

**ESTIMATING POPULATION PARAMETERS OF THE LOUISIANA
BLACK BEAR IN THE UPPER ATCHAFALAYA RIVER BASIN**

A Thesis

Presented for the

Master of Science Degree

The University of Tennessee, Knoxville

Carrie Lynne Lowe

May 2011

ACKNOWLEDGMENTS

First and foremost, I would like to thank my advisor, Dr. Joe Clark for giving me the greatest learning opportunity I could ever have. The longer I was a part of bear research with the University of Tennessee, the more I wanted to continue, and I am forever grateful for being entrusted with this project. I am also thankful for the time, guidance, and especially patience of my committee members, Dr. Lisa Muller, Dr. Arnold Saxton, and Dr. Frank T. van Manen.

I have learned never to take financial and logistical support for granted, and many people were involved in making this project happen: Maria Davidson and the Louisiana Department of Wildlife and Fisheries, Deb Fuller and the U.S. Fish and Wildlife Service, Paul Davidson and the Black Bear Conservation Coalition, Chris Clayton and RoyOMartin Lumber Management, the U.S. Geological Survey, and the University of Tennessee.

This study also would not have been possible without the cooperation of many private landowners who graciously offered access to their property. Butch Morsey was integral in helping me get started through his contacts and knowledge of the area (and more than one rescue from the mud). Thanks also to Dave Telesco, Chip Vosburg, and Dr. Bobby Fulmer for their support and interest in the project. To my Louisiana friends: Butch and Sherrie, Coonie and LeeLee, and everyone at the Lottie Wildlife camp, thank you for helping a girl from the North feel welcome. I had a lot of unique experiences in Cajun country, and owe many of them to you. I also thank Mr. John Barton, Sr. for allowing me to stay in his “Lottie Lodge,” and to Donnie Bradley for cheerfully giving me all the Krispy Kremes I could ever need.

I am grateful to my enthusiastic and hard-working technicians Kristy Craig and Kaitlin O’Connell, who endured many hours of sweat, bugs, and mud. To my fellow students in the “Bear Lab” who have come and gone, thank you for the support and friendship. From software

troubleshooting to mechanical advice to Friday lunches, you kept me going. To Jennifer, Jared, and Jennapher (my “other twin”): I don’t know what I’d do without y’all! And of course, thanks to Terry White, who kept us running as a well-oiled machine...as much as that was possible. Finally, thank you to my family, who have always been supportive, even when they had only a vague notion of what I was doing (don’t worry mom, the bear was drugged when I went down into the tree). And last but not least to Mike, without whom I never would have gotten this far.

ABSTRACT

In 1992, the Louisiana black bear (*Ursus americanus luteolus*) was granted threatened status under the Endangered Species Act primarily because of extensive habitat loss and fragmentation. Currently, the Louisiana black bear is restricted to 3 relatively small, disjunct breeding subpopulations located in the Tensas River Basin of northeast Louisiana, the upper Atchafalaya River Basin (ARB) of south-central Louisiana, and coastal Louisiana. The 1995 Recovery Plan mandates research to determine the viability of the remaining subpopulations. I conducted a capture-mark-recapture study during 2007–2009 to estimate population parameters for the ARB bear subpopulation by collecting hair samples ($n = 2,977$) from 115 barbed-wire hair traps during 8 1-week periods each summer. DNA was extracted from those hair samples and microsatellite genotypes were used to identify individuals. I analyzed encounter histories using the Huggins full heterogeneity estimator in a robust design framework in Program MARK. I compared candidate models incorporating heterogeneity, behavior, and time effects on capture using information-theoretic methods. I directly estimated apparent survival, temporary emigration, probability of capture and recapture, and probability of belonging to 1 of 2 mixtures; population abundance was a derived parameter. Apparent survival was 0.91 (SE = 0.06) and did not vary by gender or year. There was some evidence of temporary emigration for males only (0.10, 95% CI = 0.001–0.900). I modeled capture probabilities with a 2-mixture distribution for both male and females. Overall mean weekly capture probability was 0.12 (SE = 0.03) and 0.25 (SE = 0.04) for males and females, respectively. Recapture rates indicated a positive behavioral response to capture. Model-averaged mean annual abundance was 56 (SE = 4.5, 95% CI = 49–68). I calculated population density using spatially-explicit maximum-likelihood methods; model-averaged density was 0.15 bears/km² (SE = 0.03). My results updated previous abundance

estimates for the ARB bear subpopulation and will be used in a population viability analysis to determine if recovery criteria for the Louisiana black bear have been met.

TABLE OF CONTENTS

I. INTRODUCTION	1
Background	1
Justification	2
Objectives	4
II. STUDY AREA.....	4
III. METHODS	7
General Approach	7
Hair Sampling	8
Site Placement.....	8
Field Sampling	9
Genetic Analyses	10
Microsatellite Analysis	10
Subsampling.....	11
Genetic and Analysis Assumptions	12
Parameter Estimation	15
Density Estimation.....	21
IV. RESULTS	23
Hair Sampling	23
Genetic Analyses	24
Parameter Estimation	25
Density Estimation.....	27
V. DISCUSSION	28
VI. MANAGEMENT AND RESEARCH IMPLICATIONS.....	34
LITERATURE CITED	36
APPENDICES	47
APPENDIX A: TABLES.....	48
APPENDIX B: FIGURES	56
VITA.....	60

LIST OF TABLES

Table 1. Number of alleles and heterozygosity of 22 loci evaluated for efficacy to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.....	49
Table 2. Variability of microsatellite markers used to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA 2007–2009.....	50
Table 3. Summary of chi-square tests for Hardy-Weinberg equilibrium for the 7 loci used to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.....	51
Table 4. Robust design models and model selection based on AIC_c to estimate Louisiana black bear population parameters, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009, from DNA mark–recapture.	52
Table 5. Population size (N) and growth (λ) based on capture-mark-recapture analysis of hair sampling for Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.....	53
Table 6. Model selection procedures based on Akaike’s Information Criteria (AIC_c) to estimate Louisiana black bear population density (\hat{D}), Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.	54
Table 7. Reported population densities of black bear populations in the southeastern United States.	55

LIST OF FIGURES

Figure 1. Locations of 3 subpopulations of the Louisiana black bear within Louisiana, USA.	57
Figure 2. Sampling grid (2.6-km ² cell size) and locations of 115 hair-sampling sites used to collect hair from Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.	58
Figure 3. Model-averaged annual abundance estimates for the Louisiana black bear, Upper Atchafalaya River Basin, Louisiana, USA, as estimated by robust design capture-mark-recapture, 2007–2009.	59

I. INTRODUCTION

Background

The Louisiana black bear (*Ursus americanus luteolus*) is one of 16 subspecies of the American black bear (*U. americanus*) presently found in North America (Hall 1981). Historically the Louisiana black bear was common and ranged throughout the bottomland hardwood forests of Louisiana, east Texas and southern Mississippi (Hall 1981). The seasonally flooded forests of the Mississippi River floodplain provided the Louisiana black bear with its requisite escape cover, den sites (tree cavities or dense thickets), and hard and soft mast. Between the 1950s and 1970s, soybean prices were at an all-time high, facilitating extensive flood-control measures and widespread forest clearing for agriculture in the region (King et al. 2006). Forested habitat was reduced by >80% (Neal 1990). Ultimately, the forests that remained were highly fragmented and the ecosystem was converted from a forested wetland system to one dominated by agriculture interspersed with forested wetlands (King et al. 2006). This conversion from forest to agriculture threatened many species, including waterfowl, breeding songbirds, and black bears.

The Louisiana black bear is currently restricted to 3 relatively small, disjunct breeding subpopulations in Louisiana (Figure 1). The Tensas River Basin population (TRB) is in northeast Louisiana, primarily in the Tensas River National Wildlife Refuge, and is generally considered to have the largest population (Boersen 2001, Triant 2001). Remaining populations are found in the upper Atchafalaya River Basin (ARB) in south-central Louisiana and in coastal Louisiana where the Atchafalaya River flows into the Gulf of Mexico (Coastal ARB). In addition, a translocation program was conducted from 2001 to 2009 to encourage establishment of a subpopulation in suitable but unoccupied habitat located between the TRB and ARB.

Justification

Historical declines in abundance of the Louisiana black bear were based primarily on incidental reports. Despite the lack of reliable abundance estimates, the Louisiana Department of Wildlife and Fisheries (LDWF) recognized the general decline of the population and, in an effort to augment bear numbers, conducted a restocking program during the summers of 1964–1967. In the ARB, Pointe Coupee Parish received 130 bears from Cook County, Minnesota and 30 bears were released into the Tensas population (Taylor 1971). Numerous bears dispersing from the release sites were reported in states adjacent to Louisiana or were killed from vehicle collisions or poaching (Taylor 1971). The restocking was considered a failure. There was initial disagreement about whether the genetics of the Louisiana black bear were compromised by the introduction of the Minnesota bears (reviewed in Pelton [1991]). With improvements in DNA technology, however, later studies established evidence that the restocking had affected the ARB population's genetic structure. Csiki et al. (2003) found ARB bears and those of Minnesota were similar in overall genetic diversity and allele frequencies, consistent with the ARB population being mostly descended from bears from the reintroduction. Similarly, Miller et al. (1998) and Triant et al. (2004) demonstrated higher genetic variation within the ARB bear population than within the other Louisiana populations, indicating that the restocking had contributed to higher genetic diversity.

In 1992 the Louisiana black bear was listed as threatened under the U.S. Endangered Species Act (ESA) because of extensive habitat loss and fragmentation (Neal 1992). In response to the listing, the U.S. Fish and Wildlife Service (USFWS) developed the Louisiana Black Bear Recovery Plan (1995). This plan included criteria that must be met for delisting:

- (1) the existence of at least 2 viable subpopulations, one each in the Tensas and Atchafalaya River Basins,
- (2) establishment of immigration and emigration corridors between the 2 subpopulations, and
- (3) protection of habitat and travel corridors that support the 2 viable subpopulations being used as justification for delisting.

Past research on the ARB population has focused on topics related to criterion (2) and (3), and included studies of den characteristics, habitat requirements, feeding ecology, landscape movement, and taxonomy of the Louisiana black bear. Wagner (1995) used radio telemetry and activity-switch data to determine how sex and physiological state (i.e., season) affected movement extent and pattern of bears in the ARB. Pace et al. (2000) determined sources and patterns of mortality, and Hightower et al. (2002) examined the denning habitat, denning frequency, and reproductive rates of female bears in the ARB. Triant (2001) conducted the first systematic hair-sampling survey to estimate abundance and genetic diversity of the ARB population based on genetic sampling and capture-mark-recapture techniques. She sampled 142 km² of habitat using a single 15-day marking followed by a single 15-day recapture period during summer 1999, and used closed population models to derive an estimate of 41 bears (Triant et al. 2004).

The Recovery Plan specifies that population indices be evaluated and reported every 5 years and that 2 populations be viable, defined as having a $\geq 95\%$ probability of persisting over 100 years (USFWS 1995). A population viability analysis (PVA) is used to determine the probability of a population persisting over a specified amount of time (Mills 2007) for which

estimates of abundance, survival, recruitment, emigration and immigration rates, and other parameters are essential.

Objectives

My objectives were to estimate abundance (N), density (D), population growth rate (λ), and apparent survival rate (ϕ) of Louisiana black bears in the ARB subpopulation using capture-mark-recapture techniques based on genotyped hair samples. Capture-mark-recapture studies for the other 2 subpopulations are currently underway using techniques similar to my study. The eventual goal is to perform a population viability analysis for each of the Louisiana black bear subpopulations and for the metapopulation in its entirety.

II. STUDY AREA

The ARB study area was located in Pointe Coupee Parish in south-central Louisiana and consisted of approximately 270 km² of bottomland hardwood forest (Figure 1). The study area comprised approximately 20% of the total area of Pointe Coupee Parish, which included 4 incorporated towns and cities, and >40 unincorporated small communities. The study area was bordered by State Highway 1 to the east and north, U.S. Highway 190 to the south, and the Atchafalaya River to the west. Although they served as logistical boundaries for my study, U.S. Highway 190 had elevated portions that allowed movement into adjacent areas and bears were known to swim across the Atchafalaya River.

Approximately 150 km² of the forested habitat were located within the Morganza Floodway, a 6.4-km wide diversion channel designated to carry overflow waters from the Mississippi River into the Atchafalaya Basin. The Morganza Floodway was bordered by protection levees, and primarily contained bottomland hardwoods and swamps with some

clearing for agriculture. Another 97-km² tract of mostly contiguous forest was located east of State Highway 77 towards the city of New Roads. Several smaller woodlots north of the Morganza Floodway were also included in my study area, each <5 km from the next nearest tract. Timber stands were surrounded by and interspersed among an extensive network of agriculture, pastureland, and hayfields. Primary crops included sugarcane, soybeans, and cotton. Thus, the study area was divided into several fragmented sections but together included all important bear habitat in Pointe Coupee Parish.

Bear habitat primarily consisted of privately owned bottomland hardwood stands. Forestry was a major industry throughout the study area and logging practices were extensive. RoyOMartin Lumber Management, the largest landowner, generally used a continuum cut, removing all old or undesirable trees and retaining preferred young trees throughout the stands (C. Clayton, RoyOMartin, personal communication). Thus, the majority of forest stands were managed in an uneven age structure, although there were some areas in early successional stages due to occasional even-aged management. Most of the land was leased for sport hunting so all-terrain vehicle trails, limestone roads, and hunting camps occurred throughout the study area. Several major oil and natural gas pipelines traversed the ARB and oil wells and their access roads were common. There were many lakes, bayous, canals, and sloughs scattered throughout the study area. Although seasonal flooding occurred, large areas of slightly higher elevation generally remained dry throughout winter. Water levels in flooded areas were <0.5 m.

Climate in the ARB was humid subtropical, characterized by high humidity and mild winters. During 2007–2009, the average annual temperature recorded in the parish seat of New Roads (lat. 30°44'N, long. 91°22'W) was 19°C, with a high of 40°C and a low of -5°C (National Climatic Data Center [NCDC] 2010). There was an annual mean of 95 days with

temperatures $\geq 32^{\circ}\text{C}$, occurring from May through October. Annual rainfall averaged 147 cm, with a mean monthly rainfall of 7.95 cm (NCDC 2010). In addition, Pointe Coupee Parish is susceptible to hurricanes, and was one of the areas hardest-hit by Hurricane Gustav in September 2008. Gustav passed through my study area as a Category 1 storm, causing hurricane-force wind gusts and heavy damage to structures. Approximately 30 cm of rain fell that month (NCDC 2010) and the storm damaged large trees, opening the canopy and influencing the vegetation in several areas included in my study.

The study area was flat with a slope of 0–1% (Natural Resources Conservation Service [NRCS] 2009). The average elevation was 13.7 m above sea level (NCDC 2010). There were 25 soil types found in Pointe Coupee; >60% of the parish, and nearly all of my study area, was of the somewhat-poorly drained Commerce soil class, composed of silty alluvium parent materials, and the poorly-drained Sharkey class, composed of clayey alluvium parent materials (NRCS 2009).

Because of the alternating wet and dry periods and the organic matter and nutrients deposited by flooding, bottomland hardwood forests are extremely productive. Overstory species consisted primarily of water oak (*Quercus nigra*), willow oak (*Q. phellos*), Nuttall oak (*Q. nuttallii*), overcup oak (*Q. lyrata*), bitter pecan (*Carya lecontei*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), hackberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), hickory (*Carya* spp.), willow (*Salix* spp.), elm (*Ulmus* spp.), cottonwood (*Populus deltoides*), persimmon (*Diospyros virginiana*), American sycamore (*Platanus occidentalis*), water tupelo (*Nyssa aquatica*), and baldcypress (*Taxodium distichum*). Common understory species included palmetto (*Sabal minor*), giant cane (*Arundinaria gigantea*), switch cane (*A. tecta*), greenbriar (*Smilax* spp.), dogwood (*Cornus* spp.), box elder (*Acer negundo*),

fern, and poison ivy (*Toxicodendron radicans*). In areas with an open canopy, soft mast species were dense and included rattan (*Berchemia scandens*), blackberry (*Rubus* spp.), pokeberry (*Phytolacca americana*), and beautyberry (*Callicarpa americana*). Although low light intensity and prolonged inundation made groundcover sparse in areas, cover was dense where timber management practices had maintained a more open canopy and along road and trail edges.

The bottomland hardwood forests of the region provided productive habitat for a variety of wildlife species. Game species were common and included eastern wild turkey (*Melaeagris gallopavo*), white-tailed deer (*Odocoileus virginianus*), eastern cottontail (*Sylvilagus floridanus*), and squirrel (*Sciurus* spp.). Other common mammal species included coyote (*Canis latrans*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), opossum (*Didelphis virginiana*), and black bear. Feral hog (*Sus scrofa*) and the invasive nutria (*Myocaster coypus*) were frequently observed within the study area. Other characteristic species included the American alligator (*Alligator mississippiensis*) and a variety of other herpetofauna, crayfish (*Procambarus* spp.), waterfowl, wading birds, and migratory songbirds.

III. METHODS

General Approach

Livetrapping of bears often results in low capture rates that can lead to capture-mark-recapture population estimates with low precision and poor accuracy (Boulanger et al. 2002). Capture-mark-recapture for bears can also be accomplished by collecting and genotyping genetic material such as hair. Recaptures are identified by comparing genotypes of previously captured animals. Numerous researchers have used noninvasive hair collection methods to survey black bears (Woods et al. 1999, Boersen et al. 2003, Triant et al. 2004, Settlage et al. 2008, Tredick

and Vaughan 2009) and brown bears (*Ursus arctos*; Woods et al. 1999, Paetkau 2003, Boulanger et al. 2008a, Kendall et al. 2009). DNA-based survey methods (e.g., from hair, feces, feathers) have greatly advanced over the last decade and benefits include greater trapping efficiency, increased capture probabilities, decreased intrusiveness, less bias, and no loss of marks (Woods et al. 1999). Therefore, I chose to collect and genotype DNA from bear hair samples to estimate black bear population parameters based on capture-mark-recapture techniques.

Hair Sampling

Site Placement.—Movement differences among individuals result in variation in the probabilities that their hair will be sampled. One way to reduce this variation in capture-mark-recapture studies is to ensure that each animal has adequate access to traps. For each individual to have a chance of being captured, ≥ 1 trap should be located within each home range (Williams et al. 2002). Otis et al. (1978) recommended that studies be designed so animals have ≥ 4 traps available in their home range. Because female black bears typically have smaller home ranges than males (Garshelis and Pelton 1981, Smith and Pelton 1990, Schwartz and Franzmann 1992, Wooding and Hardisky 1994), I assumed that spacing traps relative to a female's home-range size allowed all individuals some probability of detection. I created a 1.6- \times 1.6-km grid using ArcView[®] GIS software (ESRI, Redlands, CA) with a goal of placing a hair-sampling site in each grid cell. Rather than placing sites in the center of each grid square, I placed them to facilitate access by roads and trails, while avoiding areas with high water levels or where landowner permission could not be obtained. By placing a hair-sampling site within each of these grid squares, I created a trapping grid whereby a mean of 6.8 hair sites were available to each female bear, based on the estimated average female spring-summer home range of 15.7 km²

in the ARB (Wagner 1995). Overall, I established 115 sites throughout forested habitats, averaging 1 hair site per 2.3 km² (Figure 2).

I maintained initial site locations through the length of the study unless the site experienced damage by logging equipment, downed trees, or flooding. I relocated 12 sites during the study. I moved 10 of these <250 m from the initial snare location, relocated one site 1.06 km from its original location to improve site distribution, and relocated another site 370 m because of logging activity.

Field Sampling.— I constructed hair-sampling stations by stretching a single strand of 4-point, 15.5-gauge barbed wire around the outside of 3 or 4 corner trees at 40–50 cm above the ground (Woods et al. 1999). If necessary to achieve this height, I filled in areas of uneven terrain with debris or blocked them off with branches. I pulled the wire tight between the corner trees using a crowbar and attached the wire with fencing staples. Bait was hung in the center of the enclosure, approximately 150 cm high, from twine stretched diagonally between corner trees. The resulting enclosure measured approximately 25 m² and was large enough to prevent a bear from reaching the bait without crossing over or under the barbed wire. Baits consisted of 2 donuts (approximately 100 grams) wrapped in small biodegradable bags (BioBag[®], BIOgroupUSA Inc., Palm Harbor, Florida). I hung a tampon soaked with artificial raspberry, honey, bacon, or anise concentrate (Mother Murphy's Laboratories, Greensboro, North Carolina) as an additional scent lure. For human safety, I attached flagging to the wire and caution tape to the corner trees. In addition, I placed a sign at each site explaining its purpose and providing my contact information.

To maintain equal trapping effort, I consistently checked all sites at a 7-day interval for 10 weeks. During each visit, I examined the site for evidence of bear visitation. Using tweezers,

I collected samples from each barb that contained ≥ 5 hairs and placed the samples in separate coin envelopes. I used this minimum standard in most cases to ensure collection of samples that were likely to produce a useful genotype in the lab (Paetkau 2003, Tredick et al. 2007). I labeled each envelope with the site ID, sample number, and date, and sealed them with tape. I used a cigarette lighter to sterilize the tweezers after collecting each sample. After hair collection was complete, I burned the entire wire with a small propane torch to prevent mixing of remaining hairs with future samples. I re-baited and re-scented sites during each visit. After returning from the field, I stored all coin envelopes at room temperature in zipper storage bags containing a small amount of color-indicating desiccant (W.A. Hammond Drierite Co. Ltd., Xenia, Ohio) to prevent degradation of DNA from moisture.

Genetic Analyses

Microsatellite Analysis.— I used microsatellite analysis to identify individual bears in the ARB from my collected hair samples. Microsatellites are a group of molecular markers that are highly variable and easy to isolate for many species (McKelvey and Schwartz 2004). A small number of microsatellite markers with high heterozygosity can provide sufficient power to identify individuals from a population, making them useful for capture-mark-recapture studies (McKelvey and Schwartz 2004). By using the polymerase chain reaction (PCR), a few copies of the small amount of DNA available in hair roots can be amplified into the many copies required for genetic analysis (Paetkau et al. 1995, Taberlet et al. 1996, Mills et al. 2000). This technique has become frequently used in population estimation and other genetic studies of bears (Csiki et al. 2003, Thompson et al. 2005, Clark and Eastridge 2006, Settlage et al. 2008, Kendall et al. 2009, Tredick and Vaughan 2009).

Microsatellite analysis for my study was conducted by Wildlife Genetics International (WGI, Nelson, British Columbia, Canada) using standard protocols (Woods et al. 1999, Paetkau 2003). An initial group of 30 randomly selected samples from 2007, assumed representative of the ARB population, was analyzed at 22 loci (A06, CPH9, CXX110, CXX20, G10B, G10H, , G10U, G10X, MSUT2, MU50, MU51, PO7, G1A, G1D, G10J, G10C, G10L, G10M, G10P, MU23, MU26, and MU59). Because of a low success rate and small number of individuals assigned with these samples, 30 additional samples were genotyped from the 2008 collection. Using 22-locus data from 24 individuals, a suite of 10 markers with the greatest allelic variability was selected for genotyping 2007–2008 samples (G1A, G1D, G10J, G10C, G10L, G10M, G10P, MU23, MU26, and MU59). That set was further reduced to the 7 most variable markers for the 2009 samples (G10C, G10L, G10M, G10P, MU23, MU26, and MU59). Additionally, the amelogenin marker was used on all samples to determine gender (Ennis and Gallagher 1994).

Subsampling.– Not all hair samples were genotyped. Analyzing all samples would likely result in multiple samples and redundant genotypes from the same individual within a single sampling period, because bears often leave multiple samples at a site and can visit multiple sites (Tredick et al. 2007). The additional number of unique individuals I would identify from a complete sample analysis would likely be minimal and would be an inefficient use of resources. Thus, I subsampled by randomly selecting 25 sites from all sites that produced a hair sample within a weekly sampling period. Then I randomly selected and analyzed 1 suitable sample from each of these 25 sites. Using the Lincoln-Peterson estimator, this was the number of samples needed to attain a coefficient of variation of $\leq 20\%$, based on an expected population size of 50–150 bears. To maximize extraction success, the minimum quality required for a suitable sample was 5 underfur or 1 guard hair (D. Paetkau, WGI, personal communication). If the sample did

not contain sufficient hairs with roots, WGI personnel randomly selected another sample from that site and sampling occasion. If no additional samples were available, WGI personnel randomly chose a sample from another site. I did not analyze any of the samples collected in the last 2 secondary periods of any year. These were initially collected to supplement the processed samples if it was determined that the first 8 secondary periods did not produce adequate capture probabilities.

Genetic and Analysis Assumptions.— An important assumption of capture-mark-recapture is that recaptured individuals are correctly identified. Error may occur when separate samples for the same individual are assigned different genotypes, causing too many individuals to be identified (Taberlet et al. 1996, Woods et al. 1999, Mills et al. 2000). Conversely, if markers are not variable enough to produce unique genotypes for each sampled individual, too few individuals may be identified (Woods et al. 1999, Mills et al. 2000, Waits et al. 2001). By selecting highly variable markers that achieve a low probability of identity, and reanalyzing pairs of samples with similar genotypes, these errors can be minimized (Woods et al. 1999). Additionally, misidentification can be reduced to an inconsequential level by maintaining rigorous standards for culling marginal samples and samples that perform poorly and by following error-checking protocols (Paetkau 2003). To minimize genotyping error and ensure accurate individual identifications, WGI discarded samples that failed at >3 markers on the first pass of standard PCR and electrophoresis methods. Samples with 1–3 misidentified pairs were reanalyzed and any samples that were still missing data (i.e., did not have complete genotypes for all markers) were discarded. The final step in error-checking was to reanalyze pairs of samples with genotypes that matched at all but 1 or 2 markers to determine if differences at those loci truly existed (D. Paetkau, personal communication, Paetkau 2003).

Although individuals cannot lose their DNA, correctly identifying individuals by their unique genotype (i.e., ‘mark’) is critical for abundance estimation. Because of the relative isolation of the ARB population, I expected that samples could be from related individuals and that multiple animals could share the same genotype at the loci being examined (Woods et al. 1999). This would result in a ‘shadow effect,’ whereby a sample may be recorded as a recapture of a single individual although it is from a different individual (Mills et al. 2000). The shadow effect inflates p , causing a negative bias in N (Mills et al. 2000). Statistical power for individual identification from molecular markers can be determined using the probability of identity statistic (PI, Mills et al. 2000). Probability of identity represents the probability that 2 individuals selected randomly from a population will have the same genotype at multiple loci (Paetkau and Strobeck 1998). The PI estimator is also commonly used to quantify levels of genetic diversity in natural populations (Paetkau and Strobeck 1994). Probability of identity can be calculated for each locus as:

$$PI_{\text{single locus}} = \sum_i x_i^4 + \sum_i \sum_{j>i} (2x_i x_j)^2,$$

where x_i and x_j are the frequencies of the i^{th} and j^{th} alleles (Paetkau and Strobeck 1994).

Probability of identity usually is multiplied across loci to give the overall PI (Taberlet and Luikart 1999). Within small or isolated populations such as the ARB, the probability of collecting hair samples from closely-related individuals is not random. This is particularly true for females and their offspring whose home ranges may overlap. The PI between siblings (PI_{sibs}) statistic is the probability that an individual and its sibling have the same genotype. This represents the upper limit of the statistical probability of observing identical genotypes based on the sampled loci (Waits et al. 2001). When x_i is the frequency of the i^{th} allele, PI_{sibs} is calculated as:

$$PI_{\text{sibs}} = 0.25 + (0.5 \sum x_i^2) + [0.5(\sum x_i^2)^2] - (0.25 \sum x_i^4).$$

Determining whether the PI is sufficiently low depends on the abundance of siblings in the population. For capture-mark-recapture studies, differentiating individuals with a probability of identity of ≤ 0.01 is sufficient (Taberlet and Luikart 1999). I calculated the PI statistics using Program GenALEx 6.1 (Peakall and Smouse 2006).

PI calculations are based on the assumptions that genetic samples are in Hardy-Weinberg equilibrium and the loci chosen for analysis are independent (Taberlet and Luikart 1999). If these assumptions are not met, biological factors (e.g., genetic drift) or sampling biases may be involved and calculations will be incorrect. In a large random mating population with no selection, mutation, or migration, allele and genotype frequencies reach equilibrium and will remain constant over time (Connor and Hartl 2004). These frequencies are in Hardy-Weinberg equilibrium if:

$$A^2 + 2Aa + a^2 = 1,$$

where A is the frequency of the dominant allele and a is the frequency of the recessive allele. The equation predicts the expected number of genotypes in the population (Lowe et al. 2004). I used the chi-square tests in GenALEx 6.1 (Peakall and Smouse 2006) to determine if frequencies of sampled genotypes deviated from Hardy-Weinberg equilibrium.

Because of large home ranges, low population densities, and long generation times, large carnivores may be susceptible to loss in genetic variation due to habitat fragmentation (Paetkau and Strobeck 1994). Genetic variation (heterozygosity) is calculated from allele frequencies at specific loci to indicate relatedness of individuals in a population. Low heterozygosity may indicate processes such as genetic drift or inbreeding. Gene flow from one population to another

results in maintenance or an increase in heterozygosity. I used the allele frequencies obtained from the microsatellite analyses to determine mean heterozygosity in the ARB.

Parameter Estimation

Because black bears have large home ranges, are secretive, often live in densely vegetated habitats, and occur in low densities, it is rare for all individuals to be detected in surveys. Consequently, estimating population size can be challenging and the results unreliable. Capture-mark-recapture methods were developed to account for this imperfect detection. By capturing and recapturing individuals in the population, the proportion of marked to unmarked animals in subsequent samples can be used to estimate capture probability (p). Assuming (1) the population is demographically and geographically closed (i.e., births, deaths, immigration, and emigration do not occur during the sampling period), (2) animals do not lose their marks during the study, and (3) all marks are noted and recorded correctly at each sampling occasion, the population size (N) equals the number of unique individuals captured (M) divided by (p):

$$N = \frac{M}{p}.$$

The above estimator is unbiased if every individual in the population has the same probability of capture. However, individual animals will have different probabilities of being detected in many instances. Some animals may avoid sampling sites, encounter fewer sites because of their home-range size, or visit a site without leaving hair, resulting in a capture probability that is almost always <1 (Williams et al. 2002). Therefore, the ability to reliably estimate abundance revolves around the ability to reliably estimate p . Otis et al. (1978) developed a series of closed population (i.e., no births, deaths, immigration, or emigration) estimators to adjust for 3 major sources of variation in the capture probability of an individual. The first source of capture variation is related to the time of sampling. For example, p can be

higher or lower at the beginning of the sampling period or it can vary over time according to some environmental variable (e.g., rainfall). Capture probability can also vary depending on previous captures. The effect of such a behavioral response can be positive (i.e., trap happy) or negative (i.e., trap shy). Finally, capture probability can vary by individual characteristics (e.g., sex, age, reproductive status, home-range location in relation to sampling grid) resulting in capture heterogeneity. Capture probabilities can also vary according to combinations of these factors.

Although estimators for closed populations are useful to account for factors that affect p , closure assumptions can be difficult to meet when studying wildlife populations (Otis et al. 1978). Open population capture-mark-recapture models make fewer assumptions, allowing additions and losses to occur during the study, and many vital rates (e.g., apparent survival and recruitment) can be estimated. However, open models are unable to incorporate individual heterogeneity or behavioral responses, often resulting in biased estimates and low precision.

The robust design introduced by Pollock (1982) combines open and closed capture-mark-recapture models to estimate abundance and other parameters. Robust design consists of 2 levels of sampling, referred to as primary and secondary sampling periods. Primary sampling occurs between periods when the population is assumed to be open. Sampling must occur during ≥ 3 of these periods, and the Cormack-Jolly-Seber (CJS) estimator is used to estimate apparent survival (ϕ), temporary emigration (γ), and population growth (λ) between the primary periods. Within each primary sampling period, several secondary sampling periods occur that are close together in time such that gains and losses to the population can be considered insignificant, and N can be estimated using closed capture models. The benefit of the robust design is that behavioral, temporal, and heterogeneity effects on capture probabilities can be estimated within secondary

sampling periods and incorporated into estimates of N , yet open population parameters (i.e., ϕ , γ , λ) can be simultaneously estimated, thus allowing for more realistic assumptions about catchability and population closure. Therefore, I used robust design methods by sampling across 3 primary sampling periods (2007, 2008, and 2009), each consisting of 8 weekly sampling periods in the summer, when reproduction was not occurring and mortality rates were low.

Capture heterogeneity is the most difficult of the capture biases to estimate (Boulanger et al. 2002, Link 2003). To better account for this bias, Huggins (1989, 1991) developed estimators of N based on initial capture probabilities but conditioned on an animal being captured at least one time during the study. Because the likelihood is conditioned only on the captured individuals, N drops out of the likelihood, the models contain only p , and N is a derived estimate. The probabilities of all observed capture histories are divided by the probability of capturing an animal at least once. Abundance is then estimated as:

$$\hat{N} = \sum_{i=1}^{M+1} \frac{1}{p_i},$$

where p_i is the capture probability for animal i , and M is the total number of captured individuals. This method removes undetected animals from the analysis, allowing individual covariates to be used to model heterogeneity in p . For example, capture probabilities can be a concern with animals whose home ranges lie largely outside the sampling grid. For grizzly bears, the distance of an animal's mean location of capture to the edge of the sampling grid has been used as an individual covariate (Boulanger and McLellan 2001, Boulanger et al. 2004). By modeling p as a function of distance from edge, the bias caused by closure violation could be estimated and the population estimates more reliable than standard closed models (Boulanger et al. 2004).

I used the results from the DNA analysis to compile encounter histories for each identified individual. Using the robust design data type in Program MARK (White and Burnham

1999), I applied the Huggins full heterogeneity model (Huggins 1989, 1991) to analyze my data. The Huggins model enables the user to model p based on a variety of individual covariates. In addition to allowing individual covariates, mixtures can be used to model unidentified sources of heterogeneity (Pledger 2000), whereby animals can be separated into groups (i.e., mixtures) with relatively homogenous capture probabilities based on a specified number of different p distributions. I used a 2-mixture model, whereby the mean capture probabilities of the first mixture (p_A) and the second mixture (p_B) were estimated, and the proportion of the population comprised of each (π and $1 - \pi$). I also developed 2-mixture models for each sex. I reported mean capture probabilities based on the 2-mixture distributions (Carothers 1973, Boulanger et al. 2008b), as $\bar{p} = \pi_1 p_1 + (1 - \pi_1) p_2$. I used the delta method to estimate variance of \bar{p} (Seber 1982, Boulanger et al. 2008b) as:

$$\begin{aligned} \text{var}(\bar{p}) &= 2 \text{cov}(\pi, p_1)(p_1 - p_2) \\ &+ 2 \text{cov}(\pi, p_2)(1 - \pi)(p_1 - p_2) \\ &+ 2 \text{cov}(p_1, p_2)\pi(1 - \pi) + \text{var}(\pi)(p_1 - p_2)^2 \\ &+ \text{var}(p_1)\pi^2 + \text{var}(p_2)(\pi - 1)^2. \end{aligned}$$

I built a number of a priori models based on bear biology and characteristics of the study area during sampling. I varied model structure to represent effects of factors such as gender and time. Parameters that were directly estimated included weekly probabilities of capture (p) and recapture (c); apparent survival rate (ϕ); probability of temporary emigration, given the animal was present during the previous primary period (γ''); and probability of remaining outside the study area, given the animal was not present during the previous primary period (γ' , Kendall et al. 1997). Annual population size (N) was a derived parameter. Annual estimates of N were used to calculate estimates of population growth (λ). I calculated growth as $\lambda = N_{t+1}/N_t$, where N_t

is the abundance estimate for primary period t and N_{t+1} is the abundance estimate for the subsequent primary period.

I expected a positive behavioral response to capture because bait was being used at the sampling sites. To test for a behavioral response within and across years, I compared models whereby capture probability did not differ from recapture probability (i.e., no behavioral response; $p = c$) to models whereby p and c were allowed to differ by a constant over the sampling period, representing a behavioral response (i.e., an additive effect; $p + c$). Additionally, I used an individual covariate for p (*CapFreq*) based on the number of secondary periods in which the animal was captured in the previous primary period (Fletcher 1994). This was to account for additional heterogeneity associated with animals that have the tendency to be captured more or less frequently than others. Animals not captured the previous year could be the result of their not having been present on my study area (i.e., temporarily emigrated) or they could have been present but simply not captured. Therefore, for models in which temporary emigration did not occur ($\gamma = 0$), I coded non-captures in the previous year as zeros. For models that included temporary emigration, I coded animals not captured the previous year as not present and used the mean number of captures for all the individuals that were detected to calculate *CapFreq* (Williams et al. 2002). Finally, I considered models whereby temporary emigration was random (i.e., the probability of emigrating during the sampling session was the same as the probability of staying away; $\gamma'' = \gamma'$), was random but differed by gender $\gamma''(g) = \gamma'(g)$, and did not occur ($\gamma'' = \gamma' = 0$). For the survival parameter (ϕ), I compared models whereby ϕ was constant with models allowing it to vary by year and gender.

I used Akaike's Information Criterion (AIC, Burnham and Anderson 2002) adjusted for small sample size bias (AIC_c, Hurvich and Tsai 1989) to compare models. I considered models

with lower AIC_c values to be better supported by the data and more parsimonious (Burnham and Anderson 2002). I compared differences in AIC_c values (ΔAIC_c) to evaluate the relative importance of models (Burnham and Anderson 2002). When 2 models had a $\Delta AIC_c < 2$, I considered both models to have equal support. I also used model weights (w_i) to compare the support of a given model containing an effect to an equivalent model without that effect (w_j) by calculating evidence ratios ($E_{i,j}$) as $E_{i,j} = w_i / w_j$. I examined the regression coefficient β (i.e., slope) and its 95% confidence interval to assess significance of effects. When the confidence interval included zero, it failed to support the importance of the effect. I accounted for the uncertainty associated with model selection by model averaging, which calculates an average value for each parameter based on AIC_c weights across the entire set of candidate models (Burnham and Anderson 2002). In this way, models with different structures can be considered at the same time, but those with greater AIC_c weights will have greater influence on the overall estimate. If a model included a parameter that was inestimable, I excluded that model from that parameter's averaging procedure. I reported unconditional variance for the parameter estimates, which includes sampling variance and variation due to model selection uncertainty.

I derived estimates of population abundance and calculated a log-based 95% confidence interval that accounts for the minimum number of bears captured (M_{t+1} , White et al. 2001) as:

$$M_{t+1} + (\hat{f}_0 / C), M_{t+1} + (\hat{f}_0 \times C),$$

$$\text{where } \hat{f}_0 = \hat{N} - M_{t+1} \text{ and } \left[C = \exp \left\{ 1.96 \left[\ln \left(1 + \frac{\widehat{\text{var}}(\hat{N})}{\hat{f}_0^2} \right) \right]^{1/2} \right\} \right].$$

Because I pooled male and female estimates to calculate annual abundance, I used the delta method to incorporate their covariances into the variance estimate (Seber 1982, Powell 2007). I

also used the delta method to calculate variance when averaging parameter estimates across years (i.e., λ and p ; Williams et al. 2002, Powell 2007).

I used the RELEASE subroutine in Program MARK (Burnham et al. 1987) to evaluate the goodness-of-fit of my capture history data to the Cormack-Jolly-Seber (CJS) model. Additionally, if assumptions of the CJS model (i.e., each marked animal has the same survival probability and captures are independent) are violated, it is necessary to adjust for overdispersion. Overdispersion is measured by the variance inflation factor (\hat{c} ; White et al. 2001); $\hat{c} > 1$ indicates the data are overdispersed, which causes the variance of the parameter estimates to be underestimated. From the CJS model output, I estimated \hat{c} from the goodness-of-fit chi-square statistic (χ^2) divided by its degrees of freedom (df).

Density Estimation

Population density is typically estimated by dividing the capture-recapture abundance estimate by the effective area sampled ($D = N/A$, where D is density, N is abundance, and A is area; Dice 1938). However, estimating the effective sampling area can be problematic when an individual's home range is not contained within the boundaries of the grid. Because of the edge effect that occurs under such circumstances, N actually applies to a larger area of unknown size (Williams et al. 2002). Temporary movements of individuals in and out of the study area during a sampling period result in capture probabilities that are biased low, an N that is biased high, and thus an overestimation of D (Karanth and Nichols 1998, Boulanger and McLellan 2001).

To address this bias, I estimated density using the spatially explicit capture-recapture (SECR) method developed by Borchers and Efford (2008). This method incorporates the locations of hair-sampling sites and the capture histories of each individual into a maximum likelihood-based model. The model consists of 2 submodels: one for the capture process (g_0),

which relates the probability of capturing an individual at a particular hair-sampling site given the distance of the site from the animal's home range center, and another for the distribution of animal home ranges in the sampling grid (σ ; Efford et al. 2004, Borchers and Efford 2008).

Behavioral, temporal, and individual heterogeneity effects on the detection probability can be included, and can be modeled to affect g_0 , σ , or both. Trap-site covariates, 2- or 3-class finite mixtures, and differences in density among areas or time may also be modeled.

I used Program DENSITY (version 4.4, <http://www.otago.ac.nz/density/>, accessed 25 January 2011) to build models as similar as possible to my top models in the robust design analysis. I included a behavioral response for g_0 in all models. I modeled individual heterogeneity in the g_0 parameter using sex as a covariate. To more closely match my robust design models I also attempted to analyze all sessions (i.e., years) together rather than separately, to model a 2-class mixture allowing g_0 to vary by a sex covariate. I modeled detection as a hazard and half-normal function (Efford et al. 2008). I modeled the number of captured individuals as a Poisson distribution, which assumes that animals are distributed randomly across the landscape and may extend beyond the edge of the sampling grid, and as a binomial distribution, which assumes a discrete, 'island' landscape (Borchers and Efford 2008). Because SECR is based on maximum likelihood, I again used AIC_c for model comparison. I calculated model-averaged density estimates and unconditional variance. I applied a habitat mask because my study area contained a considerable amount of non-habitat that would bias density estimates. I used the National Land Cover Database (U. S. Geological Survey 2001) to delineate bear habitat in Pointe Coupee Parish. The land-cover categories only included woody wetlands, cultivated crops, and pasture-hay which I reclassified as habitat (woody wetlands) and non-habitat (cultivated crops and pasture-hay). I calculated the buffer width, or extent beyond

my sampling grid to be used in the estimation of g_0 and σ , using the root pooled spatial variance (RPSV) $\times 4$ (Efford et al. 2004). This resulted in a buffer width of approximately 11.5 km. I used a mesh of $64X = 64Y$ grid points over my sampling area for the analysis.

Because many reported densities for bear populations in the southeastern U.S. have not been calculated using SECR, I also calculated density using the traditional method of density estimation ($D = N/A$) to allow comparison. I used the habitat mask previously described to exclude non-habitat. I estimated the effective sampling area by extending the sampling grid boundary by 2,236 m, which was the radius of mean spring-summer home ranges of females in the ARB (Dice 1938, Wagner 2005). To estimate population density, I divided my model-averaged abundance estimate by the effective sampling area, exclusive of non-habitat.

IV. RESULTS

Hair Sampling

I began field sampling in July 2007 and concluded in August 2009. Because of additional time required to set up the initial hair-sampling sites, sampling began approximately 4 weeks later in 2007 than in 2008 and 2009, each of the latter beginning the first week of June and ending the second week of August. I baited and checked 115 hair-sampling sites on 7-day intervals for 10 weeks during each summer. In 2007, I collected 432 hair samples from 69 different traps (60% of trap sites), with a mean of 24 traps per week producing samples. In 2008, I collected 981 samples from 102 traps (89%), with a mean of 45 traps per week producing samples. In 2009, I collected 1,564 samples from 113 traps (98%), with a mean of 63 traps per week producing samples. The total number of hair samples collected over all 3 primary periods was 2,977. Every site produced ≥ 1 sample over the course of my study.

Genetic Analyses

For the 2007 hair-sampling season, 167 of the 432 samples (39%) were chosen for microsatellite analysis of which complete multilocus genotypes were obtained for 102 (61% success). Due to a lack of suitable samples, my goal of 25 samples extracted per period was not achieved for periods 1 through 5. For 2008, 182 of the 981 collected samples (19%) were chosen for analysis, of which complete genotypes were obtained for 153 (84% success). For 2009, 201 of the 1,564 collected samples (13%) were chosen for analysis, of which complete genotypes were obtained for 170 (85% success). The lower success rate in 2007 was attributed to lower quality samples, with a mean number of usable guard hairs per extraction of only 2.75, in comparison to 6.0 and 5.8 guard hairs in 2008 and 2009, respectively. The majority of the samples in 2008 and 2009 were extracted from ≥ 3 guard hairs. Of the 425 samples that were assigned individual identities, 411 (97%) produced multilocus genotypes that were fully replicated in ≥ 1 other sample; this high rate would only be expected if samples that were from the same individual had been correctly genotyped (D. Paetkau, WGI, personal communication; Paetkau 2003).

I identified 32 unique individuals in 2007 and 36 in 2008; 21 bears were captured in both years. In 2009, 53 individuals were captured, including 30 recaptures from 2007 or 2008 and 23 new captures. Overall, I identified 70 different individuals: 97 captures of 26 males and 328 captures of 44 females. The mean number of captures per individual was 7.5 (SD = 6.8) for females and 3.7 (SD = 5.0) for males. Males were more likely to be identified by a single sample ($n = 10 \text{ M}:4 \text{ F}$). I captured 18 males (69%) and 17 females (39%) in only a single year. One female was captured 36 times over the entire study and 1 male was captured 21 times. The mean number of different sites where an individual was captured was 3.3 (SD = 3.1) for males and 4.4

(SD = 3.2) for females. The mean maximum distance between all capture locations of individual bears was 4.25 km and the mean distance between successive capture locations of individuals was 2.84 km.

The original 22-locus suite had a mean of 3.7 alleles per locus (SD = 0.98, range 1–6) and a mean observed heterozygosity (H_o) of 0.64 (SE = 0.05; Table 1). The 7 markers used to identify individual genotypes had a mean of 4.3 alleles per locus (SD = 0.49, range 4–5) and mean H_o of 0.75 (SE = 0.02; Table 2), which represented a sufficient level of marker variability to differentiate individuals (Paetkau 2003). There was no difference ($P < 0.050$) between expected and observed heterozygosities so none of the loci deviated from Hardy-Weinberg equilibrium (Table 3).

For the 70 individuals identified in the ARB, individual locus PI estimates ranged from 0.098–0.130 and overall PI was 1.3×10^{-6} (Table 2). This represents a 1 in 769,230 chance of observing 2 individuals with identical genotypes in the ARB population. The probability of identity between siblings (PI_{sibs}) estimates for individual loci ranged from 0.40–0.47, and overall PI_{sibs} was 3.2×10^{-3} representing a 1 in 312 chance of observing identical genotypes in 2 related individuals. Based on these results, the probability of encountering identical genotypes based on the 7 most variable microsatellite loci was sufficiently low for capture-mark-recapture analysis.

Parameter Estimation

There were 28 models in my candidate set. Eleven of these had no support, with AIC_c weights of 0 and ΔAIC_c values >25 ; 17 models had ΔAIC_c values <7.53 (Table 4). The top 2 models carried approximately half the total weight of the model set ($w_1 = 0.25$, $w_2 = 0.23$, $\Delta AIC_c = 0.188$). The next 3 models each carried weights of 0.08–0.09. The subsequent 13 models were poorly supported, with weights ranging from 0.002 to 0.06.

Of the top 2 models, the only difference was the individual covariate of capture frequency during the previous primary period (*CapFreq*). Several of the other supported models also contained *CapFreq*. However in all cases, the slope of this parameter did not differ from zero (e.g., $\beta = 0.735$, 95% CI = -0.133–1.603 for Model 1), but model fit was improved, as indicated by a decrease in deviance ($Dev_{Model\ 1} = 1,246.90$, $Dev_{Model\ 2} = 1,249.19$). Parameters that were consistently supported in the weighted models were those in which apparent survival (ϕ) was constant with no time (t) or sex (g) variation and no temporary emigration ($\gamma'' = \gamma' = 0$). Models with sex-specific capture probabilities were well supported and there was strong support for a positive behavioral effect on p . Mixture distributions (π) were well supported, but models where π varied by gender were not. There was some support for constant, random temporary emigration of males ($\gamma'' = \gamma' = 0.10$, 95% CI = 0.001–0.90) but γ was inestimable for females. Models in which capture probabilities were allowed to vary across time were not well supported. No gender or time variation was supported for ϕ .

Apparent survival for males and females across both survival periods was 0.91 (SE = 0.06). The proportion of males in the first mixture ($\pi = 0.87$, SE = 0.07), when held constant across primary periods, had a capture probability of 0.08 (SE = 0.03) and in the second mixture ($\pi = 0.13$) had a capture probability of 0.37 (SE = 0.12). For females, the first capture heterogeneity mixture ($\pi = 0.86$, SE = 0.07), when held constant across primary periods, had a capture probability of 0.20 (SE = 0.04) and the second mixture ($\pi = 0.14$) had a capture probability of 0.62 (SE = 0.11). Mean weekly capture probabilities across all 24 secondary periods for both mixtures was 0.12 (SE = 0.03) for males and 0.25 (SE = 0.04) for females. Based on those probabilities, male bears that were present on my study area during all sampling periods had a 95.3% probability of being captured at least once and that probability for females

was 99.9%. Annual male abundance estimates for 2007–2009, respectively, were 22 (SE = 6.20, 95% CI = 15–43), 16 (SE = 4.80, 95% CI = 11–33), and 31 (SE = 7.78, 95% CI = 22–56). Respective annual female abundance estimates for 2007–2009 were 24 (SE = 3.01, 95% CI = 21–35), 32 (SE = 3.18, 95% CI = 24–43), and 42 (SE = 3.82, 95% CI = 38–55). The combined estimate of N for males and females, averaged across primary periods, was 56 (SE = 4.51, 95% CI = 49–68) with a coefficient of variation of 8.1%. Population growth varied considerably by gender and by interval (Table 5). The pooled growth rate for males and females across both intervals was 1.32 (SE = 0.07).

The result of the goodness-of-fit test was not significant ($\chi^2_{81} = 53.1$, $P = 0.993$) with the estimate of $\hat{c} = 0.656$ indicating the assumptions of the global CJS model were not violated. Therefore, I did not adjust for overdispersion in the data.

Density Estimation

The model-averaged density estimate based on the SECR method was 0.15 bears/km² (SE = 0.03). Models with detection represented by the hazard function received more support than the half-normal function (Table 6). In most cases, the Poisson and binomial distributions were equally supported. All models contained a behavioral response to capture, sex-specific individual heterogeneity for capture, or both. No models with individual heterogeneity represented in a 2-class mixture were estimable. In addition, neither models with added complexity of movement parameter effects were estimable, nor were models that included between-session parameters. For the 2007 data, the most supported model represented 66% of the model weight and modeled only a behavioral effect for the g_0 parameter. In 2008 and 2009, 4 of 5 models in the model set had $\Delta AIC_c < 2$, and several models were virtually identical with

evidence ratios <1 from the next model. My density estimate based on the traditional buffer strip method, after excluding non-habitat, was 0.18 bears/km².

V. DISCUSSION

My estimate of black bear abundance ($N = 56$) was greater than that of the only previous estimate for the ARB from 1999 ($N = 41$; Triant et al. 2004). However, direct comparison may not be warranted. Triant et al. (2004) sampled approximately 142 km², with a sampling grid based on areas known to have received bear use as determined by previous radio-telemetry locations. In contrast, my effective sampling area included all previously sampled areas plus an additional ≈ 160 km² of habitat. Consequently, sampled populations were different for the 2 studies. Sampling for the earlier study occurred over 2 15-day periods in a single year, and the modified Lincoln-Peterson closed-population estimator was used to estimate abundance. This is a simple estimator that can not account for capture heterogeneity, typically resulting in estimates that are biased low (Pollock et al. 1990). If the Triant et al. (2004) estimate indeed is biased low and only applied to approximately half my sampled area, my abundance estimate could be interpreted as indicative of a population decline. However, direct comparisons between the estimates may not be justified because of the differences in sampling area, sampling duration, and method of analysis used in the 2 studies.

My estimates of apparent survival were high between years ($\phi = 0.91$ for both time steps), so survival within the 8 weeks of sampling was even higher, supporting the assumption of demographic closure. Because permanent emigration is included in the estimate of ϕ , this also suggests low rates of egress between years. My apparent survival estimate was comparable to that of the Tensas River Basin population (0.91, SE = 0.08; Hooker 2010) and survival in both

studies did not vary greatly over time or by gender. This finding is not surprising given that both populations were un hunted due to their protection under the Endangered Species Act. High survival rates have also been reported in other black bear populations in the southeastern U.S. during periods of no hunting, such as the Osceola National Forest population in Florida (0.97, females only; Dobey et al. 2005) and the White River National Wildlife Refuge population in Arkansas (0.94, Clark and Eastridge 2006).

My results from the conventional method of density estimation were comparable to my model-averaged estimate using the SECR method. Typically, density estimates based on abundance are biased due to underestimation of the effective study area size and lack of geographic closure. However, given the discrete boundaries of bear habitat in my study area, estimating the effective study area likely was accurate. Clark et al. (2010) reported similar findings from a bear study in Arkansas, which also consisted of a discrete habitat/non-habitat matrix. When compared with reported densities of other black bear populations in the southeastern U.S., the density of the ARB population was most similar to the Osceola National Forest population in Florida (Table 7), also a small, protected population. The ARB bear density was low compared with TRB (0.66 bears/km², Hooker 2010). Although the two areas contain similar habitat, there are important differences that may have influenced densities. The TRB population is found primarily in the Tensas River National Wildlife Refuge, which was established in 1980 and prior to the listing of the Louisiana black bear. Therefore, this population resided in a protected area managed for wildlife, potentially facilitating recovery earlier than the ARB. In addition, agriculture surrounds the refuge and includes corn which may provide an artificial but stable food supply to reinforce reproduction (Dobey et al. 2005). Considering the high density and estimated growth rate reported for the TRB (1.04, Hooker

2010), that population may be nearing carrying capacity. The low density and high growth rate from my study suggest the ARB population may still be growing.

My annual estimates of N for females were similar to the number of females I captured annually, indicating that I captured a high proportion of the females that were in my study area (Table 5). There was also an annual increase in N for females ($\lambda = 1.32$, $SE = 0.06$). Because female bears do not typically disperse or only disperse a short distance, this increase suggests recruitment via reproduction rather than immigration. Given the life history of black bears (i.e., age of reproduction, litter size, and 2-year birth cycle), this rate would be very high (Bunnell and Tait 1981, Clark et al. 2005, Dobey et al. 2005, Clark and Eastridge 2006). This high growth rate may be biologically plausible under certain circumstances. Growth rate is the sum of survival and recruitment rates (f). Given an annual survival rate of 0.91, it would require 0.41 female recruits per adult female per year in the ARB to achieve this growth rate. This high level of recruitment for bears may be possible for short periods of time. For example, food resources can fluctuate, and a year of scarce food resources may initiate synchronous reproduction in bears (Rogers 1987, Elowe and Dodge 1989, Dobey et al. 2005). If a large cohort of cubs was produced prior to my study in response to a food shortage, sampling of that cohort could have resulted in the high recruitment I observed. If so, the high growth rate may not be sustained because reproductive rates typically vary for bears (Dobey et al. 2005, Garshelis et al. 2005) and contribute as much or more to variation in λ than survival in protected bear populations (Mitchell et al. 2009).

In contrast to females, variation in annual estimates of N for males was high, leading to a high standard error for male growth rate (0.14, Table 5). In each primary period the coefficient of variation for males was >20%, which exceeds desirable precision of population estimates

(Pollock et al. 1990). Heterogeneity of capture probabilities is the most likely cause of high annual variation and is one of the major challenges in estimating population parameters of bears using DNA methods. It is to be expected that individual differences such as the animal's size, age, or behavior influence its capture probability (Boulanger et al. 2004) and these sources are unidentifiable from DNA data. Smaller populations require greater capture probabilities for estimates to be precise and unbiased. Boulanger et al. (2004) recommended capture probabilities ≥ 0.20 for reliable parameter estimates using DNA mark-recapture techniques. Because my density of sampling sites was high, it is likely that females with their smaller home ranges had sufficient opportunity to encounter sampling sites. This is reflected in the high mean capture probability for females ($p = 0.25$). For females, even the individuals belonging to the "difficult-to-catch" mixture had adequate probability of capture ($p = 0.20$). Although males have larger home ranges (Wagner 1995) and the opportunity to encounter even more sampling sites, male capture probabilities were much lower, with 87% of males having a $p = 0.08$, and 13% with $p = 0.13$.

One possible explanation for capture heterogeneity in males may be related to movement on and off my sampling grid. Males make greater movements than females when dispersing, seeking food, or finding mates. Additionally, they are not encumbered by offspring as females may be. As previously mentioned, portions of Highway 190 on the southern border were elevated and would facilitate bear crossing into adjacent habitat and nearby Sherburne Wildlife Management Area. Also, habitat was present on the west side of the Atchafalaya River. White et al. (2000) found male bears twice as likely to cross rivers as females in the Mississippi Alluvial Valley. Males are also more likely to spend time traveling between habitat fragments (Marchinton 1995, Anderson 1997). Anderson (1997) found that seasonal use of corridors in the

TRB was highest during the summer. Males moved readily between tracts via wooded corridors and agricultural fields, whereas females traveled between tracts infrequently and only between corridor-linked tracts. This would allow them less time on the grid and a decreased probability for those individuals to be captured due to fewer trap encounters. Regardless, my estimates of apparent survival, which includes permanent emigration, were high which does not support this explanation.

Immigration of relocated nuisance bears also may have affected estimates of male abundance. The adjacent Sherburne Wildlife Management Area is commonly used as a release site for nuisance bears captured from the coastal population (M. Davidson, LDWF, personal communication). The majority of these bears likely were killed by human-related causes or traveled back to the coast soon after release (M. Davidson, LDWF, personal communication), so their contribution to the ARB population is presumably low. However, it is feasible they entered my sampling grid. Given my estimates of male abundance, variation in even a small number of released nuisance bears (e.g., 8 males were relocated to Sherburne in 2008) could have contributed to the variation in abundance that I observed.

One important advantage of hair sampling is that initial captures likely have little negative effect on recapture probabilities. However, of all males captured during the study, 38% (10/26) were only captured once. It is possible they were visiting sites and simply not being caught, due to avoidance of the wire after initial capture or design of the sampling device. For example, I documented numerous occasions each week when a bear removed the bait from the site and did not leave hair on the wire, as evidenced by canine marks in the bait bag or hairs stuck to the scent rag. Boulanger et al. (2004) used GPS-collared bears to document this, and found that 37% of bears encountering a hair-sampling site did not leave a hair sample. I used a

digital game camera (Cuddeback,[®] Non Typical Inc., Green Bay, Wisconsin, USA) to document bear activity at some of my hair-sampling sites in 2008 and 2009. This was also done in the TRB in 2008 (Hooker 2010). In both study areas, multiple videos and still photos revealed bears of various sizes crossing the barbed wire at a site and leaving no hair sample. Many of the large adults avoided the wire by stepping over or on it; in some cases male genitalia were visible and in other cases the bear was presumed to be an adult male based on its large size. Another consideration for lack of collectible samples is that bears in Louisiana molt during the summer and some only have patchy areas of hair remaining which could affect the probability that hair would be snagged when contacting the wire. Hooker (2010) obtained multiple videos of large male bears entering a site with their nearly hairless underside and hindquarters contacting the wire but leaving no hair sample.

Hair sampling in my study area was extended to 2010–2011, and sampling was modified to a 2-wire system in an attempt to decrease capture heterogeneity, particularly for males. Rather than placing the wire at a height of 40–50 cm from the ground, a bottom wire was placed at a height of 35 cm and a top wire at 70 cm. This design should increase capture probabilities by forcing bears of different sizes to contact at least 1 wire. Preliminary results from the 2010 capture data suggest the 2-wire system was effective in decreasing sampling bias for males (K. O’Connell, University of Tennessee, personal communication). The sex ratio of all captures in my study using 1 wire was 44 F:26 M whereas the sex ratio for the 2010 capture data was 22 F:20 M, with 2 new females and 9 new males identified. Additionally, females were identified almost equally from samples collected from the top and bottom wires, whereas 63% of the males were identified from samples collected from the top wire (D. Paetkau, WGI, personal communication).

VI. MANAGEMENT AND RESEARCH IMPLICATIONS

Although this study provides initial abundance and growth rate estimates, the short time span did not allow accurate estimation of process variance (i.e., temporal and spatial) for population viability analysis (Mills 2007). Population monitoring should continue in the ARB to further refine and improve precision of my parameter estimates. The two additional years of sampling of this population should better capture process variance over time, particularly with the population growth rate and male abundance estimates. The additional data could also provide important insights regarding female recruitment.

DNA capture-mark-recapture studies are in progress to obtain reliable estimates of the other 2 subpopulations. Data collection in the TRB occurred during 2006–2008, resulting in a population estimate of 294 bears (Hooker 2010). That project is expected to continue through 2011. For the Coastal ARB population, data collection began in the summer of 2010 and will end in 2012. Individually, these data will allow assessment of viability of the subpopulations. Collectively, the data will provide insights into the functioning of the Louisiana black bear as a metapopulation.

Bears in the ARB subpopulation occur in an area of fragmented habitat. Although some ingress and egress occurs, these individuals likely are males only. Based on my annual abundance estimates for females ($N = 24, 32, \text{ and } 42, CV = 9\%–12.5\%$), the ARB population remains vulnerable to environmental and demographic stochasticity because of its small size and isolation. Given estimated vital rates, the PVA will help to predict risks to the population under various conditions (Mills 2007), including simulations of stochastic events and management actions (e.g., effects of mortality from a hunting season).

Bears in the ARB subpopulation occur in a highly fragmented landscape. Although genetic connectivity may be maintained by male ingress and egress, movement of both sexes between populations is important for demographic viability (Proctor et al. 2005). Without such movements, the ARB population would be demographically isolated and vulnerable to stochastic events (Proctor et al. 2005). To facilitate demographic connectivity, establishment and maintenance of habitat corridors between the ARB and TRB populations would be important. A GPS-collar study is being conducted to investigate interchange of dispersing bears among the subpopulations and identify corridors that facilitate such connectivity (J. Laufenberg, University of Tennessee, personal communication). Because approximately 90% of land within historic range of the Louisiana black bear is privately owned, establishing such corridors is challenging. Lands enrolled in the Wetland Reserve Program (WRP) and other conservation incentive programs for private lands may be crucial to create these corridors. Evidence already exists that WRP lands with early successional forests have contributed to recovery of the Louisiana black bear. For example, in the past 7 years, several litters of cubs have been reported on WRP lands adjacent to Tensas River National Wildlife Refuge (University of Tennessee, unpublished data).

LITERATURE CITED

- Allen, T. G. 1999. Black bear population size and habitat use on the Alligator River National Wildlife Refuge, North Carolina. Thesis, University of Tennessee, Knoxville, USA.
- Anderson, D. A. 1997. Corridor use, feeding ecology, and habitat relationships of black bears in a fragmented landscape in Louisiana. Thesis, University of Tennessee, Knoxville, USA.
- Beausoleil, R. A. 1999. Population and spatial ecology of the Louisiana black bear in a fragmented bottomland hardwood forest. Thesis, University of Tennessee, Knoxville, USA.
- Boersen, M. R. 2001. Abundance and density of the Louisiana black bear on the Tensas National Wildlife Refuge. Thesis, University of Tennessee, Knoxville, USA.
- Boersen, M. R., J. D. Clark, and T. L. King. 2003. Estimating black bear population density and genetic diversity at Tensas River, Louisiana using microsatellite DNA markers. *Wildlife Society Bulletin* 31:197–207.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64:377–385.
- Boulanger, J., and B. McLellan. 2001. Closure violation in DNA-based mark-recapture estimation of grizzly bear populations. *Canadian Journal of Zoology* 79:642–651.
- Boulanger, J., G. C. White, B. N. McLellan, J. Woods, M. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. *Ursus* 13:137–152.
- Boulanger, J., G. Stenhouse, and R. Munro. 2004. Sources of heterogeneity bias when DNA mark-recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. *Journal of Mammalogy* 85:618–624.

- Boulanger, J., K. C. Kendall, J. B. Stetz, D. A. Roon, L. P. Waits, and D. Paetkau. 2008a. Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. *Ecological Applications* 18.
- Boulanger, J., G. C. White, M. Proctor, G. Stenhouse, G. Machutchon, and S. Himmer. 2008b. Use of occupancy models to estimate the influence of previous live captures on DNA-based detection probabilities of grizzly bears. *Journal of Wildlife Management* 72:589–595).
- Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears—implications. Pages 75–98 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. John Wiley and Sons, New York, New York, USA.
- Brandenberg, D. M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, USA.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph No. 5, Bethesda, Maryland, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Carothers, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29:79–100.
- Clark, J. D. 1991. Ecology of two black bear (*Ursus americanus*) populations in the Interior Highlands of Arkansas. Dissertation, University of Arkansas, Fayetteville, USA.
- Clark, J. D., and R. Eastridge. 2006. Growth and sustainability of black bears at White River National Wildlife Refuge, Arkansas. *Journal of Wildlife Management* 70:1094–1101.

- Clark, J. D., R. Eastridge, and M. J. Hooker. 2010. Effects of exploitation on black bear populations at White River National Wildlife Refuge. *Journal of Wildlife Management* 74:1448–1456.
- Clark, J. D., F. T van Manen, and M. R. Pelton. 2005. Bait stations, hard mast, and black bear population growth in Great Smoky Mountains National Park. *Journal of Wildlife Management* 69:1633–1640.
- Conner, K., and D. L. Hartl. 2004. *Primer of ecological genetics*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Conner, M. M., and G. C. White. 1999. Effects of individual heterogeneity in estimating the persistence of small populations. *Natural Resources Modeling* 12:109–127.
- Csiki, I., C. Lam, A. Key, E. Coulter, J. D. Clark, R. M. Pace III, K. G. Smith, and D. D. Rhoads. 2003. Genetic variation in black bears in Arkansas and Louisiana using microsatellite DNA markers. *Journal of Mammalogy* 84:691–701.
- Dice, L. 1938. Some census methods for mammals. *Journal of Wildlife Management* 2:119–130.
- Dobey, S., D. V. Masters, B. K. Scheick, J. D. Clark, M. R. Pelton, and M. E. Sundquist. 2005. Ecology of black bears in the Okefenokee–Osceola Ecosystem. *Wildlife Monographs* 158.
- Drewry, J. M. 2010. Population abundance and genetic structure of black bears in coastal South Carolina. Thesis, University of Tennessee, Knoxville, USA.
- Efford, M. G., D. K. Dawson, and C. S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation* 27:217–228.

- Efford, M. G., D. L. Borchers, and A. E. Byrom. 2008. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 in D. L. Thomson, E. G. Cooch, and M. J. Conry, editors. Modeling demographic processes in marked populations. Springer-Verlag, New York, New York, USA.
- Ennis, S., and T. F. Gallagher. 1994. PCR based sex determination assay in cattle based on the bovine Amelogenin locus. *Animal Genetics* 25:425–427.
- Fletcher, D. J. 1994. A mark–recapture model in which sighting probability depends on the number of sightings on the previous occasion. Pages 105–110 in D. J. Fletcher and B. F. J. Manly, editors. Statistics in ecology and environmental monitoring. University of Otago Press, Dunedin, New Zealand.
- Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. *Journal of Wildlife Management* 45:912–925.
- Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, New York, USA.
- Hellgren, E. C., and M. R. Vaughan. 1989. Demographic analysis of a black bear population in the Great Dismal Swamp. *Journal of Wildlife Management* 53:969–977.
- Hightower, D. A., R. O. Wagner, and R. M. Pace III. 2002. Denning ecology of female American black bears in south central Louisiana. *Ursus* 13:11–17.
- Hooker, M. J. 2010. Estimating population parameters of the Louisiana black bear in the Tensas River Basin, Louisiana, using robust design capture-mark-recapture. Thesis, University of Tennessee, Knoxville, USA.
- Huggins, R. M. 1989. On the statistical analysis of capture-recapture experiments. *Biometrika* 76:133–140.

- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Hurvich, C. M. and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration: stochastic model. *Biometrika* 52:225–247.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- Kendall, W. L., J. D. Nichols, and E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock’s robust design. *Ecology* 78:563–578.
- Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. MacCleod, D. Paetkau, G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. *Journal of Wildlife Management* 73:3–17.
- King, S. L., D. J. Twedt, and R. R. Wilson. 2006. The role of the wetland reserve program in conservation efforts in the Mississippi River Alluvial Valley. *Wildlife Society Bulletin* 34:914–920.
- Link, W. A. 2003. Nonidentifiability of population size from capture-recapture data with heterogeneous detection probabilities. *Biometrics* 59:1123–1130.
- Lowe, A., S. Harris, and P. Ashton. 2004. *Ecological genetics: design, analysis and application*. Blackwell Publishing, Oxford, United Kingdom.
- Marchinton, F. B. 1995. Movement ecology of black bears in a fragmented bottomland hardwood habitat in Louisiana. Thesis, University of Tennessee, Knoxville, USA.

- Martorello, D. A. 1998. Ecology of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, USA.
- McKelvey, K. S., and M. K. Schwartz. 2004. Genetic errors associated with population estimation using noninvasive molecular tagging: problems and new solutions. *Journal of Wildlife Management* 68:439–448.
- Miller, D. A., E. M. Hallerman, M. R. Vaughan., and J. W. Kasbohm. 1998. Genetic variation in black bear populations from Louisiana and Arkansas: examining the potential influence of reintroductions from Minnesota. *Ursus* 10:335–341.
- Mills, L. S. 2007. Conservation of wildlife populations: demography, genetics and management. Blackwell Publishing, Malden, Massachusetts, USA.
- Mills, L. S., J. J. Citta, K. P. Lair, M. K. Schwartz, and D. A. Tallmon. 2000. Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. *Ecological Applications* 10:283–294.
- Mitchell, M. S., L. B. Pacifici, J. B. Grand, and R. A. Powell. 2009. Contributions of vital rates to growth of a protected population of American black bears. *Ursus* 20:77–84.
- National Climatic Data Center [NCDC]. National Oceanic and Atmospheric Administration. 2010. Annual Climatological Summary. <<http://cdo.ncdc.noaa.gov/ancsum/ACS>>. Accessed 20 September 2010.
- Natural Resources Conservation Service [NRCS]. U.S. Department of Agriculture. 2009. Custom Soil Resource Report for Pointe Coupee Parish, Louisiana. <<http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx/>>. Accessed 6 March 2011.

- Neal, W. A. 1990. Proposed threatened status for the Louisiana black bear. *Federal Register* 55(120):25341–25345.
- Neal, W. A. 1992. Threatened status for the Louisiana black bear and related rules. *Federal Register* 57(4):588–595.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62.
- Pace, R. M. III, Anderson, D. R., and S. Shively. 2000. Sources and patterns of mortality in Louisiana black bears. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 54:365–373.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12:1375–1387.
- Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- Paetkau, D., and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bears. *Molecular Ecology* 4:347–354.
- Paetkau, D., and C. Strobeck. 1998. Ecological genetic studies of bears using microsatellite analysis. *Ursus* 10:299–306.
- Peakall, R., and P. E. Smouse. 2006. Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology* 6:288–295.
- Pelton, M. R. 1991. Black bears in the Southeast: to list or not to list? *Eastern Workshop on Black Bear Research and Management* 10:155–161.
- Pledger, S. A. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics* 56:434–442.

- Pollock, K. H. 1982. A capture-recapture design robust to unequal capture probability. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference from capture-recapture experiments. *Wildlife Monographs* 107.
- Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949–954.
- Proctor, M. F., B. N. McLellan, C. Strobeck, and R. M. R. Barclay. 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B: Biological Sciences*. 272:2409–2416.
- Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56:426–431.
- Seber, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- Seber, G. A. F. 1982. *The estimation of animal abundance*. Charles Griffin, London, United Kingdom.
- Settlage, K. E., F. T. van Manen, J. D. Clark, and T. L. King. 2008. Challenges of DNA-based mark-recapture studies of American black bears. *Journal of Wildlife Management* 72:1035–1042.
- Smith, T. R. 1985. *Ecology of black bears in a bottomland hardwood forest in Arkansas*. Dissertation, University of Tennessee, Knoxville, USA.
- Smith, T. R., and M. R. Pelton. 1990. Home ranges and movements of black bears in a bottomland hardwood forest in Arkansas. *International Conference on Bear Research and Management* 8:213–218.

- Taberlet, P., S. Griffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with low DNA quantities using PCR. *Nucleic Acids Research* 26:3189–3194.
- Taberlet, P. and G. Luikart. 1999. Non-invasive genetic sampling and individual identification. *Biological Journal of the Linnean Society* 68:41-55.
- Taylor, D. F. 1971. A radio-telemetry study of the black bear (*Euarctos americanus*) with notes on its history and present status in Louisiana. Thesis, Louisiana State University, Baton Rouge, USA.
- Thompson, L. M., F. T. van Manen, and T. L. King. 2005. Geostatistical analysis of allele presence patterns among American black bears in eastern North Carolina. *Ursus* 16:59–69.
- Tredick, C.A., and M. R. Vaughan. 2009. DNA-based population demographics of black bears in coastal North Carolina and Virginia. *Journal of Wildlife Management* 73:1031–1039.
- Tredick, C. A., M. R. Vaughan, D. F. Stauffer, S. L. Simek, and T. Eason. 2007. Sub-sampling genetic data to estimate black bear population size: a case study. *Ursus* 18:179–188.
- Triant, D. A. 2001. Estimating population size and genetic diversity of two populations of black bears in south central Louisiana. Thesis, Louisiana State University, Baton Rouge, USA.
- Triant, D. A., R. M. Pace III, and M. Stine. 2004. Abundance, genetic diversity and conservation of Louisiana black bears (*Ursus americanus luteolus*) as detected through noninvasive sampling. *Conservation Genetics* 5:647–659.
- U. S. Geological Survey. 2001. Multi-resolution land characteristics consortium. National land cover database. <<http://www.mrlc.gov/index.php>>. Accessed 25 January 2011.

- U.S. Fish and Wildlife Service [USFWS]. 1995. Louisiana black bear (*Ursus americanus luteolus*) recovery plan. U.S. Fish and Wildlife Service, Southeast Regional Office, Atlanta, Georgia, USA.
- Wagner, R. O. 1995. Movement patterns of black bears in south central Louisiana. Thesis, Louisiana State University, Baton Rouge, USA.
- Waits, L. P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology* 10:249–256.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.
- White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of Program Mark. Pages 368–377 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century*. Proceedings of the second international wildlife management congress. The Wildlife Society, Bethesda, Maryland, USA.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use and mortality of black bears in north-central Florida. *International Conference on Bear Research and Management* 9:349–356.
- Woods, J. G., D. Paetkau, D. Lewis, B. L. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. *Wildlife Society Bulletin* 27:616–627.

APPENDICES

APPENDIX A: TABLES

Table 1. Number of alleles and heterozygosity of 22 loci evaluated for efficacy to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.

Locus	<i>n</i>^a	A^b	H_o^c	H_e^d
MU23	70	5	0.81	0.75
G10M	70	5	0.79	0.72
G10C	70	4	0.80	0.72
MU26	70	4	0.69	0.69
G10L	70	4	0.70	0.66
G10P	70	4	0.77	0.65
MU59	70	4	0.69	0.65
G10J	45	3	0.71	0.64
G1D	45	4	0.69	0.65
G1A	45	4	0.64	0.55
G10U	23	4	0.91	0.75
MSUT2	23	6	0.61	0.73
CXX110	23	4	0.43	0.72
G10X	23	4	0.48	0.66
CXX20	23	4	0.87	0.63
G10H	23	3	0.52	0.62
P07	23	3	0.65	0.60
CPH9	23	3	0.52	0.52
G10B	23	3	0.43	0.46
MU50	23	3	0.35	0.36
A06	23	3	0.30	0.31
MU51	23	1	0.00	0.00

^a Number of bears identified using given locus.

^b Number of observed alleles.

^c Observed heterozygosity.

^d Expected heterozygosity.

Table 2. Variability of microsatellite markers used to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA 2007–2009.

Locus	H_o	H_e	A	PI	PI_{sib}
G10M	0.79	0.72	5	0.13	0.42
G10P	0.77	0.65	4	0.17	0.47
MU59	0.69	0.65	4	0.17	0.47
G10L	0.70	0.66	4	0.19	0.47
MU23	0.81	0.75	5	0.10	0.40
MU26	0.69	0.69	4	0.15	0.44
G10C	0.80	0.72	4	0.13	0.42
\bar{x}	0.75	0.69	4.3	0.15	0.44
Overall PI				1.3×10^{-6}	3.2×10^{-3}

H_o= observed heterozygosity; H_e = expected heterozygosity; A = number of alleles;
 PI = probability of identity; PI_{sib} = probability of sibling identity.

Table 3. Summary of chi-square tests for Hardy-Weinberg equilibrium for the 7 loci used to identify individual Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009. *P*-value represents significance value for test of difference between H_0 and H_e for that locus across all genotyped samples.

Locus	df	χ^2	<i>P</i>-value
G10M	10	11.22	0.34
G10P	6	7.25	0.30
MU59	6	2.97	0.81
G10L	6	5.15	0.53
MU23	10	17.87	0.06
MU26	6	5.84	0.44
G10C	6	8.62	0.20

Table 4. Robust design models and model selection based on AIC_c to estimate Louisiana black bear population parameters in the Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009, from DNA capture-mark-recapture. I modeled apparent survival (ϕ), probability of temporarily leaving the study area (γ''), probability of remaining off the study area (γ'), proportion of the population belonging to 1 of 2 heterogeneity mixtures (π), capture probability (p), and recapture probability (c) as functions of time (t), sex (g), t and g as an additive effect ($t + g$), t and g interaction ($t \times g$), the first primary period differing from the second 2 primary periods ($tfirstyr$), or number of secondary periods in which the animal was captured in the previous primary period ($CapFreq$). I modeled c as a behavioral response (*behavior*), no behavioral response ($p = c$), or independent (p, c). I modeled temporary emigration as random ($\gamma'' = \gamma'$) or no movement ($\gamma'' = \gamma' = 0$). I also modeled parameters as constant (\cdot).

Model Number	Model	AIC_c	ΔAIC_c^a	w_i^b	K^c	Dev
1	{ $\phi(\cdot), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,261.27	0.00	0.25	7	1,246.91
2	{ $\phi(\cdot), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g) = c(\text{behavior})$ }	1,261.46	0.19	0.23	6	1,249.19
3	{ $\phi(t), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,263.36	2.09	0.09	8	1,246.89
4	{ $\phi(\cdot), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(g), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,263.36	2.09	0.09	8	1,246.89
5	{ $\phi(\cdot), \gamma''(\cdot) = \gamma'(\cdot), \pi(\cdot), p(\text{mix}, g = c(\text{behavior}))$ }	1,263.55	2.28	0.08	7	1,249.19
6	{ $\phi(\cdot), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g), c(\text{mix}, g)$ }	1,264.06	2.79	0.06	8	1,247.59
7	{ $\phi(t+g), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,264.93	3.65	0.04	9	1,246.34
8	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g = c(\text{behavior}))$ }	1,265.27	4.00	0.03	8	1,248.80
9	{ $\phi(\cdot), \gamma''(g) = \gamma'(g) = 0, \pi(g), p(\text{mix}, g) = c$ }	1,266.61	5.34	0.02	6	1,254.33
10	{ $\phi(t \times g), \gamma''(\cdot) = \gamma'(\cdot) = 0, \pi(\cdot), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,266.66	5.39	0.02	10	1,245.93
11	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g = c)$ }	1,266.78	5.50	0.02	7	1,252.41
12	{ $\phi(g), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g = c(\text{behavior}))$ }	1,267.05	5.78	0.01	9	1,248.46
13	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g, tfirstyr = c(\text{behavior}))$ }	1,267.09	5.82	0.01	9	1,248.50
14	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g, CapFreq = c(\text{behavior}))$ }	1,267.15	5.87	0.01	9	1,248.55
15	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(g), p(\text{mix}, g = c(\text{behavior}))$ }	1,267.18	5.91	0.01	9	1,248.59
16	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(\cdot), p(\text{mix}, g, t = c(\text{behavior}))$ }	1,268.76	7.49	0.01	10	1,248.04
17	{ $\phi(\cdot), \gamma''(g) = \gamma'(g), \pi(g), p(\text{mix}, g = c)$ }	1,268.81	7.53	0.01	8	1,252.33

^a Relative difference between AIC_c of model and AIC_c of model with lowest AIC_c .

^b Model weight.

^c Number of model parameters including intercepts.

Table 5. Number of individuals captured (M_{t+1}) and estimates of population size (N) and growth (λ) based on robust design capture-mark-recapture analysis of hair sampling for Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.

Sex and year	M_{t+1}	N	N SE	95% CI	λ	λ SE
Male						
2007	12	22.3	6.2	15.4–42.0		
2008	9	16.4	4.8	11.3–32.8	0.736	0.042
2009	17	31.2	7.8	22.1–56.1	1.898	0.270
Female						
2007	20	24.0	3.0	21.1–34.9		
2008	27	31.7	3.2	28.4–42.6	1.322	0.064
2009	36	42.1	3.8	38.0–54.8	1.327	0.047
Pooled						
2007	32	46.3	7.5	37.4–69.9		
2008	36	48.1	6.2	40.7–67.3	1.029	0.038
2009	53	73.3	9.4	61.5–101.2	1.613	0.137

Table 6. Model selection procedures based on Akaike's Information Criteria (AIC_c) to estimate Louisiana black bear population density (\hat{D}), Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009. Hazard (HZ) and Half-normal (HN) detection functions were considered, as were Poisson and binomial distributions. The probability of detection parameter (g_0) was modeled as a function of sex (h) and behavior (B). The hazard function also incorporates a shape parameter (b). Spatial scale (σ) was modeled as constant (\cdot)

Model and year	AIC_c^a	ΔAIC_c	w_i^b	Model likelihood	\hat{D} (no. bears/km ²)	SE
2007						
HZ Poisson: $g_0(B), b(B), \sigma(\cdot)$	913.25	0.00	0.663	1.00	0.138	0.024
HZ Poisson: $g_0(Bh), b(Bh), \sigma(\cdot)$	916.02	2.77	0.166	0.250	0.138	0.024
HZ Binomial: $g_0(Bh), b(Bh), \sigma(\cdot)$	916.02	2.77	0.166	0.250	0.139	0.024
HZ Poisson: $g_0(h), b(h), \sigma(\cdot)$	923.19	9.94	0.005	0.067	0.111	0.020
HN Poisson: $g_0(bh), \sigma(\cdot)$	973.22	59.97	6E-14	9E-14	0.136	0.024
model-averaged \hat{D} and SE					0.138	0.024
2008						
HZ Poisson: $g_0(Bh), b(Bh), \sigma(\cdot)$	1,339.49	0.00	0.301	1.00	0.122	0.020
HZ Binomial: $g_0(Bh), b(Bh), \sigma(\cdot)$	1,339.49	0.00	0.301	1.00	0.123	0.019
HZ Poisson: $g_0(B), b(B), \sigma(\cdot)$	1,340.51	1.02	0.181	0.600	0.121	0.026
HZ Poisson: $g_0(h), b(h), \sigma(\cdot)$	1,340.97	1.48	0.143	0.477	0.119	0.020
HN Poisson: $g_0(bh), \sigma(\cdot)$	1,342.27	2.78	0.075	0.249	0.123	0.020
model-averaged \hat{D} and SE					0.122	0.025
2009						
HZ Poisson: $g_0(h), b(h), \sigma(\cdot)$	1,612.50	0.00	0.371	1.00	0.183	0.025
HZ Poisson: $g_0(B), b(B), \sigma(\cdot)$	1,612.88	0.38	0.307	0.827	0.187	0.026
HZ Binomial: $g_0(Bh), b(Bh), \sigma(\cdot)$	1,614.21	1.71	0.158	0.425	0.187	0.025
HZ Poisson: $g_0(Bh), b(bh), \sigma(\cdot)$	1,614.21	1.71	0.158	0.425	0.187	0.026
HN Poisson: $g_0(bh), \sigma(\cdot)$	1,620.95	8.45	0.005	0.015	0.187	0.026
model-averaged \hat{D} and SE					0.186	0.025

^aAkaike's Information Criterion adjusted for small n .

^bAkaike weight.

Table 7. Reported population densities of black bear populations in the southeastern United States.

Locality	Bears/km²	Reference
Camp Lejeune, North Carolina	0.02	Brandenburg (1996)
Carvers Bay, South Carolina	0.04	Drewry (2010)
White Rock, Arkansas	0.08	Clark (1991)
Dry Creek, Arkansas	0.09	Clark (1991)
Okefenokee Swamp, Georgia	0.12	Dobey et al. (2005)
Osceola National Forest, Florida	0.14	Dobey et al. (2005)
White River National Wildlife Refuge, Arkansas	0.22–0.25	Clark et al. (2010)
Upper Atchafalaya River Basin, Louisiana	0.15–0.18	This study
White River National Wildlife Refuge, Arkansas	0.29	Smith (1985)
Lewis Ocean Bay, South Carolina	0.31	Drewry (2010)
Tensas River National Wildlife Refuge, Louisiana	0.36	Boersen et al. (2003)
Great Dismal Swamp, North Carolina – Virginia	0.47–0.68	Hellgren and Vaughan (1989)
Big Pocosin, North Carolina	0.53	Martorello (1998)
Tensas River Basin, Louisiana	0.66	Hooker (2010)
Alligator River National Wildlife Refuge, North Carolina	0.86	Allen (1999)
Gum Swamp, North Carolina	1.35	Martorello (1998)
Deltic Tracts, Tensas River Basin, Louisiana	1.43	Beausoleil (1999)

APPENDIX B: FIGURES

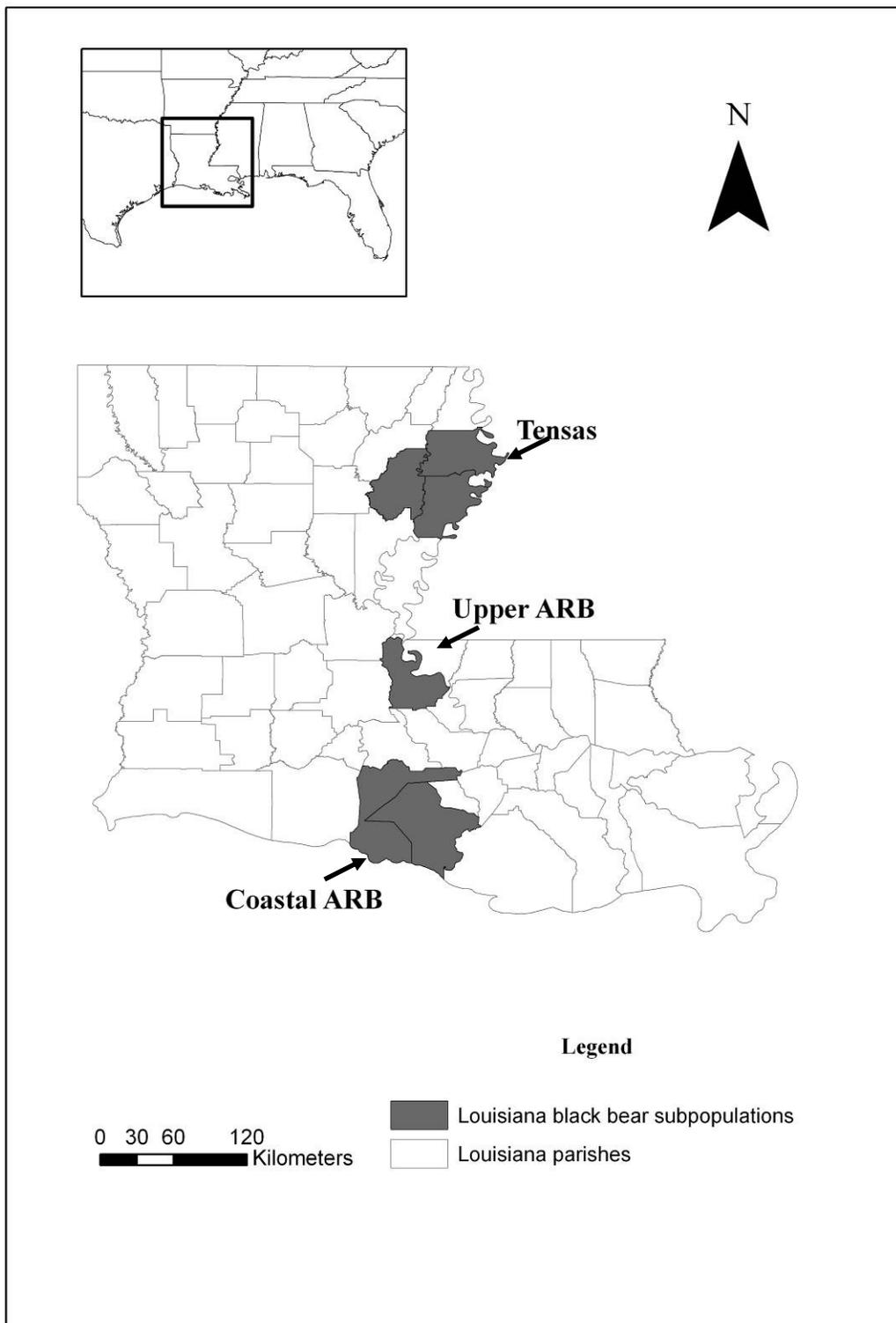


Figure1. Locations of 3 subpopulations of the Louisiana black bear within Louisiana, USA.

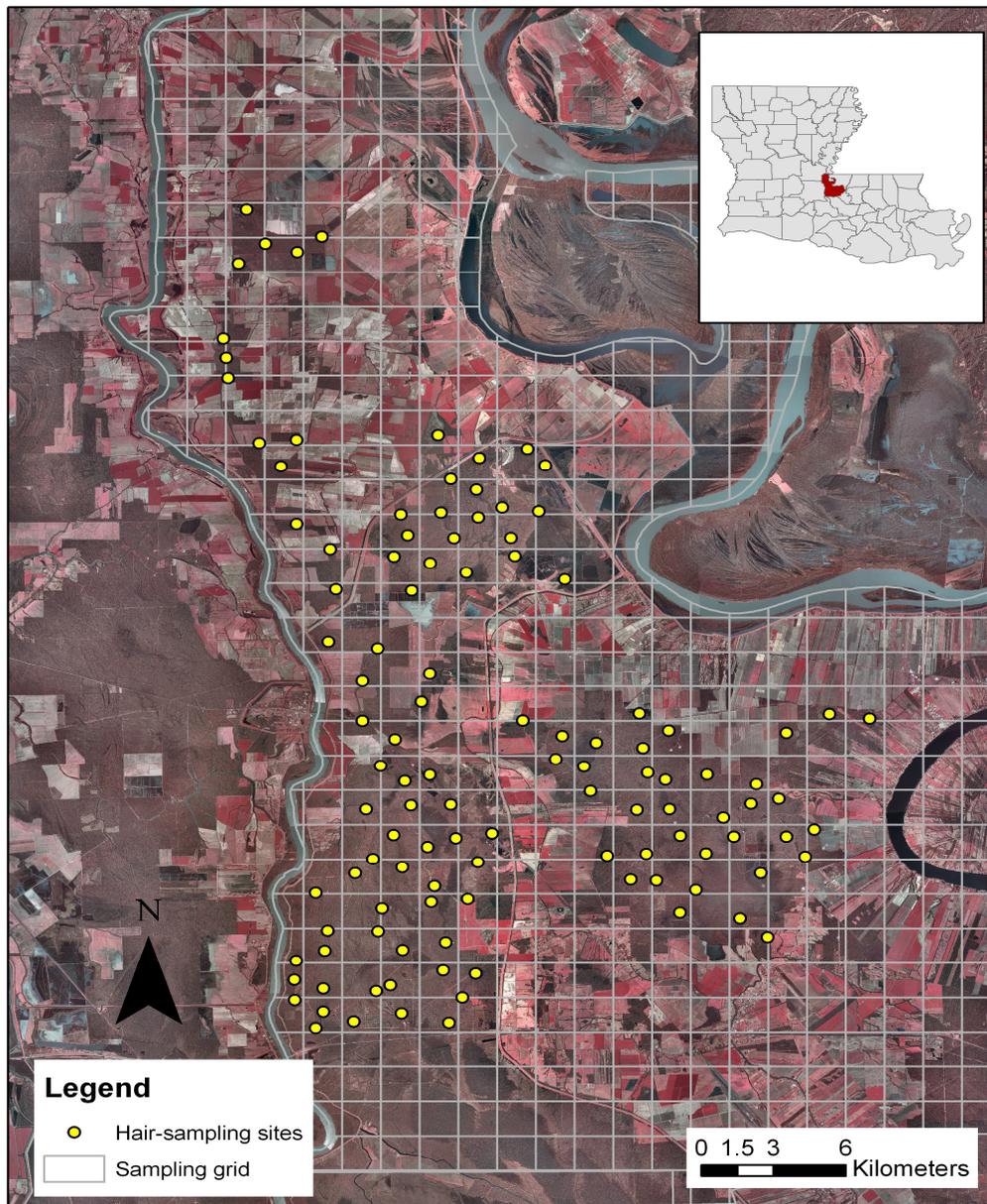


Figure 2. Sampling grid (2.6-km² cell size) and locations of 115 hair-sampling sites used to collect hair from Louisiana black bears, Upper Atchafalaya River Basin, Louisiana, USA, 2007–2009.

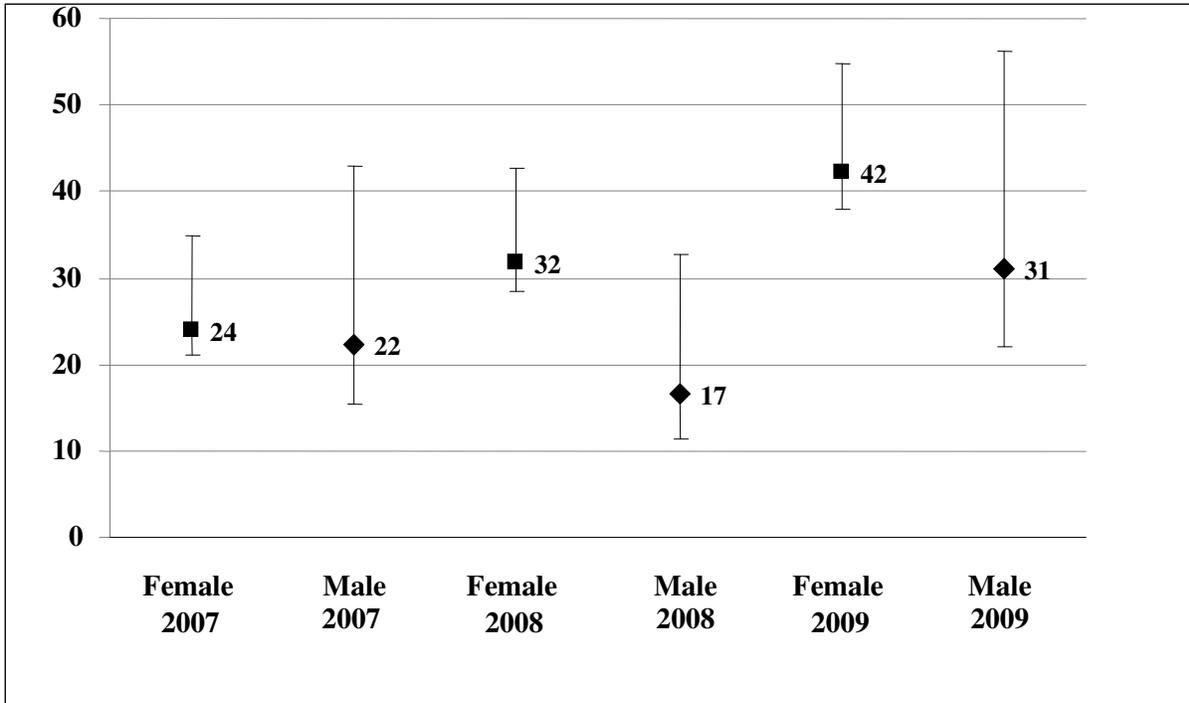


Figure 3. Model-averaged annual abundance estimates for the Louisiana black bear, Upper Atchafalaya River Basin, Louisiana, USA, as estimated by robust design capture-mark-recapture, 2007–2009. Vertical lines represent 95% confidence intervals.

VITA

Carrie L. Lowe was born in Grand Rapids, Michigan on 5 March 1979 and grew up in Holland, Michigan. She received Bachelor's degrees in Biology and Psychology from Hope College in 2001. She spent several years working as a wildlife field technician on a variety of studies, including a sea turtle project in Georgia and fisher and marten surveys in the Sierra Nevada Mountains. Prior to graduate school, Carrie was involved with black bear studies for the University of Tennessee in the Great Smoky Mountains National Park, White River, Arkansas, and in Louisiana. She received her Master's degree in Wildlife and Fisheries Science from the University of Tennessee in May 2011.