult	No
747	747-2010	M	10/15/2010	Nuisance; euthanized	Middle aged	Yes
718	718-2010	M	11/1/2010	Mortality; illegally shot	Yearling	Yes
756	CO1-08-J12-001T	F	11/25/2010	Mortality; illegally shot	Young adult	Yes
768	768-2010	M	12/2/2010	Mortality; caught in hog-snare	Sub adult	Yes
NA	CO1-07-M28-004B	M	12/14/2010	Nuisance; euthanized	Old adult	Yes
814	814-2011	M	12/16/2010	Relocated/shot	Sub adult	Yes
NA	CO1-06-N33-001B	F	12/29/2010	Roadkill	Unknown	Yes
NA	CO1-04-O30-001T	M	12/30/2010	Roadkill	Unknown	Yes
805	CO1-05-M29-001T	M	12/30/2010	Relocated to Sherburne WMA	Young adult	Yes
NA	CO1-01-K27-001B	?	1/1/2011	Train kill	Unknown	Yes
806	CO1-05-O33-001T	M	1/15/2011	Relocated/shot	Middle aged	Yes
816	NA	M	1/15/2011	Relocated to Red River WMA	Unknown	No
NA	CMORT2011-1	F	2/1/2011	Roadkill	Sub adult	No
818	CO2-08-M29-001B	M	2/6/2011	Relocated/returned	Sub adult	Yes
802	CO1-02-M30-001T	M	4/16/2011	Relocated to Red River WMA; returned twice	Unknown	Yes
NA	CO1-03-I24-001B	F	7/11/2011	Roadkill	Young adult	Yes
NA	CO1-03-O33-001B	M	7/16/2011	Roadkill	Young adult	Yes
NA	NA	M	8/22/2011	Unknown mortality	Unknown	No

Table 10. Continued.

LDWF ID	UT ID	Sex	Date	Notes	Age Class	DNA sampled
NA	NA	F	11/14/2011	Roadkill	Unknown	No
NA	CMORT5-2011	M	11/28/2011	Roadkill	Young adult	No
NA	CMORT6-2011	M	12/3/2011	Mortality; illegally shot	Sub adult	No
NA	CMORT7-2011	M	12/20/2011	Mortality; incidental to research	Unknown	No
24	NA	M	1/3/2012	Relocated to Red River WMA	Young adult	No
748	NA	F	1/5/2012	Roadkill	Unknown	No
NA	CO2-08-M26-001T	M	1/5/2012	Roadkill	Young adult	Yes
NA	NA	M	2/1/2012	Roadkill	Unknown	No
NA	CMORT2-2012	M	2/18/2012	Roadkill	Unknown	No
NA	CMORT3-2012	M	8/13/2012	Roadkill	Sub adult	No
810	NA	M	8/21/2012	Relocated to Red River WMA	Sub adult	No
NA	CMORT4-2012	F	10/30/2012	Roadkill	Young adult	No
NA	CO2-01-O35-003B	F	11/12/2012	Roadkill	Middle aged	Yes
NA	CMORT6-2012	F	11/14/2012	Roadkill	Yearling	No
NA	CO1-08-P31-001T	F	11/24/2012	Roadkill	Young adult	Yes
NA	CMORT8-2012	M	11/26/2012	Roadkill	Cub	No
NA	CMORT9-2012	Unknown	11/26/2012	Roadkill	Cub	No

Table 11. Black bear population densities in the southeastern USA.

Study Area	Bears/km ²	Reference
Camp Lejeune, NC	0.02	Brandenburg (1996)
Carvers Bay, SC	0.04	Drewry (2010)
White Rock, AR	0.08	Clark and Smith (1994)
Dry Creek, AR	0.09	Clark and Smith (1994)
Okefenokee Swamp, GA	0.12	Dobey et al. (2005)
Osceola National Forest, FL	0.14	Dobey et al. (2005)
Upper Atchafalaya River Basin, LA	0.15	Lowe (2011)
White River National Wildlife Refuge, AR	0.22	Clark et al. (2010)
Lewis Ocean Bay, SC	0.31	Drewry (2010)
Lower Atchafalaya River Basin, LA	0.35	This study
Big Pocosin, NC	0.53	Martorello (1998)
Great Dismal Swamp, NC/VA	0.52–0.66	Hellgren and Vaughan (1989)
Tensas River Basin, LA	0.66	Hooker (2010)
Alligator River National Wildlife Refuge, NC	0.86	Allen (1999)
Gum Swamp, NC	1.35	Martorello (1998)
Deltic Tracts, Tensas River Basin, LA	1.43	Beasoleil (1999)

APPENDIX B: FIGURES

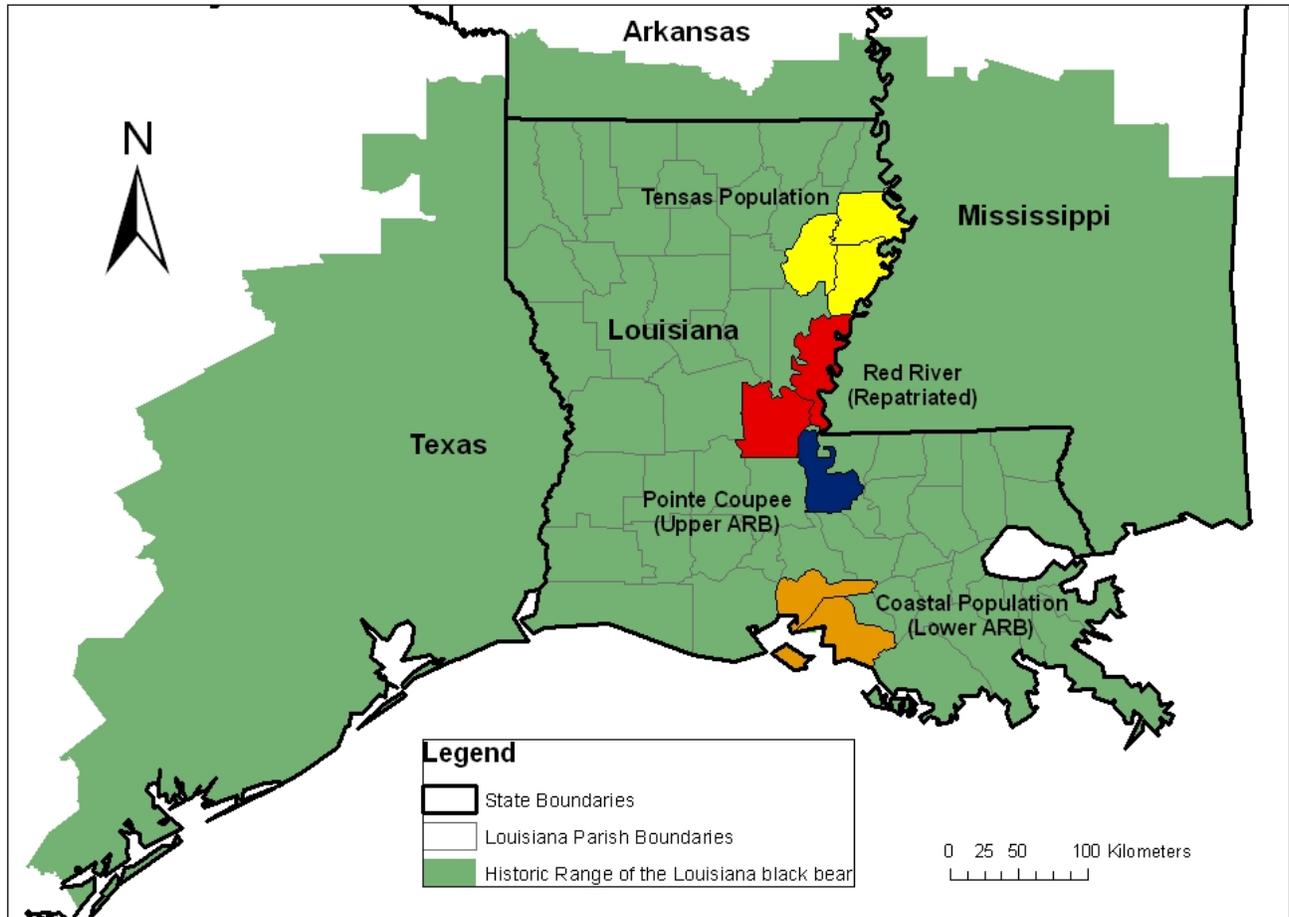


Figure 1: Historic range of the Louisiana black bear in Louisiana, Arkansas, Mississippi, and Texas, USA, and Louisiana parishes occupied by breeding populations 2010–2012.

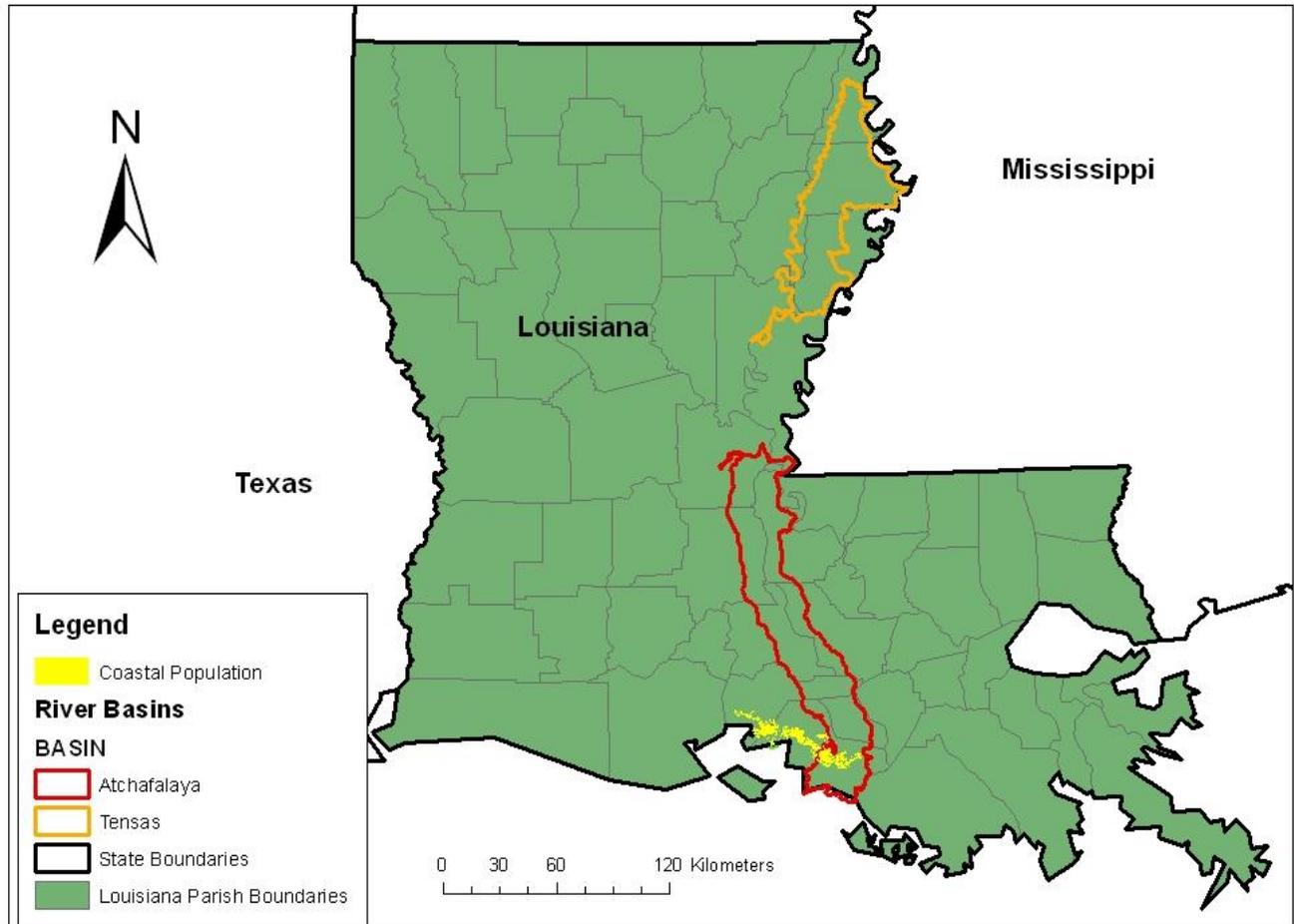


Figure 2: Location of Louisiana black bear habitat in St. Mary and Iberia parishes, 2010–2012.

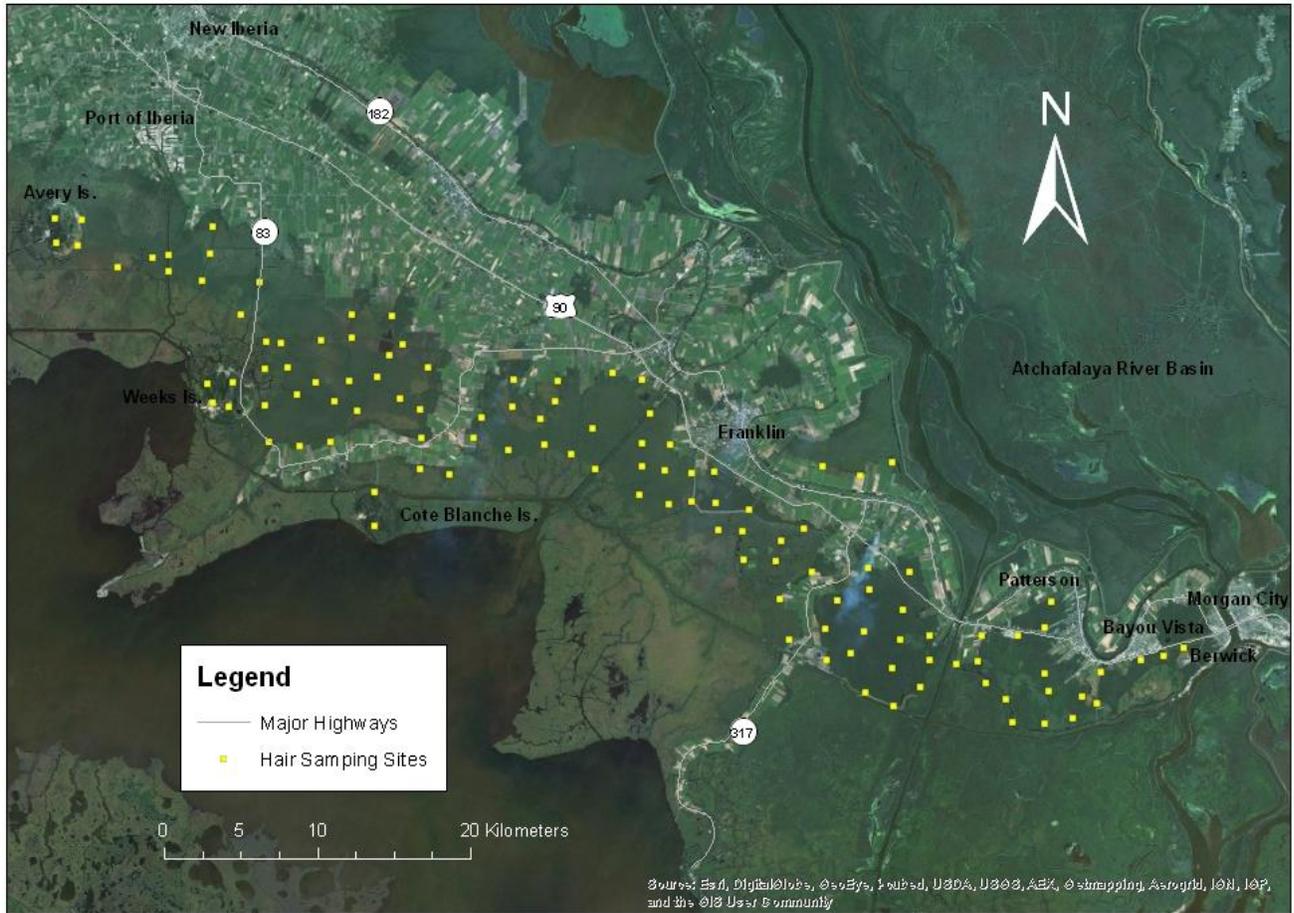


Figure 3: Location of 118 stations used for hair-sampling of Louisiana black bears in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012.

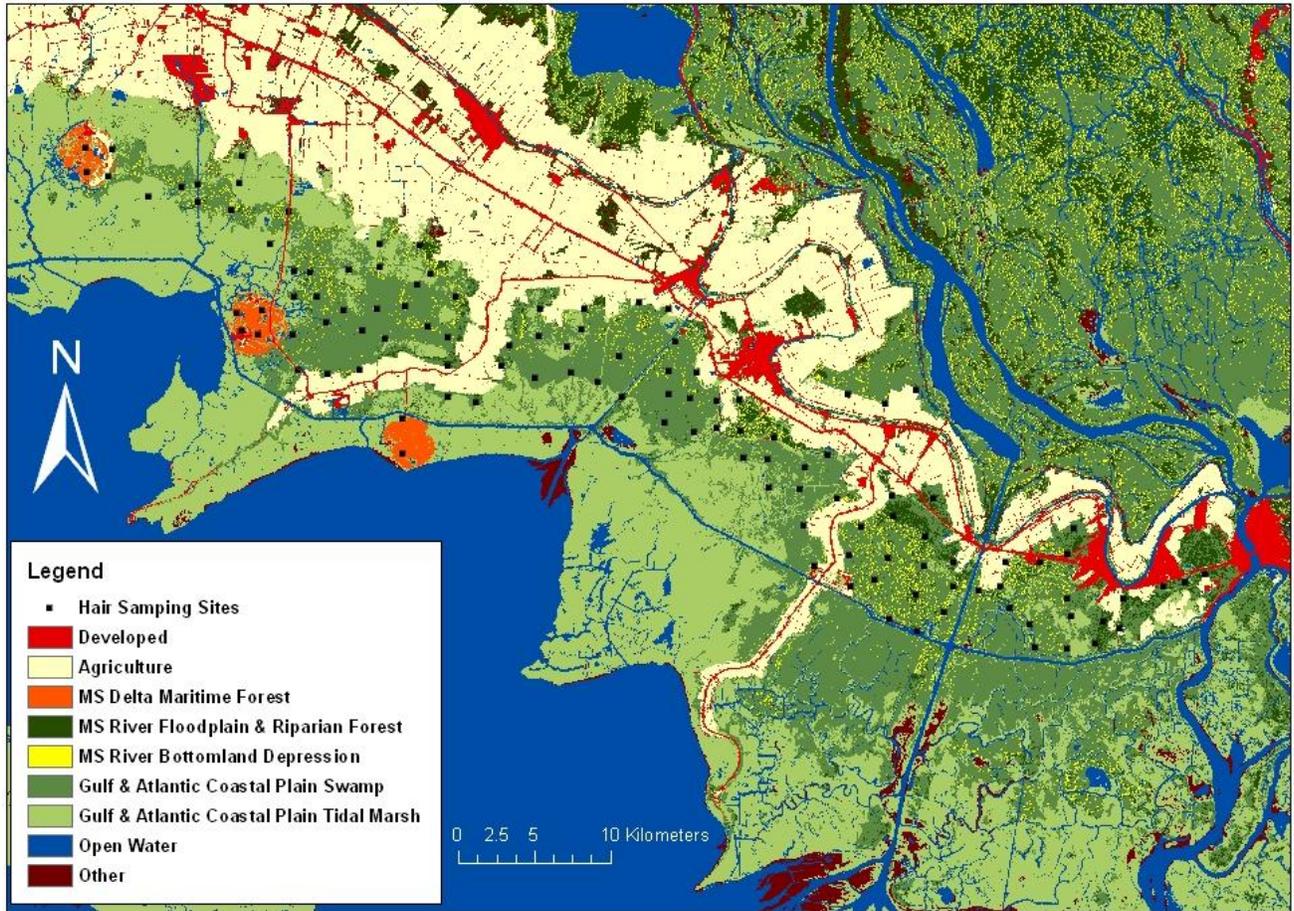


Figure 4: Eight landcover classifications comprise >95% of the coastal study area. Percentages of these 8 and percent canopy were used as covariates in SECR to predict density of Louisiana black bears in coastal Louisiana, USA, 2010–2012.



Figure 5: A barbed wire corral for collecting hair samples from Louisiana black bears. I constructed 118 hair collection sites in 2010–2012 in St. Mary and Iberia parishes, Louisiana, USA.

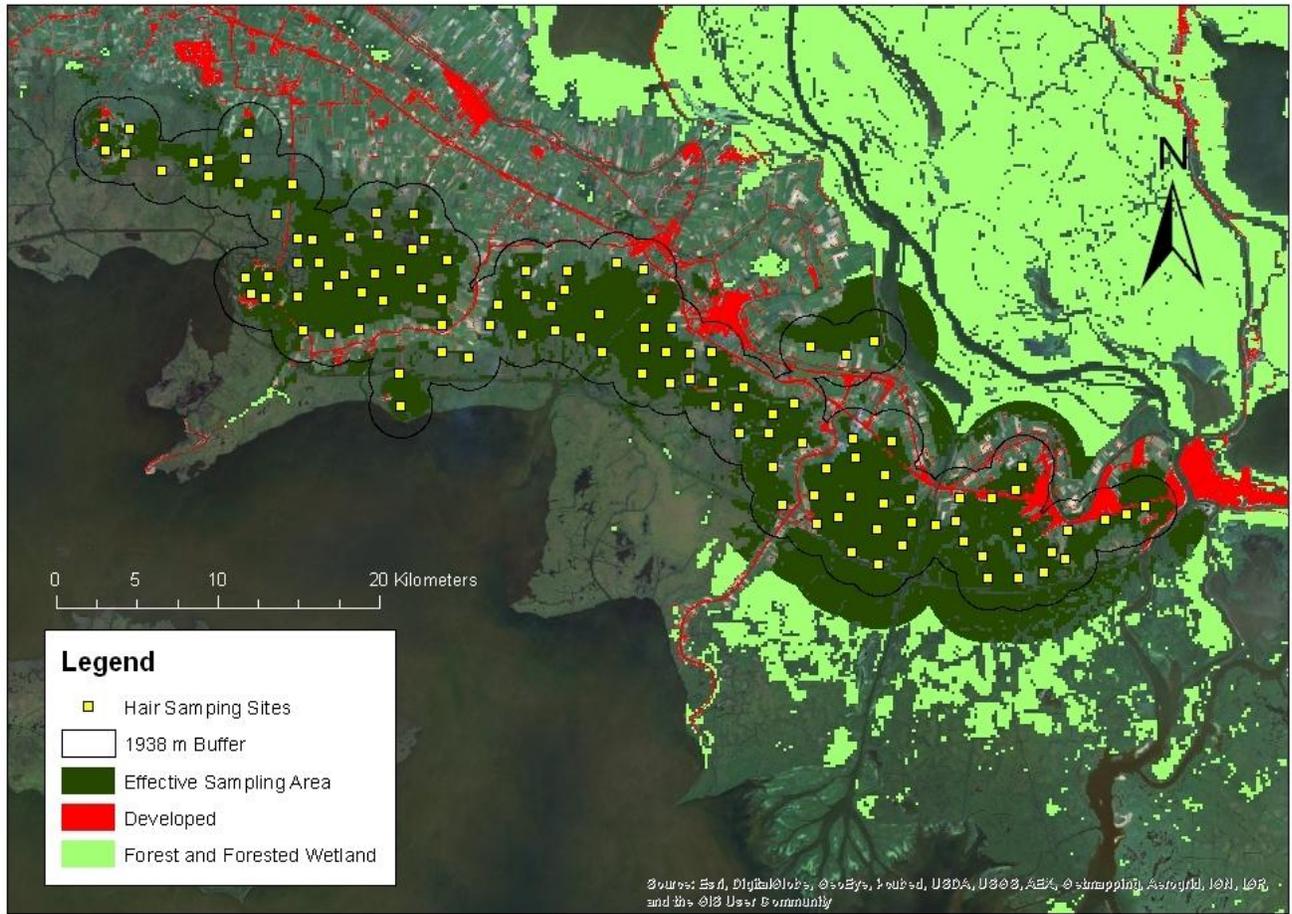


Figure 6: Average Louisiana black bear female home range radii (1,938 m) circumscribed around 118 hair collection sites operated in 2010–2012, forest cover within a 4,000 m SECR buffer, and forest cover adjacent to the sampling area in coastal Louisiana, USA.

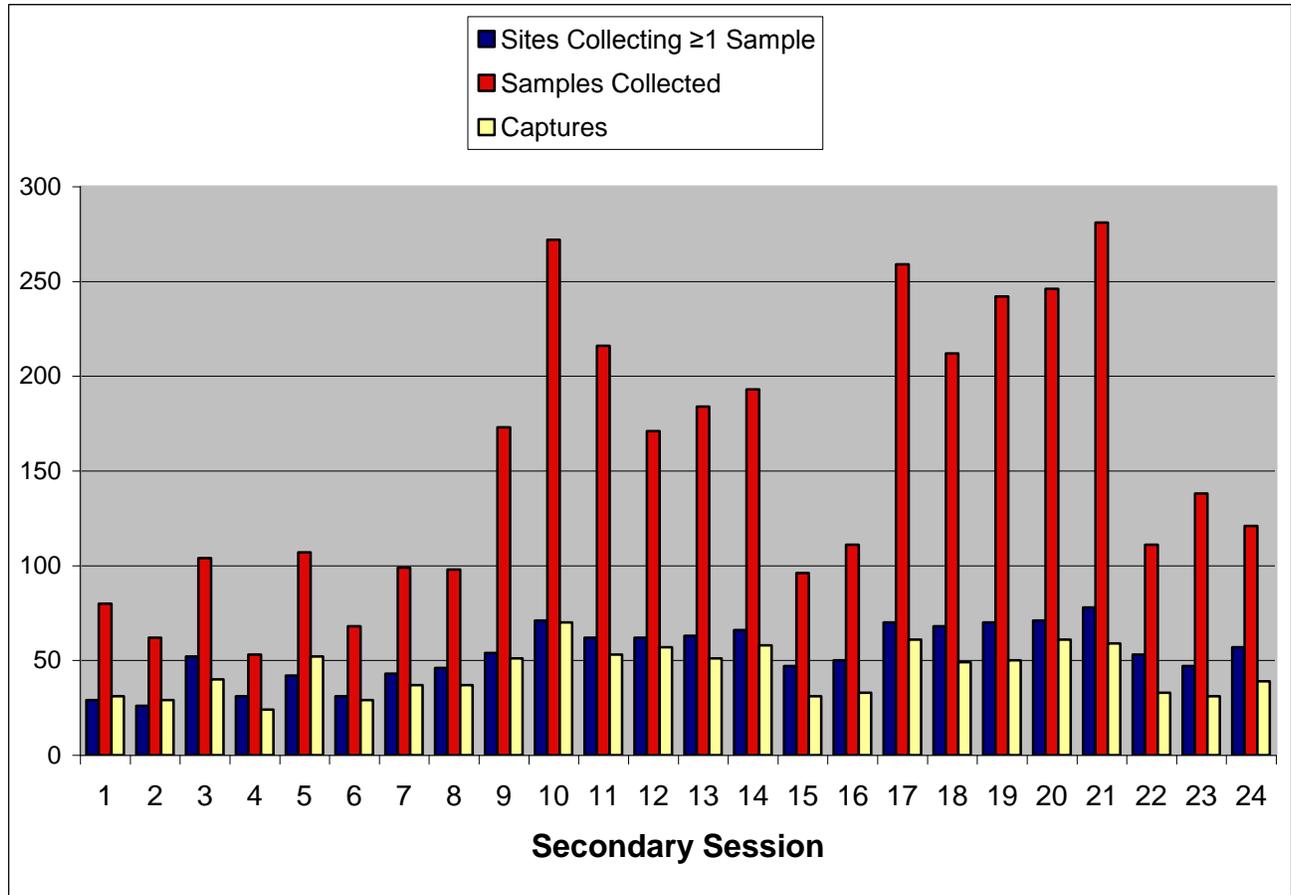


Figure 7: Collection rates of samples from Louisiana black bears in coastal Louisiana, USA. Sites collecting ≥ 1 hair-sample, samples collected, and captures (detection of a single individual at a single site) are shown for 24 sampling occasions. Sessions 1 to 8 were collected in 2010, 9 to 16 in 2011, and 17 to 24 in 2012.

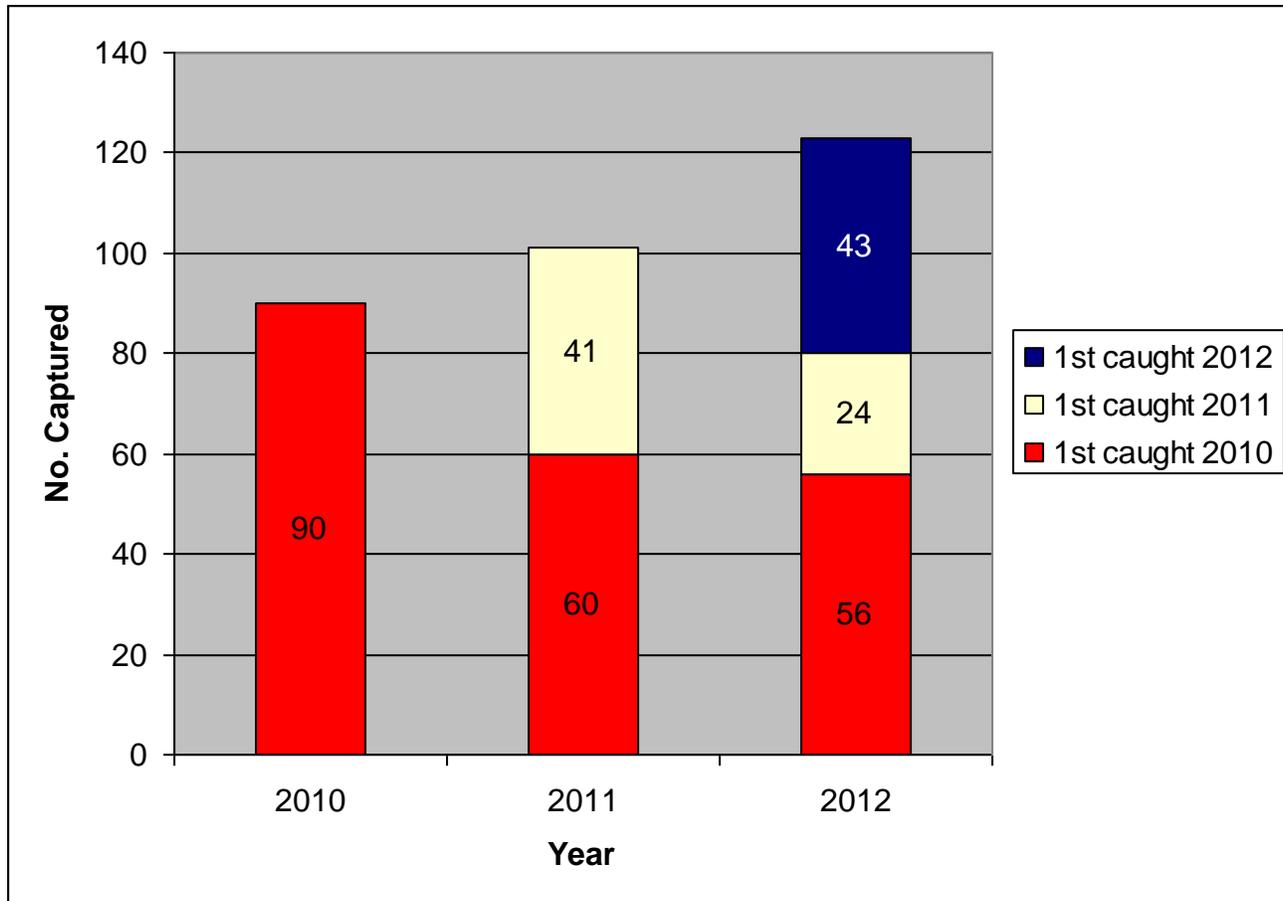


Figure 8: Capture histories for Louisiana black bears 2010–2012 in coastal Louisiana, USA.

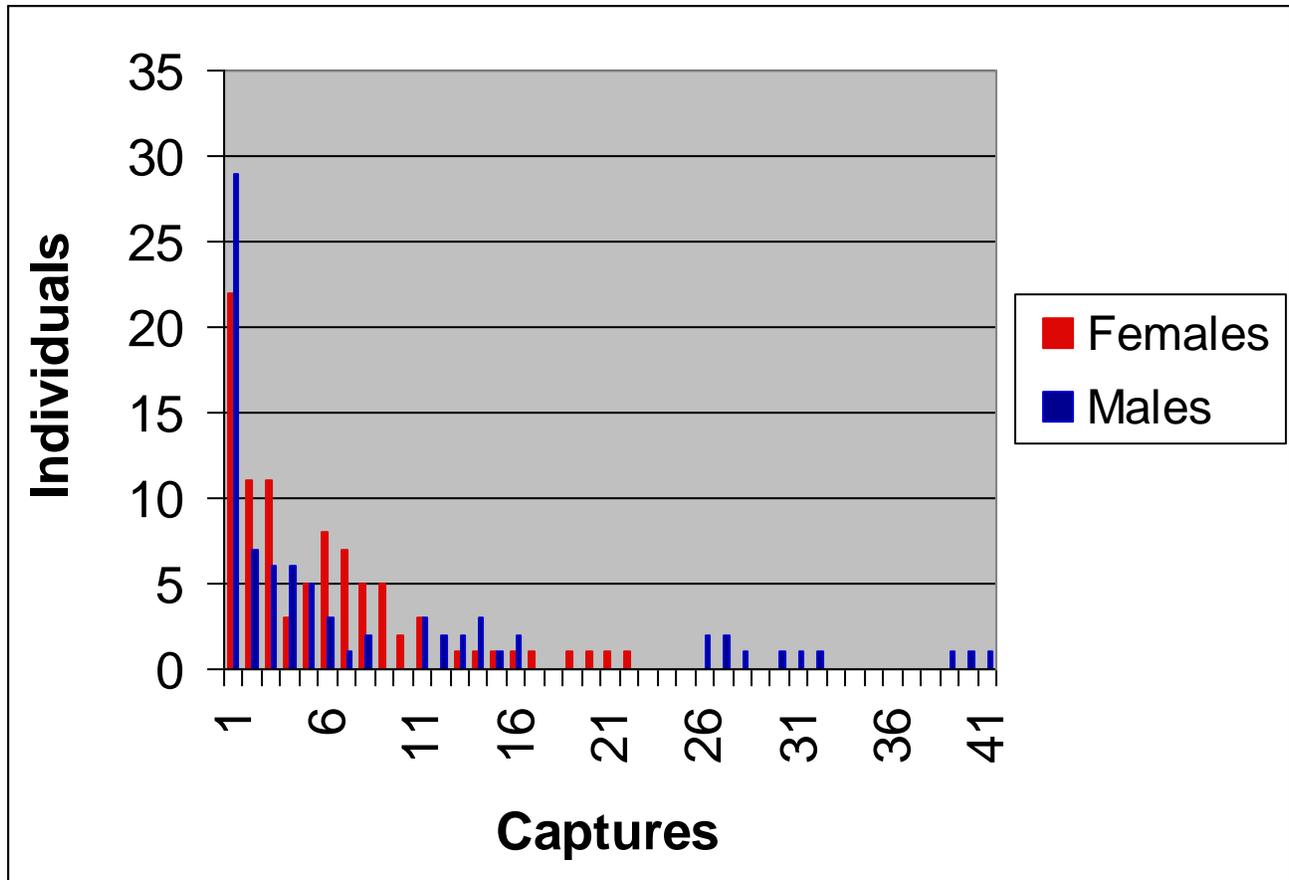


Figure 9: Capture distribution of Louisiana black bears, 2010–2012, in coastal Louisiana, USA. Individual males were encountered up to 41 times with a mean of 8.07 encounters at 4.3 sites and females up to 22 times with a mean of 5.56 encounters at 2.3 sites.

Model Averaged Abundance Estimates

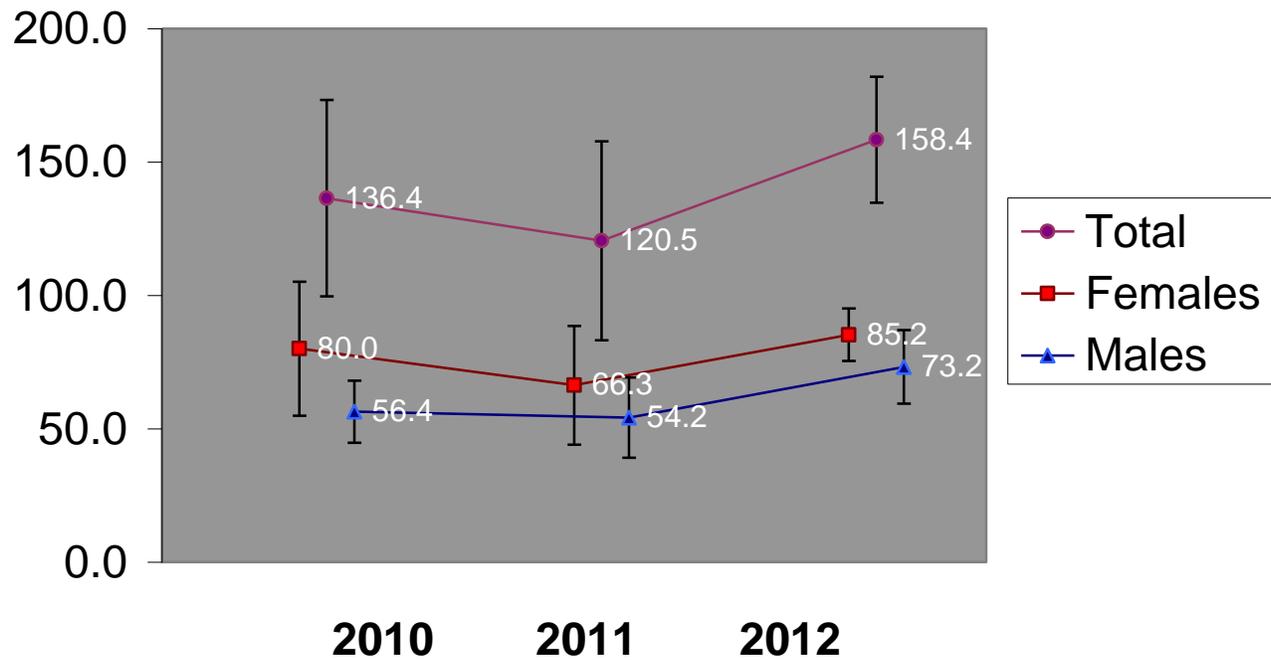


Figure 10: Annual abundance estimates of Louisiana black bears in coastal Louisiana, USA, 2010–2012.

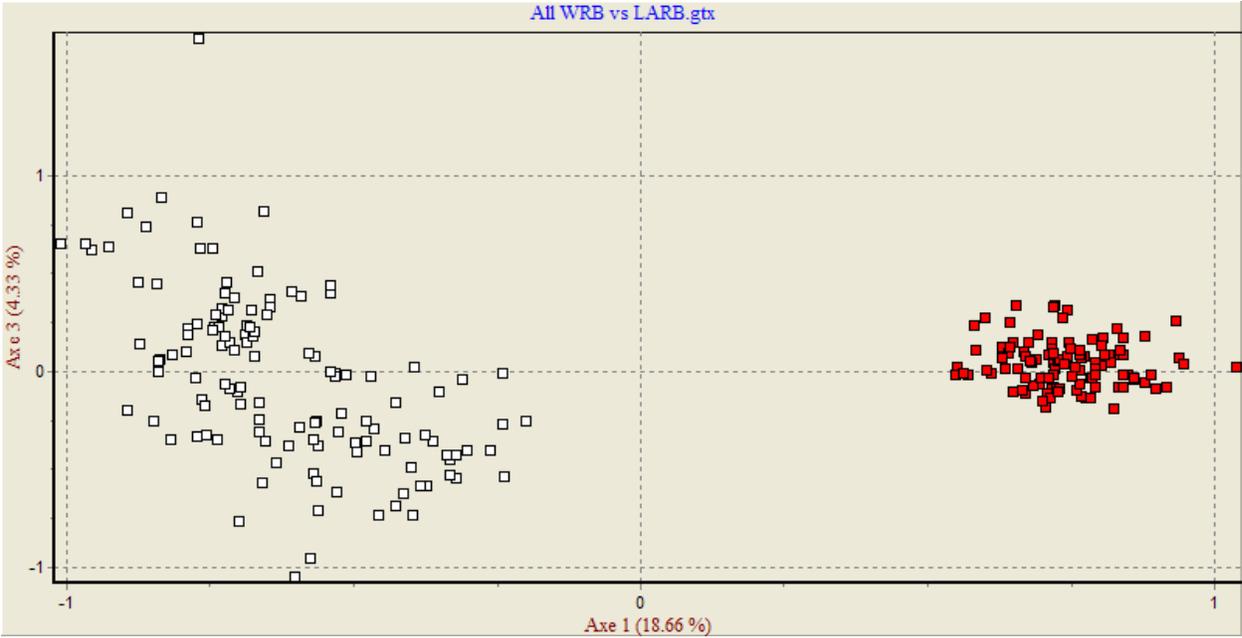


Figure 11: Correspondence analysis of 105 black bears sampled in the White River Basin, Arkansas, USA, 2004–2007 (red) vs. 127 Louisiana black bears from the Lower Atchafalaya River Basin, Louisiana, USA, sampled from 2010–2012 (white).

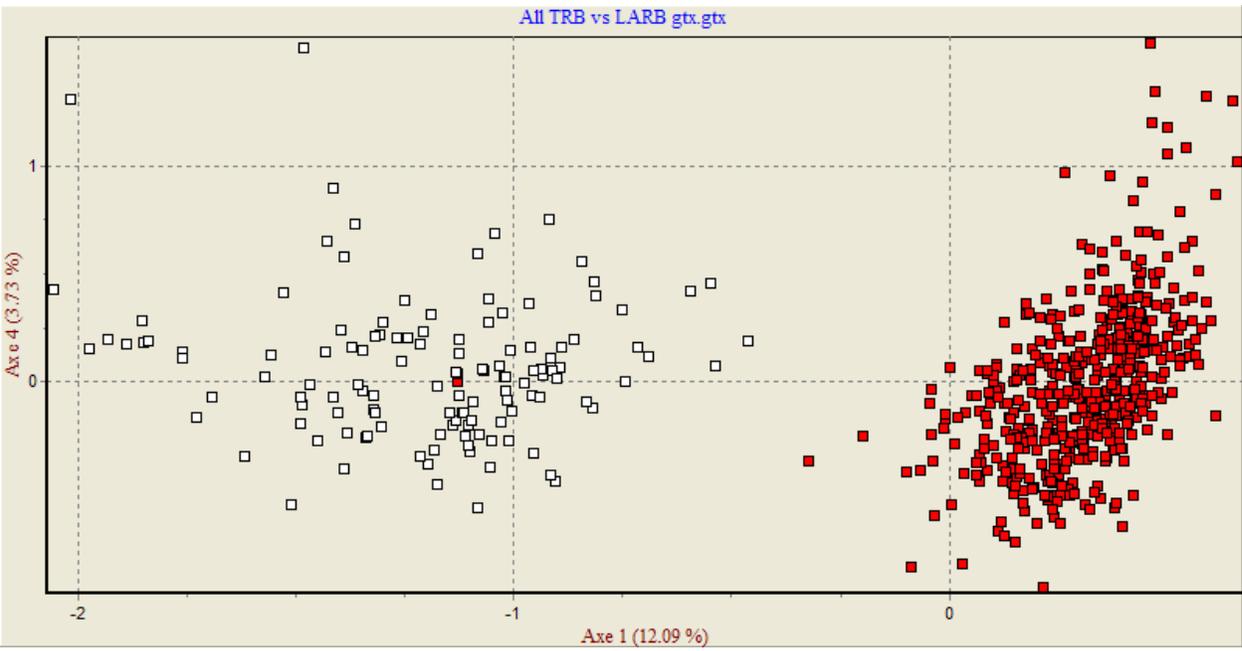


Figure 12. Correspondence analysis of 498 Louisiana black bears sampled in the Tensas River Basin, Louisiana, USA, from 2006–2012 (red) vs. 127 from the Lower Atchafalaya River Basin, Louisiana, USA, sampled from 2010–2012 (white). One female sampled at Tensas assigned genetically to the coastal population.

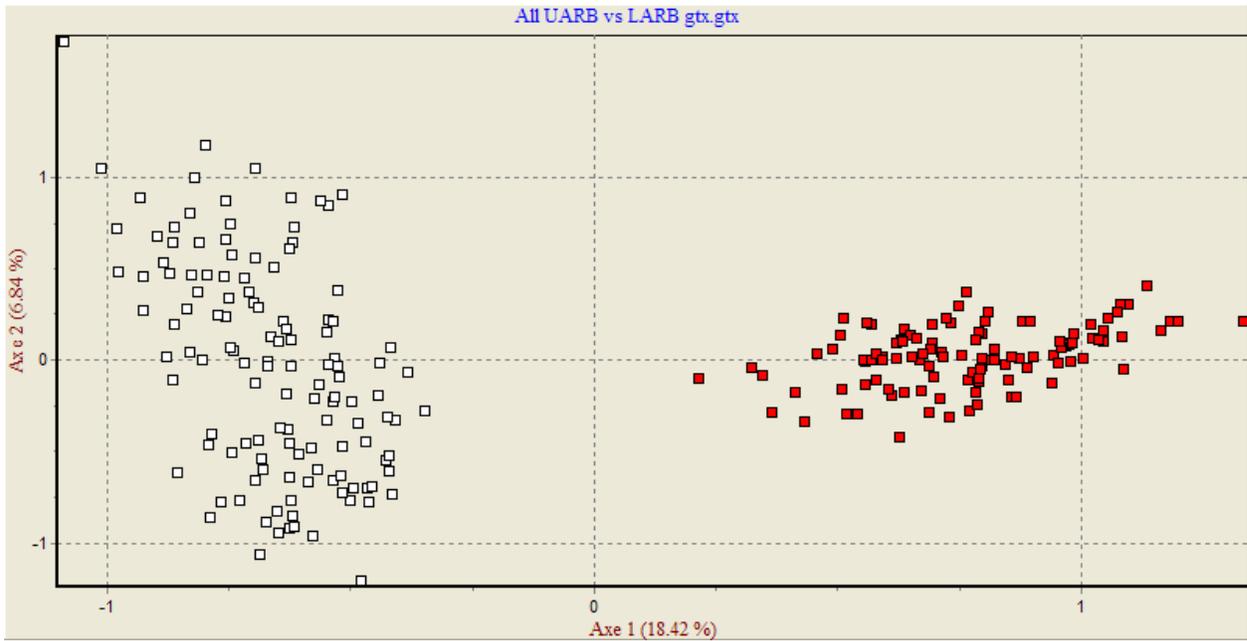


Figure 13. Correspondence analysis of 109 Louisiana black bears sampled in the Upper Atchafalaya River Basin, Louisiana, USA, from 2007–2012 (red) vs. 127 sampled in the Lower Atchafalaya River Basin, Louisiana, USA, from 2010–2012 (white).

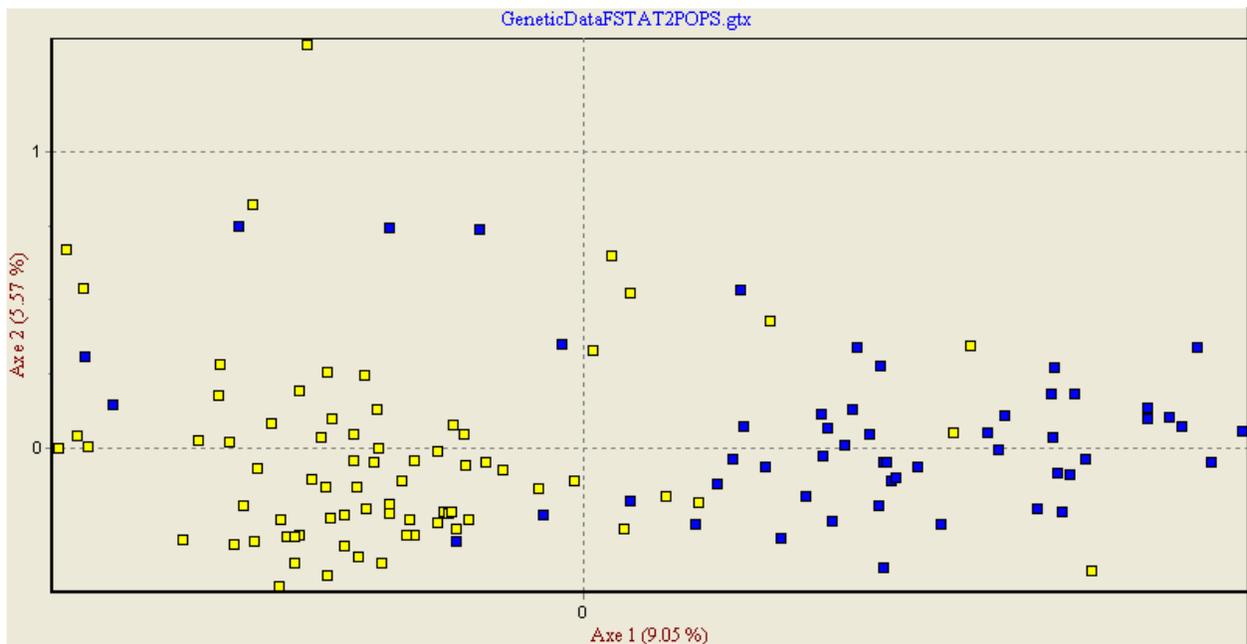


Figure 14: Correspondence analysis of 74 Louisiana black bears (gold) sampled in the western section of the study area (zones 1 through 4) vs 53 individuals (blue) sampled in the eastern section (zones 5 and 6) in coastal Louisiana, USA, 2010–2012.

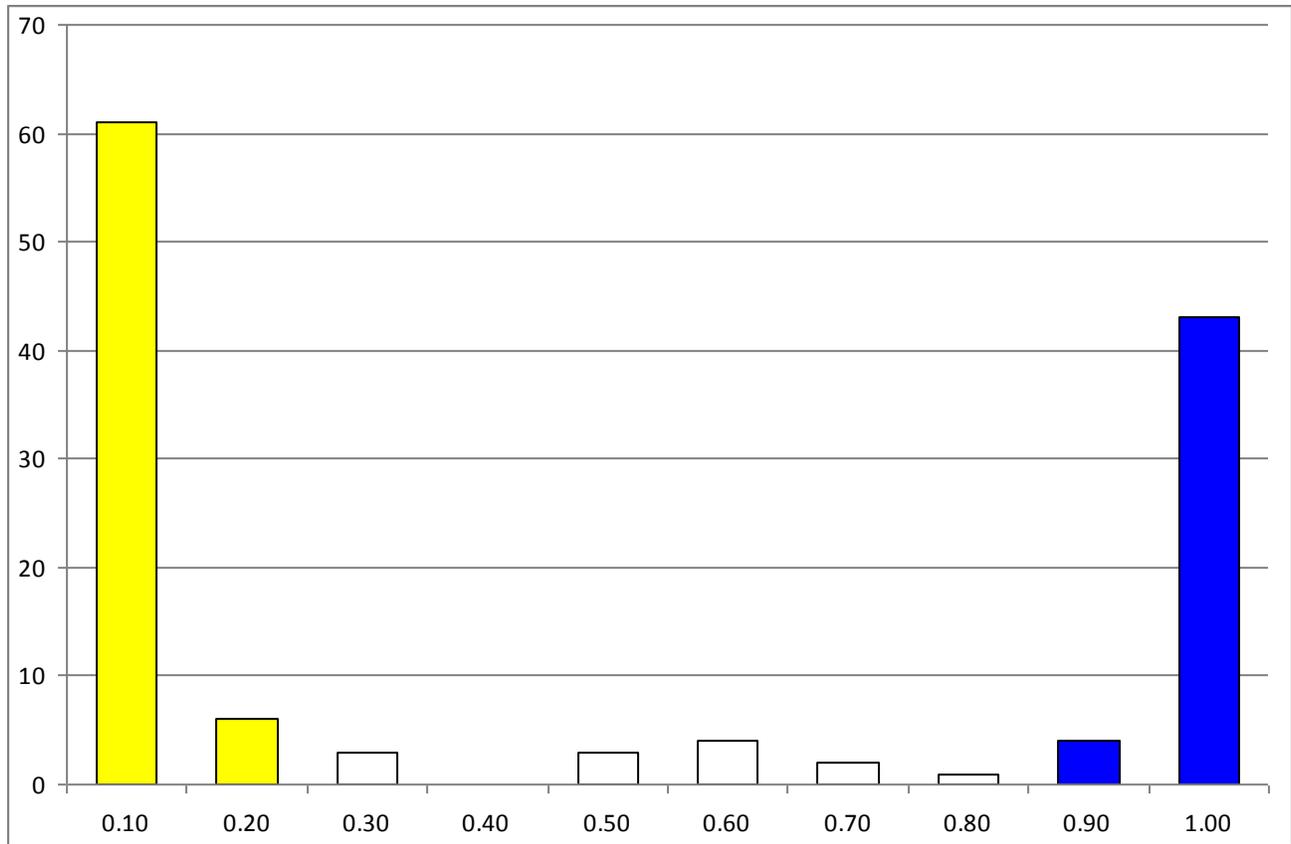


Figure 15: Genetic assignments by Program STRUCTURE of 127 Louisiana black bears sampled in St. Mary and Iberia parishes, Louisiana, USA, from 2010–2012. Blue: >0.75 assignment to population 1, Gold: >0.75 assignment to population 2. White: 0.25-0.75 assignment to either population.

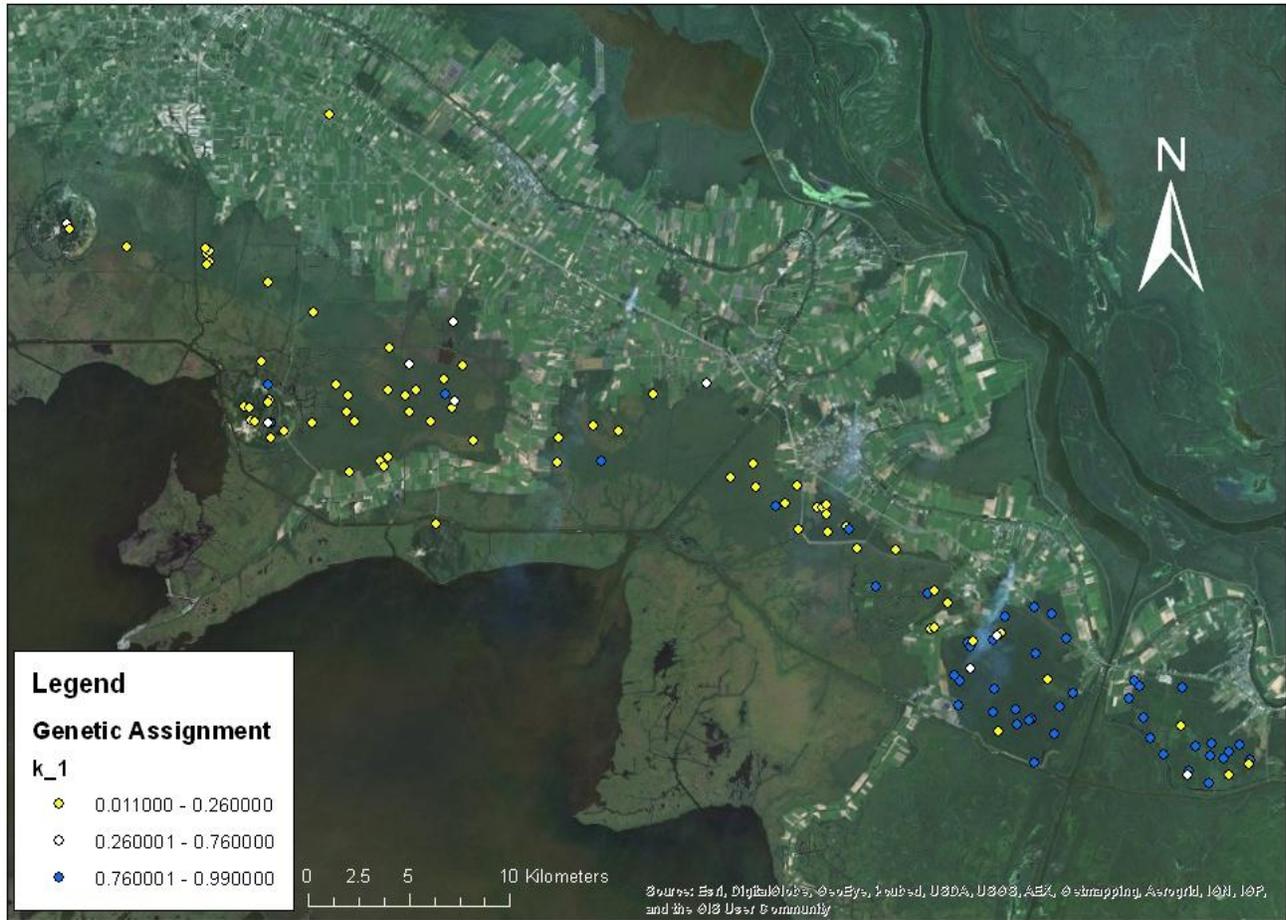


Figure 16: Detection-based home range centers for Louisiana black bears in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012, color categorized by genetic assignment. Blue: >0.75 assignment to population 1, Gold: >0.75 assignment to population 2. White: 0.25-0.75 assignment to either population.

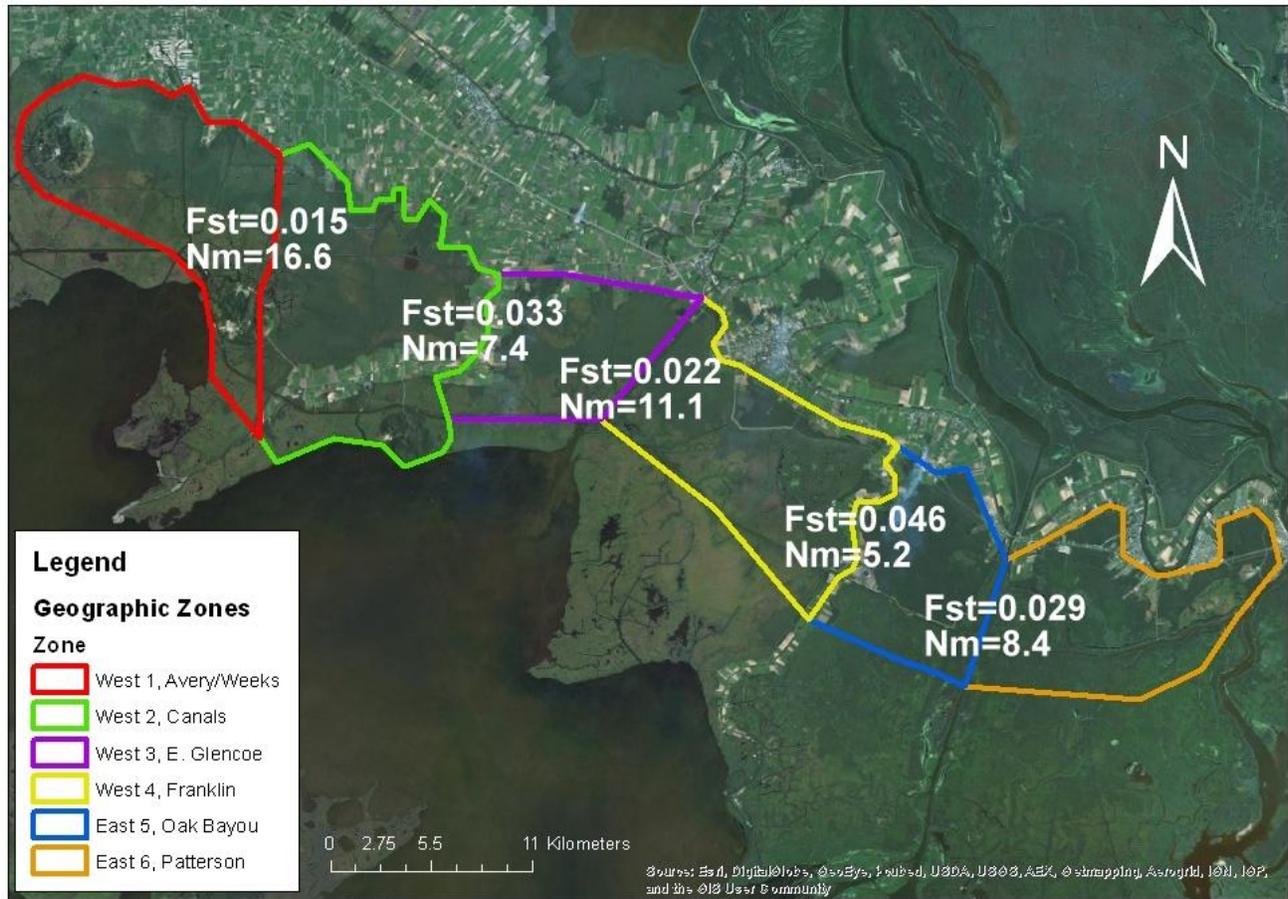


Figure 17: Geographic zones 1–4 West, and 5 and 6 East used to measure F_{ST} between Louisiana black bears in coastal Louisiana, USA, 2010–2012. Pairwise F_{ST} values and estimated number of migrants per generation (Nm) between adjacent zones are shown.

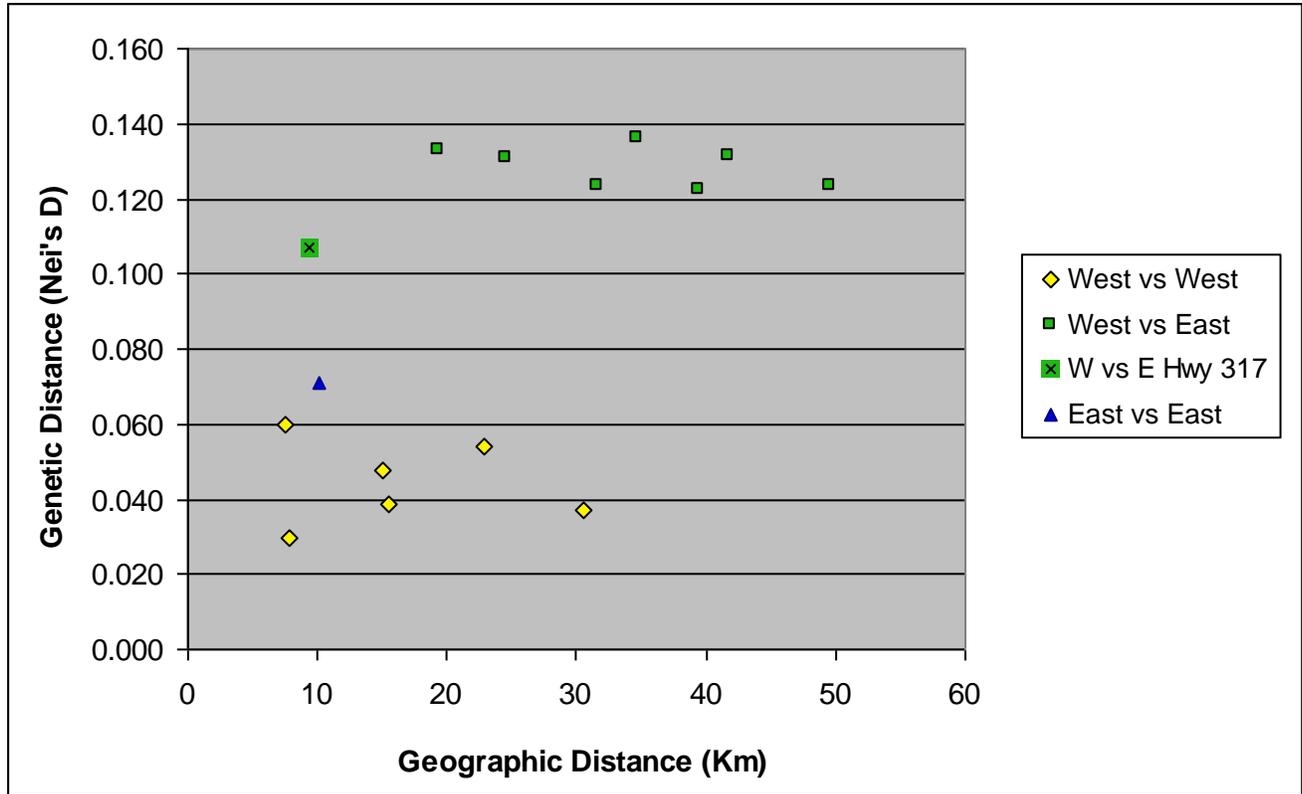


Figure 18: Genetic distance (Nei's D) vs geographic distance (km) between geographically categorized groups of Louisiana black bears in St. Mary and Iberia parishes, Louisiana, USA, 2010–2012. W vs E Hwy 317 is the distance between zones 4 east and 5 west.

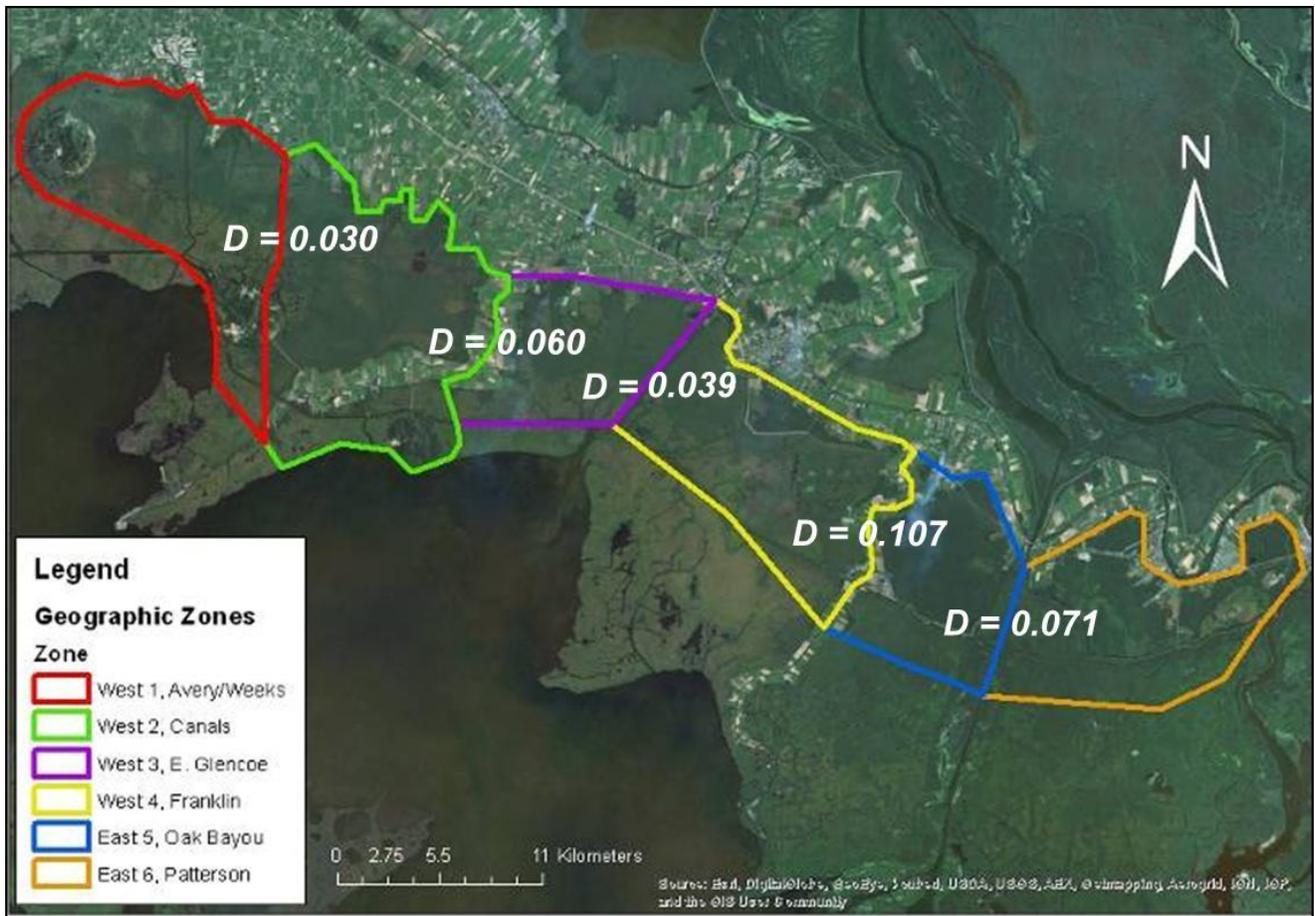


Figure 19: Geographic zones 1–4 West, and 5 and 6 East used to measure genetic distance between Louisiana black bears in coastal Louisiana, USA, 2010–2012. Pairwise Nei's D values between adjacent zones are shown.

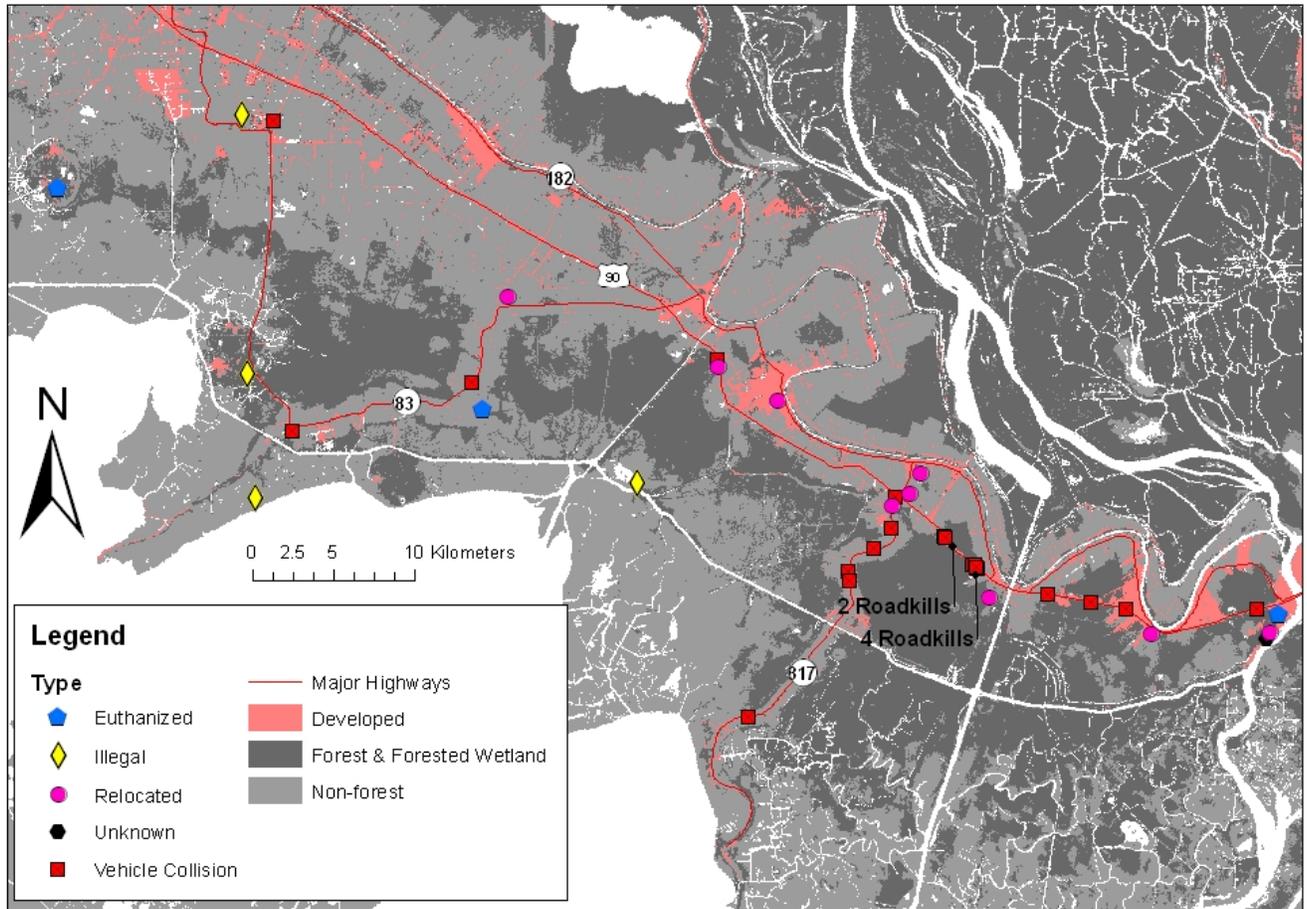


Figure 20: Geographic distributions of deaths and relocations of Louisiana black bears from St. Mary and Iberia parishes, Louisiana, USA, 2010–2012.

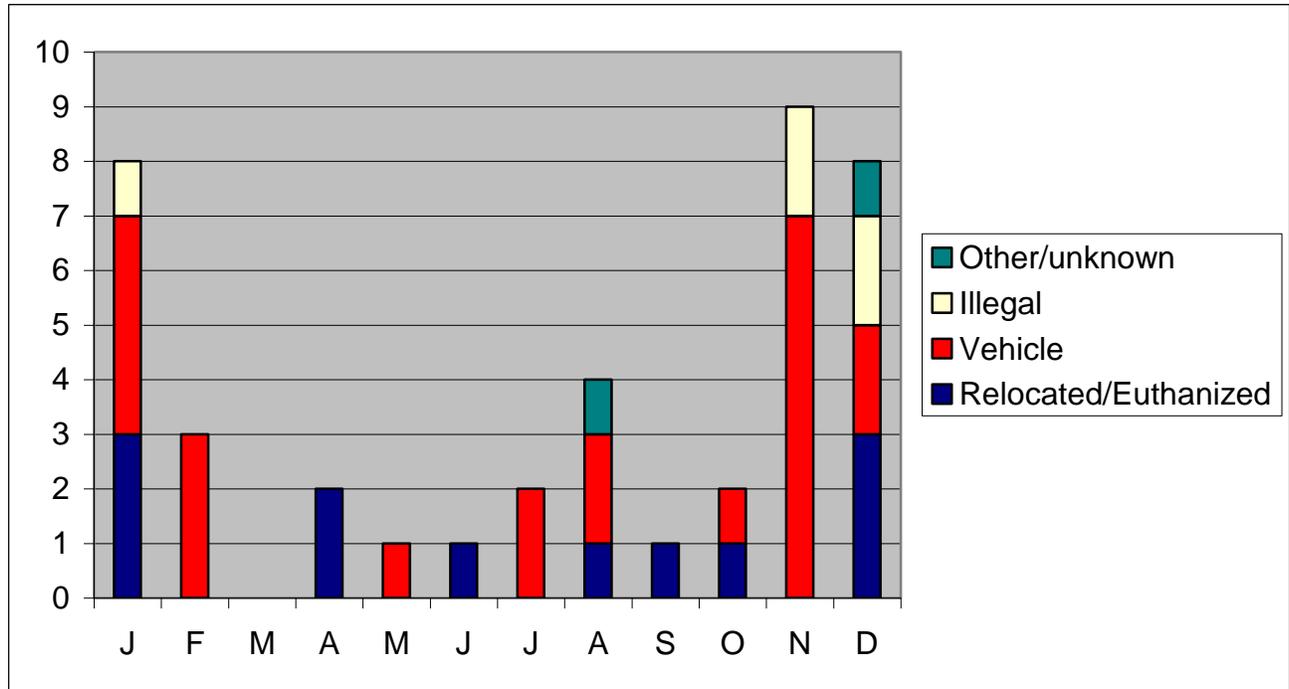


Figure 21: Causes and monthly distribution of losses from the Louisiana black bear population, coastal Louisiana, USA, 2010–2012.

VITA

Jesse Charles Troxler, son of Bill and Joyce Troxler, was born in Knoxville, Tennessee on August 30, 1981. He graduated from Karns High School in 2000 and completed his B.S. in Wildlife and Fisheries Science at the University of Tennessee in 2005. Between semesters, he worked as a technician on a ruffed grouse study in North Carolina and black-tailed prairie dog and wolverine projects in Montana. He also visited Brazil several times with the UT Christian Student Center. In Joao Pessoa he met his future wife Juliana Notaro. Following graduation, he worked on river otters in Missouri, black bears in Arkansas and Louisiana, brown bears in Wyoming, and pygmy rabbits in Idaho. He and Juliana were married in 2009 and lived 2 years in Washington D.C. They returned to Knoxville where Jesse received an M.S. in Wildlife and Fisheries Science with a minor in Statistics in December, 2013.