

To the Graduate Council:

I am submitting herewith a thesis written by Michael James Hooker entitled “Estimating population parameters of the Louisiana black bear in the Tensas River Basin, Louisiana, using robust design capture-mark-recapture.” I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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**ESTIMATING POPULATION PARAMETERS OF THE LOUISIANA
BLACK BEAR IN THE TENSAS RIVER BASIN, LOUISIANA, USING
ROBUST DESIGN CAPTURE-MARK-RECAPTURE**

A Thesis

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Michael James Hooker

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DEDICATION

This thesis is dedicated to all who have stood along a bayou's edge, in fading light, watching muddy water fill a bear track and wondered.

“If Sam Fathers had been his mentor and the backyard rabbits and squirrels his kindergarten, the wilderness the old bear ran was his college and the old male bear itself, so long unwifed and childless as to have become its own ungended progenitor, was his alma mater”

William Faulkner *-from The Bear*

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ABSTRACT

The Louisiana black bear (*Ursus americanus luteolus*) is listed as a threatened species under the protection of the Endangered Species Act of 1973. The Louisiana Black Bear Recovery Plan calls for research regarding bear population viability and biology. From July 2006 to August 2008 I conducted a 3-year robust design capture-mark-recapture study of bears in the Tensas River Basin of northeast Louisiana. I used microsatellite genotypes from DNA extracted from hair samples to identify individual bears. Robust design encounter histories of bears were analyzed using Huggins full heterogeneity models in Program MARK. I ranked models using Akaike's Information Criterion (AIC). I used model averaging to account for model selection uncertainty. Apparent survival rate, temporary emigration, the probability of an individual coming from 1 of 2 mixtures, and the probability of capture and recapture were estimated from encounter histories. Population abundance was a derived parameter. I used abundance estimates to calculate density, and population growth. Apparent survival did not differ by gender or year and was 0.91 (95% CI = 0.62–0.98). There was no temporary emigration. Models in which capture probabilities varied by mixtures were favored over models lacking mixtures. For both genders and across all years, >80% of individuals were in a mixture with capture probabilities ranging from 0.02 to 0.03 for males and 0.07 to 0.08 for females. Estimates for recapture were higher than capture indicating a positive behavioral response to being captured for females. Model-averaged estimates of abundance for females were 143 (95% CI = 113–204), 106 (95% CI = 83–151), and 133 (95% CI = 100–195) and for males were 198 (95% CI = 117–360), 116 (95% CI = 69–209), and 185 (95% CI = 112–323) during 2006, 2007 and 2008, respectively. Mean population size for both genders averaged across years was 294 (SE = 31) and density was 0.66 bears/km² (SE = 0.07). Video and photographic evidence suggested that adult males were

less likely to be sampled while visiting hair snares. I offer suggestions to reduce this heterogeneity bias.

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I. INTRODUCTION

The American black bear (*Ursus americanus*) is the most common and widely distributed North American ursid (Pelton 2003) but the current range represents only approximately 62% of its historical range (Pelton and van Manen 1994). In many areas of North America black bears are numerous, sustain high levels of hunter harvest, and are sometimes considered pests. In other regions, however, black bears are found only in small, isolated, and remnant populations or have been extirpated (Pelton 1982). The Louisiana black bear (*U. a. luteolus*), one of 16 subspecies of American black bear (Hall 1981), exemplifies the former.

Prior to the twentieth century the Louisiana black bear was distributed across present-day east Texas, Louisiana, and southern Mississippi (Fig. 1, Hall 1981). Little is known about population levels at the time of European settlement but it is thought that the Louisiana black bear was abundant (Lowery 1974). Le Page du Pratz (1758) documented bear hunting along the lower Mississippi River in the mid-eighteenth century. Theodore Roosevelt, in his essay “In the Louisiana Canebrakes” indicated that prior to his 1907 Louisiana bear hunt, bears had been plentiful along the river bottoms of the region (Schullery 1997). Over-exploitation and loss of habitat greatly reduced Louisiana black bear abundance and distribution (Neal 1992). In 2007, biologists from Louisiana, Mississippi, and Texas estimated that 450–600, 60–70, and <150 bears existed in each of these respective states (Davidson 2008, Garner 2008, Young 2008). However, the reported estimates for Mississippi and Texas include black bear subspecies other than the Louisiana black bear.

Within Louisiana, there are 3 distinct subpopulations of the Louisiana black bear. One subpopulation, generally considered to be the most abundant (M. Davidson, Louisiana Department of Wildlife and Fisheries, personal communication), is located within the Tensas

River Basin in northeast Louisiana. The remaining 2 subpopulations are located within the upper and lower Atchafalaya River Basin, respectively. The populations are commonly referred to as the Tensas population, the Pointe Coupee population (named for Pointe Coupee Parish), and the Coastal population (named for its proximity to the Gulf Coast of Louisiana).

Justification

In 1992, citing dwindling numbers and loss of habitat, the U. S. Fish and Wildlife Service (USFWS) granted the Louisiana black bear a status of ‘threatened’ under the rules set forth by the Endangered Species Act of 1973 (Neal 1992). Charged with the conservation and recovery of threatened and endangered species, the USFWS drafted the Louisiana Black Bear Recovery Plan (USFWS 1995). The plan lists the following 4 actions needed for the recovery of the Louisiana black bear:

- 1) restoration and protection of bear habitat,
- 2) information and education programs,
- 3) protection and management of bear populations, and
- 4) research on population viability and bear biology.

Furthermore, the Louisiana Black Bear Recovery Plan lists as the criteria for removing the bear from the list of federally threatened species:

- 1) 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 the habitat and interconnecting corridors that support each of the 2 viable subpopulations used as justification for delisting.

Beginning in the mid-1990s, several research projects were conducted to address the above actions. Three projects had the specific goal of establishing abundance estimates for the 3 subpopulations of the Louisiana black bear within Louisiana. Beausoleil (1999) used live-trapping and re-sighting via camera-traps to estimate abundance of bears in the Deltic Tracts. The Deltic Tracts are 4 small, isolated forest patches totaling about 2,675 ha in the northern Tensas River Basin. Beausoleil (1999) estimated 50 bears in that area. Boersen (2001) used capture-mark-recapture (CMR) to sample an additional 32,939 ha of bear habitat in the Tensas River Basin. He identified individual bears using microsatellite markers and derived an estimate of 119 animals using closed population mark-recapture models. Combined, Boersen (2001) and Beausoleil (1999) sampled 35,614 ha (86%) of approximately 41,000 ha of bear habitat in the Tensas River Basin. Using genetic sampling and mark-recapture models, Triant (2001) estimated 41 and 77 bears for the Pointe Coupee and Coastal populations, respectively.

These studies represented the first scientific efforts to estimate abundance of Louisiana black bear populations. Since that time, considerable improvements have been made in the methodology by which wildlife population abundance is estimated. For example, closed (Otis et al. 1978, Chao 1987, Chao 1989, Chao et al. 1992) and open population estimators (i.e., Jolly-Seber; Jolly 1965, Seber 1965) have been combined by the robust design model (Pollock 1982), which is a combination of closed and open models. The robust design is capable of estimating parameters that are not estimable with closed or Jolly-Seber models alone (Kendall et al. 1995). Improved methods of estimating capture heterogeneity also have been developed, such as inclusion of individual covariates (Huggins 1989) and finite mixtures (Pledger 2000). Lastly, estimation based on a single best model has been replaced by ranking models using information theory and multi-model inference (e.g., model averaging; Burnham and Anderson 2002).

Since the conclusion of the earlier projects, a number of factors have changed that could have influenced bear population dynamics at Tensas River Basin. Although hunting has been prohibited, the Tensas population was used as a source for a bear repatriation project that began March 2001. Between March 2001 and March 2008, 41 female bears and 89 cubs were removed from the Tensas River Basin and relocated to bear habitat between the Tensas River Basin and the area inhabited by the Pointe Coupee population (Benson 2005; M. Davidson, Louisiana Department of Wildlife and Fisheries, unpublished data). The habitat base has changed as well with the addition of substantial areas of early successional habitat in the Tensas River Basin due to federal Conservation Reserve (CRP) and Wetland Reserve Programs (WRP). To measure the effect of such impacts on the Tensas population and to make sound decisions regarding future bear conservation practices, up-to-date abundance estimates were needed.

Finally, recovery of the Louisiana black bear under the Endangered Species Act requires a demonstration of population viability for 2 of the 3 subpopulations. Population viability analysis (PVA) requires reliable estimates of population parameters such as abundance and apparent survival. This project was intended to establish baseline parameter estimates that could be used in PVA. Similar projects are currently being conducted for the Pointe Coupee and Coastal populations. Combined, these projects will document the conservation status of the Louisiana Black Bear and determine if the criteria for recovery have been met.

Objectives

My objectives were to estimate abundance (N), apparent survival (ϕ), density (D), and population growth (λ) of the Louisiana black bear subpopulation in the Tensas River Basin using genotypic identification of individual bears and robust design CMR techniques. To better estimate these parameters of interest, I also estimated the nuisance parameter capture probability

(p). A nuisance parameter is one which is not of direct interest but is integral in estimating parameters that are of interest. My goal was to estimate these parameters with a level of precision such that their coefficient of variation (CV) was $\leq 20\%$.

II. STUDY AREA

My study area was located on the western floodplain of the Mississippi River in the 620-km² Tensas River Basin in northeastern Louisiana (Fig. 2). The study area consisted of approximately 41,000 ha of bottomland hardwood forest adjacent to Tensas Bayou in East Carroll, Franklin, Madison, Richland, and Tensas parishes. I delineated an approximate study area based on the political boundaries encompassing the Tensas River National Wildlife Refuge (28,733 ha; TRNWR), Big Lake Wildlife Management Area (4,986 ha; Big Lake WMA), Buckhorn Wildlife Management Area (4,558 ha; Buckhorn WMA), and several small, privately owned forest tracts including the 4 Deltic Tracts: Blue Cat (525 ha), Wade Bayou (610 ha), Panther Lake (730 ha), and Brownie Woods (810 ha, Fig. 3). The study area was 5,386 ha larger than the combined area for which Beausoleil (1999) and Boersen (2001) derived population estimates.

My study area was irregular in shape and divided into several portions that were not conterminous. Big Lake WMA was directly adjacent to the southwest portion of TRNWR. Buckhorn WMA was approximately 3 km south of TRNWR and was separated from TRNWR and Big Lake WMA by a span of agricultural lands and Louisiana State Route 4, a 2-lane highway. The Deltic Tracts were approximately 3.5 km north of the northernmost tip of TRNWR and were separated from TRNWR by open agricultural land and Interstate 20, a 4-lane, divided highway. The 4 Deltic Tracts were separated from one another by distances ranging from 1.5 to 3.5 km. Despite its discontinuity and irregular shape, the study area encompassed almost all black bear habitat in the upper Tensas River Basin.

My study area was primarily comprised of bottomland hardwood forest interspersed by many lakes, bayous, and sloughs. Overstory species included willow oak (*Quercus phellos*),

water oak (*Q. nigra*), Nuttall oak (*Q. texana*), overcup oak (*Q. lyrata*), sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), American elm (*Ulmus americana*), sweet pecan (*Carya illinoensis*), water locust (*Gleditsia aquatica*), and baldcypress (*Taxodium distichum*). The understory was predominated by palmetto (*Sabal minor*), greenbrier (*Smilax* spp.) and poison ivy (*Toxicodendron radicans*). Dense thickets of giant switchcane (*Arundinaria gigantea*) were common along bayous and at forest edges. In areas where forest management practices had maintained a more open canopy and along road and trail edges, soft-mast species such as blackberry (*Rubus* spp.), American beautyberry (*Callicarpa americana*), and pokeberry (*Phytolacca americana*) were abundant.

The region supported a diverse and abundant community of >400 species of birds, fish, mammals, reptiles, and amphibians (USFWS 2010). Game species such as white-tailed deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*) were abundant. Waterfowl, mostly absent during the summer months, congregated by the thousands to winter on the natural water bodies of the region and the man-made impoundments managed for waterfowl hunting and as waterfowl rest areas. The Order Carnivora was well represented by coyotes (*Canis latrans*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and black bears, but mountain lions (*Puma concolor*) and red wolves (*Canis rufus*) had been extirpated. Feral hogs (*Sus scrofa*), considered absent from the region during the late-1900s, occurred within the study area.

Lands surrounding the study area were sparsely populated by humans and dominated by farmsteads, vast agricultural fields lightly interspersed by wooded bayous, and small woodlots managed for timber harvest and sport hunting. The nearest human population centers were Tallulah (10 km, population 9,189) and Delhi (8 km, population 3,066) in Louisiana and

Vicksburg (30 km, population 26,407) in Mississippi (U.S. Census Bureau 2002). Crops included corn, soybeans, cotton, rice, and sorghum.

The topography of the Tensas River Basin is flat to slightly undulating with 0–8% slopes and a mean elevation of 26 m above National Geodetic Vertical Datum (USGS 1995). The channel slope of the Tensas River at Tendal, Louisiana (Latitude 32° 25' N, Longitude 91° 22' W) is 0.2 m/km (USGS 1995). Soils are mostly of the Tensas-, Sharkey-, or Alligator-Series, alluvial in nature, and poorly drained but highly fertile (USDA 1968).

Summers in the Tensas River Basin are hot and humid. Late-afternoon thunder storms are not uncommon. Winters are cool and rainy. The average monthly high and low temperatures recorded at Tallulah (Latitude 32° 24' N, Longitude 91° 11' W) during January 2006–December 2008 were 24°C and 12°C, respectively (NOAA 2009). During the same 3- year period, there were 226 days during which the high temperature was $\geq 32^{\circ}\text{C}$ and 113 days when the low temperature was $\leq 0^{\circ}\text{C}$. Annual precipitation averaged 137 cm (NOAA 2009).

III. METHODS

Robust Design Capture-mark-recapture

Wildlife science has a long history of needing, developing, and improving techniques to estimate animal abundance. One widely used method is CMR. Simply stated, animals from a population are sampled via capture (e.g., live-capture, sighting, collection of genetic material) and marked (e.g., ear-tags, genetic identification) for future identification. The proportion of the population captured in the first sample is:

$$\frac{n_1}{N},$$

where n_1 is the number of sampled animals and N is the entire population. A second sample is taken from the same population. The ratio of unmarked animals in the second sample (n_2) to marked animals in the second sample (m_2) is such that:

$$\frac{m_2}{n_2} \approx \frac{n_1}{N}.$$

Population abundance can then be estimated as:

$$N = \frac{n_1 n_2}{m_2}.$$

This is the Lincoln-Petersen estimator, the most basic model to estimate population abundance (Pollock 2000). Assumptions of this method are:

- 1) the population is closed to gains and losses,
- 2) all animals have an equal chance of being captured,
- 3) capture does not affect the probability of being recaptured, and
- 4) marks are not lost.

Because these assumptions are often violated, Otis et al. (1978) described models designed to account for several types of capture biases (M). For example, they describe models

whereby p could vary as a function of time (t), as a function of behavioral response to previous capture experience (b ; i.e., “trap-happy” or “trap-shy” behavior), or as a function of individual capture heterogeneity (h ; e.g., gender, reproductive status, innate differences between individual animals). These models were characterized as M_t , M_b , and M_h , along with the null model (M_0), whereby capture probabilities are equal for all individuals and across time. Combinations of different capture biases were also accommodated (i.e., M_{tb} , M_{th} , M_{bh} , and M_{tbh}). The various models were combined into the software program CAPTURE along with a model selection routine and goodness-of-fit test (Rextad and Burnham 1992). However, appropriate estimators for 3 of the 8 models (M_{tb} , M_{th} , and M_{tbh}) were lacking at the time.

Estimators of N have also been developed for instances when the population may be open, either demographically (i.e., births, deaths) or geographically (i.e., immigration, emigration). The Jolly-Seber estimator (Jolly 1965, Seber 1965) can provide estimates of N when the closure assumption is violated if sampling occurs during ≥ 3 intervals. The Jolly-Seber estimator also provides estimates of apparent survival (ϕ ; i.e., the proportion of animals that survive and do not emigrate) and number of births (B). However, if capture probability biases are not accounted for estimates of N will be biased and lack precision (Carothers 1973, Gilbert 1973).

Pollock (1982) introduced the robust design, a combination of open and closed models. The robust design involves sampling during primary and secondary periods, whereby the population is closed during secondary sampling and open during primary sampling. For example, a population could be sampled during a series of short secondary sampling periods when geographic and demographic closure can be assumed. These secondary periods would constitute 1 primary sampling period. This sampling scheme would then be repeated at a later

time, after a presumed population change due to births, mortalities, ingress, or egress. If this scenario occurs over ≥ 3 primary sampling periods the robust design can be used, whereby N is estimated for each of the secondary sampling periods when closure is assumed, and ϕ and other parameters associated with population change can be estimated for the primary sampling periods. Thus, the robust design combines the best attributes of open and closed models, enabling researchers to estimate parameters associated with population change (e.g., ϕ) and accounting for capture effects that could bias estimates of N . At the time of Pollock's introduction of the robust design, the method was an ad hoc procedure and all parameters of interest were not estimable in a maximum likelihood. Simultaneous estimation of all parameters within a maximum likelihood framework is now possible, which provides more flexibility and precision (Kendall et al. 1995). The ability to account for capture heterogeneity with covariates (Huggins 1989, 1991) and finite mixtures (Pledger 2000) has greatly improved estimator reliability. Finally, robust design models can be used to estimate additional parameters compared with previous techniques, such as temporary emigration (γ'' and γ' , Kendall et al. 1997), population growth (λ), and recruitment between primary sampling periods (Pradel 1996).

CMR experiments involving wildlife species have been revolutionized by at least 2 developments in the field of genetics. First, identification of individuals is now possible based on patterns of allelic variation at individual microsatellite loci (Mills et al. 2000, McKelvey and Schwartz 2004). Second, polymerase chain reaction (PCR) allow genetic analysis to be conducted on samples containing small amounts of DNA, as is often the case with non-invasively collected hair samples (Goossens et al. 1998, Taberlet et al. 1996). Consequently, modern genetic methodology has enabled researchers to reliably identify individual animals based on non-invasively collected biological samples containing miniscule amounts of DNA.

I established a robust design sampling framework based on a series of secondary sampling periods during 3 consecutive summers (primary sampling period). For each secondary sampling period, I assumed the population to be demographically and geographically closed. For the primary sampling periods, I assumed the population was open. The closure assumption during summer sampling was reasonable because black bears have relatively low rates of mortality and are parturient during one specific time of year (i.e., January-February). Also, I sampled virtually all the forested habitat in the vicinity of my study area so I considered permanent ingress and egress to be minimal. I conducted 8 secondary sampling periods within each of 3 primary sampling periods and used likelihood-based robust design methods to estimate N , ϕ , γ' , γ'' , p , and the probability of recapture (c).

I used an information-theoretic approach for this study. I used a priori and post-hoc considerations in developing a set of candidate models that included parameters of interest as well as nuisance parameters. I compared and ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c , Burnham and Anderson 2002). I used the rank of a given model within the set of candidate models and the difference between a given model's AIC_c score and the AIC_c score of other models in the candidate set (ΔAIC_c) as a gauge of support. Likewise, I compared variations of a particular parameter across models to test the importance of parameters. I thereby tested:

- 1) whether ϕ varied by gender and time (i.e., year),
- 2) whether p varied by gender and time (i.e., year and week),
- 3) whether bears exhibited temporary emigration or if emigration was random, and
- 4) whether bears exhibited a behavioral response to capture and, if so, if the response was positive (i.e., trap-happy) or negative (i.e., trap-shy).

Hair Sampling

Hair snare placement.—Simple random sampling is not required for mark-recapture and in some cases can be detrimental to success (Williams et al. 2002). A completely random approach is not as important as ensuring that all individuals have a non-zero chance of being captured (i.e., detected). White et al. (1982) recommended a systematic layout to ensure equal spacing between traps. Otis et al. (1978) suggested a sampling intensity of 4 traps per home range. Based on the estimated size of a solitary female bear's summer home range in habitat similar to that of my study area (10 km²; Smith and Pelton 1990), I established a sampling grid with a cell size of 1.6 km × 1.6 km. I used a Geographic Information System (GIS) to overlay a grid with cell sizes of 2.6 km² on a map of the study area (Fig. 4). I placed one hair snare per sampling grid cell and attempted to maintain spacing between snares. Thus, I achieved a site density of 3.8 hair snares per solitary-female home range.

I maintained initial site locations throughout both primary and secondary sampling periods except in instances when a site was destroyed by falling trees, logging equipment, or flooding. In those instances, I constructed new hair snares <200 m from the original site. Ten hair snares were relocated (173 –3,022 m) between primary sampling periods to improve sampling coverage of the study area.

Sample collection.—I collected bear hair samples using barbed-wire hair snares similar to those first described by Woods et al. (1999). I constructed hair snares using 15.5-gauge, high-tensile barbed wire with 4 prongs per barb and barb spacing of 12.7 cm (Goucho[®], Bekaert Corporation, Marietta, Georgia, USA). A single strand of wire was stretched around 3 to 5 tree trunks so that the wire between trees was about 2 to 3 m in length and 50 cm from the ground. I secured the wire in place on the tree trunk with galvanized fencing staples and used heavy-duty

nylon cable ties (U-LINE[®], Waukegan, Illinois, USA) stretched across the corners to maintain wire tension.

I baited each site with about 100 g of bakery sweets (e.g., donuts, cookies, fruit pies) and a small cotton cloth soaked with liquid artificial raspberry, honey, sassafras, or anise flavor concentrate (Mother Murphy's[®] Greensboro, NC). Bait was contained in a small biodegradable bag (BioBag[®], BIOgroupUSA Inc., Palm Harbor, Florida, USA) and suspended from a string and centered within the perimeter wire such that bears could not obtain the bait without entering the enclosure. Height of the bait was approximately 150 cm, which prevented access by non-target animals (e.g., raccoons and opossums [*Didelphis virginianus*]).

I visited each site at intervals of approximately 7 days. I inspected each site for evidence of animal visitation (e.g., tracks, scat, missing bait) and each barb on the perimeter wire for presence of hair. Bear hair was collected from any barb that contained ≥ 5 hairs, with each barb representing an individual sample. I removed hairs from barbs using metal tweezers and placed the sample into pre-labeled #2 coin envelopes. A flame was passed across the tweezers to prevent cross-contamination of samples. Once all samples were collected, I passed a flame over the entire perimeter wire to remove any uncollected hair or other debris. I replaced baits and added additional scent attractant to the cotton cloth. I cataloged all sample envelopes and placed them in a sealed container with a small amount of #8 color-indicating desiccant (W. A. Hammond, DRIERITE Co. LTD, Xenia, Ohio, USA).

Subsampling.—Analysis of all collected hair samples was cost prohibitive and would likely have resulted in needless repeated recaptures of the same bear at the same hair snares each week, because bears often leave >1 sample when visiting a site (Tredick et al. 2007). Therefore, I randomly selected 25 hair snares from all the hair snares that produced a collectable hair sample

during a secondary sampling period, and analyzed 1 hair sample from each of these 25 hair snares. Hair snares that failed to produce an adequate sample for DNA extraction (i.e., ≥ 1 guard hair root or ≥ 5 undercoat hairs) were replaced by the next available site from a randomized list of hair snares.

Microsatellite Analysis

Microsatellite analysis was performed by Wildlife Genetics International (WGI, Nelson, British Columbia, Canada). The number of loci needed to distinguish between individual animals within a population varies based on the variability or heterozygosity of the individual loci. Therefore, an initial group of randomly selected samples was analyzed at 22 loci (A06, CPH9, CXX110, CXX20, G10B, G10C, G10H, G10J, G10L, G10M, G10P, G10U, G10X, G1D, GA1, MSUT2, MU23, MU26, MU50, MU51, MU59, and P07; Paetkau and Strobeck 1994, Paetkau et al. 1995, Taberlet et al. 1997, Kitahara et al. 2000, Breen et al. 2001) to select optimal markers. A suite of 7 loci that demonstrated the greatest allelic variability, thereby maximizing individual identification within the Tensas Population, was used to generate individual genotypes (G10M, G10P, G1D, MSUT2, MU23, MU26, and MU50). A region of the Amelogenin gene was used to determine gender (Ennis and Gallagher 1994).

Calculated from allelic frequencies at specific loci, heterozygosity is an indicator of how closely individuals within a population are related and provides the basis for a number of assumptions that must be met for reliable identification of individuals using microsatellites. For example, observed heterozygosity (H_O) can be compared with expected heterozygosity (H_E), the expected allelic frequencies of a population under Hardy-Weinberg equilibrium. The principle of Hardy-Weinberg equilibrium is based on the assumption that the population is large, mating is random, and that there is no selection, mutation, or migration (Wessells and Hopson 1988).

When these assumptions are met, allele frequencies reach equilibrium and remain constant across generations (Weir 1990, Connor and Hartl 2004). Thus, the equation

$$p^2 + 2pq + q^2 = 1$$

predicts the expected number of genotypes where p is the frequency of the dominant allele and q is the frequency of the recessive allele (Lowe et al. 2004). I used the Microsoft Excel extension GenAlEx 6.1 (Peakall and Smouse 2006) to test for conformation to Hardy-Weinberg equilibrium.

Another assumption for capture-mark-recapture is that individuals are uniquely marked; that assumption can be violated when ≥ 2 individuals share the same genotype at examined loci. This is referred to as the shadow effect, and can negatively bias estimates of population abundance (Mills et al. 2000). Shadow effects occur when too few loci or loci with low heterozygosity are selected (McKelvey and Schwartz 2004). I calculated the probability of identity statistic (PI) as a metric of how well a molecular marker distinguished between individuals. It measures the frequency at which 2 unrelated individuals from a population would be expected to have the same genotype at multiple loci (Paetkau and Strobeck 1998). The PI for a single locus with multiple alleles is calculated as:

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

where p_i and p_j are the frequencies of the i th and j th alleles, assuming the allele genotypes are in Hardy-Weinberg proportions (Taberlet and Luikart 1999). Overall PI (PI_{overall}) for multiple loci can be calculated by multiplying probabilities across loci:

$$PI_{\text{overall}} = \prod (PI_{\text{single locus}}).$$

PI_{overall} values are valid if the loci are independent and are biased low if they are not (Mills et al. 2000). Multi-locus genotypes within small isolated populations may not be independent due to

shared ancestry within families (Taberlet and Luikart 1999). Therefore, I used the probability of identity between siblings (PI_{sibs}) as a conservative upper bound of the statistical probability of observing identical genotypes based on the sampled loci (Waits et al. 2001). The probability of identity between siblings is calculated as:

$$PI_{sibs} = 0.25 + (0.5 \sum p_i^2) + [0.5 (\sum p_i^2)^2] - (0.25 \sum p_i^4),$$

where p_i is the frequency of the i th allele (Taberlet and Luikart 1999).

Genotyping errors can also result from sampling and in the laboratory and translate into individuals being misidentified with concomitant biases in abundance estimates (McKelvey and Schwartz 2004). Genotyping errors include allelic dropout and false alleles (Taberlet and Luikart 1999, McKelvey and Schwartz 2004). Follicles from non-invasively collected hair may contain variable amounts of template DNA, possibly resulting in the amplification of only 1 of 2 alleles in a heterozygote pair producing a false homozygote (McKelvey and Schwartz 2004). These false alleles are artifacts of the amplification process and can be misinterpreted as true alleles and appear as a capture of a new individual (Taberlet and Luikart 1999, McKelvey and Schwartz 2004). Genotyping errors can be reduced with appropriate laboratory and sampling techniques. For example, by only collecting samples containing ≥ 5 hairs (i.e., more available template DNA) the success rate of DNA extraction and amplification will be elevated (Goossens et al. 1998). Using the optimal number of microsatellite markers can also reduce genotyping error (e.g., my loci selection as described above; Paetkau and Strobeck 1994, Thompson 2003). Another method used by WGI to reduce the potential of genotyping errors is the selective reanalysis of mismatched genotypes (Paetkau 2004). Selective reanalysis was performed on genotypes which differed by ≤ 3 loci. The mismatched loci within these genotypes were scrutinized for evidence of allelic dropout or other genotyping errors.

Parameter Estimation

I created encounter histories for each identified bear and analyzed those histories as a robust design data type in Program MARK (White and Burnham 1999). I used the Huggins full heterogeneity model, which can incorporate individual and group covariates (Huggins 1989, 1991) and finite mixtures (Pledger 2000). Parameters directly estimated by the model were apparent survival (ϕ), temporary emigration parameters (γ' , γ''), the probability of belonging to 1 of 2 finite mixtures (π) with different capture probabilities, probability of capture (p), and probability of recapture (c). Population abundance (N) is conditioned out of the likelihood of Huggins models and is a derived parameter (Huggins 1989, 1991).

I developed a series of a priori models and fit them to the capture data. I considered models where ϕ was held constant (i.e., time and gender invariant) or varied by gender. I did not include models whereby ϕ varied by year. Bears are long lived and typically have high rates of survival. There were no events (e.g., severe weather events, extreme food shortages) that would have drastically altered annual survival during this study.

In the context of robust design CMR, temporary emigration (γ) is the probability that an animal is temporarily unavailable for capture during ≥ 1 of the primary sampling occasions. Permanent emigration is not estimable except as a component of ϕ . Kendall et al. (1995, 1997) extended the definition by introducing γ'' , which is the probability of an animal being unavailable for sampling during a primary sampling period provided it was available at a previous period and γ' which is the probability that, once an individual is unavailable, it remains unavailable during the following period. I developed and compared models based on random temporary emigration ($\gamma' = \gamma''$) and on no temporary emigration ($\gamma' = \gamma'' = 0$; Kendall et al. 1995, 1997). I developed random emigration models whereby γ'' was constant, varied by gender, or varied by gender and

time. Likewise, γ' was modeled as constant or varied by gender; γ' could not vary by time because there was only 1 emigration time step in this 3-year study.

I modeled capture probability (p) as a constant or allowed it to vary by gender, year or gender $\times$ year interaction. I also created an individual covariate (*CapFreq*) to estimate capture heterogeneity of p and used the Huggins (1989, 1991) estimator to incorporate that effect. Covariate *CapFreq* was the frequency at which a bear was captured in a previous primary period (Fletcher 1994 as cited by Williams et al. 2002). Individuals with a greater propensity for being captured presumably would have a greater frequency of captures in the previous year. When animals are not captured during a previous year, interpretation depends on whether or not the population exhibits temporary emigration. If the population is geographically closed, animals with a *CapFreq* value of 0 are considered available for capture but not detected. If the population is not geographically closed, an animal with a *CapFreq* value of 0 could be absent from the sampling grid or present but not detected; the mean capture frequency should be used in such instances (Williams et al. 2002). I used a covariate value of 0 for bears not captured in the previous year. I also created a temporal group covariate, *JDate*, which was the Julian date of the onset of sampling for the 3 primary sample periods. The onset of sampling grew progressively earlier each primary period and by doing so, the temporal relationship between the sampling period and annual biological events (e.g., mating season, availability of agricultural crops for protective cover and food) was altered. I fit models with and without covariate *JDate* to determine what effect the staggered sampling schedule had on p , and I also included models with gender interactions (e.g., *CapFreq** g , *JDate** g). Similarly, I included models where the covariate *CapFreq* was applied to only one gender.

I created models where p was estimated for 2 finite mixtures within genders, either expressed as a function of gender, or gender and time. After initial analyses, I made the post-hoc decision to model π as a function of time for females only while allowing the male π to remain constant across primary periods. I also included models where π was fixed at 1 for females in the third primary period (i.e., no mixture). These decisions were based on patterns seen in preliminary results.

Lastly, I modeled recapture probabilities (c) as being equal to p (i.e., no behavioral response) or additive to p (i.e., evidence of a behavioral response). The numeric sign of the parameter's beta value (β) indicates if the effect was positive or negative. Because I used baits at the hair snares, albeit small amounts, I expected a positive response to capture. However, preliminary analyses indicated extreme differences in capture probabilities of males and females. I therefore made the post-hoc decision to include models containing a behavioral effect for females only (*Behavior-F*) and a behavior $\times$ gender interaction (*Behavior * g*).

I ranked candidate models using Akaike's Information Criterion with a second-order correction for small sample size (AIC_c), with the most parsimonious model having the lowest AIC_c score. The difference between the top model and other models in the candidate set (ΔAIC_c) provides a relative measure of empirical support for a given model. Models with $\Delta AIC_c \leq 2$ are considered to be well supported whereas models with $\Delta AIC_c > 10$ have almost no support (Burnham and Anderson 2002). Another measure of model support is model weight (w_i). Model weight represents the evidence for a given model being the best model compared with all models in the candidate set, based on the assumption that the best model is included. Model weights were calculated as:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)}$$

where R is the number of models in the candidate set and r is the first model in the summation (Burnham and Anderson 2002). To account for model selection uncertainty, I used model averaging to derive final parameter estimates:

$$\hat{\theta} = \sum_{i=1}^R w_i \hat{\theta}_i$$

where $\hat{\theta}$ denotes a model averaged estimate of a given parameter with unconditional variance:

$$\widehat{\text{var}}(\hat{\theta}) = \left[\sum_{i=1}^R w_i \sqrt{\widehat{\text{var}}(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \theta)^2} \right]^2$$

(Burnham and Anderson 2002).

I calculated asymmetrical log-based 95% confidence intervals (CI) for N , based on the minimum population size (M_{t+1}) as:

$$[M_{t+1} + (\hat{f}_0/C) \cdot M_{t+1} + (\hat{f}_0 \cdot C)]$$

where

$$\hat{f}_0 = \hat{N} - M_{t+1} \text{ and}$$

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

(White et al. 2001). I used the annual estimates of N to calculate estimates of population growth (λ) and density (D). I calculated population growth rate as:

$$\lambda = \frac{N_{t+1}}{N_t},$$

where N_t is the abundance estimate for a given primary period and N_{t+1} is the abundance estimate for the subsequent primary period. I calculated population density as:

$$D = \frac{N}{A},$$

where N is the abundance estimate for a given primary period and A is the effective sampling area. I determined A using the buffer strip method (Dice 1938). I circumscribed each hair snare with a radius equal to the radius of an average summer home range of female bears without cubs <1 year old (Benson 2005). Land within the boundary created by the outermost extent of these overlapping circles was the effective sampling area (Fig. 8). However, not all lands within this boundary represented bear habitat so I used land-cover data to only include lands classified as forest (U.S. Geological Survey 2001). Calculating λ and D and computations involving other parameter estimates (e.g., N and p) involve combining estimates with differing and sometimes related variances (i.e., covariance). To appropriately represent the error of such estimates, I used the delta method (Powell 2007).

IV. RESULTS

Hair Sampling

I conducted hair sampling from early July to mid-September in 2006, from mid-June to mid-August in 2007, and from early June to early August in 2008 (Fig. 5). I sampled for 10 weeks during year 1 of my study because I did not know what sample sizes to expect. After I determined that the number of hair samples was adequate, I sampled for 8 weeks the following 2 years. I operated 209 hair snares for 22 of the 26 secondary sampling periods; there were 207 hair snares during the first 3 secondary periods of 2006 and 206 hair snares during the first secondary period of 2008. The mean distance between hair snares was 1,230 m (SD = 28.9). I visited hair snares at intervals of 5 to 9 days (mode = 7 days).

I collected 4,451 hair samples across all sampling periods. The mean number of samples per secondary period was 171 (SD = 80.0, range = 98–324; Fig. 6). The mean number of hair snares per secondary sampling period with hair samples was 77 (SD = 27.8, range = 35–126). Overall, 201 of the 209 hair snares produced ≥ 1 sample. The 8 hair snares that never produced a sample were located in the southern portion of the study area, of which 5 were on Buckhorn WMA. The mean number of samples collected per site was 2.2 (SD = 1.7, range = 1–30, mode = 1).

Microsatellite Analysis

I excluded all samples collected in the last 2 secondary periods of 2006 from microsatellite analysis to maintain 8 secondary periods per primary period. Many selected samples did not meet the minimum criteria of 1 guard hair root or 5 undercoat hairs, and samples from 30–40 hair snares typically were required to produce the desired 25 samples per secondary period (D. Paetkau, WGI, personal communication). Once extracted, if a sample failed to

amplify or otherwise did not result in an adequate genotype, it was not replaced with another sample. The genotyping success rate was 89.5% (D. Paetkau, WGI, personal communication).

Marker selection.—The first 29 samples selected were genotyped based on 22 loci (Table 1). Marker MU51 appeared to be fixed at 1 allele in 17 samples, failed in 3 others, and was removed from consideration. The 22-locus suite had an average of 3.31 (SD = 0.3, range 1–5) alleles per locus and a mean observed heterozygosity (H_O) of 0.47 (SE = 0.04). Based on the number of alleles per locus and the maximum allele frequencies, 7 of the 21 loci were selected to be used for the remainder of the genotyping procedures. The 7-locus suite had an average of 4.9 (SD = 0.5) alleles per locus and an H_O of 0.66 (SE = 0.03).

After initial microsatellite analysis of 600 samples (i.e., 25 samples $\times$ 8 secondary periods $\times$ 3 primary periods), there was an unexpected number of individuals only captured once and relatively few males had been captured. Preliminary CMR analysis revealed capture probabilities <0.2 with males having lower capture probabilities than females. To increase p , I submitted 154 samples from previously unselected hair snares from the first 8 secondary periods of 2006 to WGI for analysis. Of those 154 samples, 134 were successfully genotyped. The additional samples were pooled with previous samples to construct capture histories.

Microsatellite analysis of the first sample set resulted in 8-locus genotypes (including the Amelogenin gender locus) of 181 individuals (male 74: female 107). Analysis of the second sample added 15 males and 6 females for a total of 202 bears (89 male: 113 female). Overall, there were 675 captures of 202 individuals. The average number of captures per individual was 1.9 (SD = 1.76) and 4.4 (SD = 3.8) for males and females, respectively. Bears captured ≤ 2 times ($n = 120$) were 58% males whereas bears captured >10 times ($n = 9$) were all females; 2 females were captured 18 times each. The mean distance between captures was 4,898 m (SD = 611 m)

for males and 1,593 m (SD = 102 m) for females. The mean proportion of recaptures involving a bear revisiting a hair snare where it had been previously captured was 0.04 (SD = 0.05) and 0.29 (SD = 0.03) for males and females, respectively.

Probability of Identity.—The probability of identity for the 7-locus suite plus the Amelogenin gender locus was 1.7×10^{-6} , equating to an almost 1 in 600,000 chance of encountering 2 individuals from the Tensas population with the identical allelic pattern at the 8 loci. The sibling probability of identity was 3.0×10^{-3} or a 1 in 335 chance of encountering 2 related individuals with the same 8-locus genotype.

Parameter Estimation

Model Comparison.—Seventeen of the 28 models (Models 12–28) in the candidate set were not supported, with model weights of 0 and ΔAIC_c values > 20 (Table 2). The most supported model (Model 1) had almost half the total weight for the model set ($w_1 = 0.49$) and the 5 highest ranked models (Models 1–5) accounted for almost all model weight ($\sum w_1-w_5 = 0.98$).

Supported models (Models 1–11) included constant ϕ (i.e., time and gender invariant apparent survival), no temporary emigration ($\gamma'' = \gamma' = 0$), and p varying by gender and by 2 finite mixtures within each gender. The proportion of animals in each of the finite mixtures varied by gender and in 10 of the 11 weighted models (Models 1–10) π varied by primary period for females while remaining constant across years for males. The single model in which π varied across years for males was the lowest supported model (Model 11) and received almost no weight ($w = < 0.01$) and a ΔAIC_c of 17.71.

All weighted models (Models 1–11) included a behavioral effect (i.e., $c \neq p$) for females only (*Behavior-F*), for both genders (*Behavior*), or as a behavioral effect by gender interaction (*Behavior*g*). The highest-ranked model (Model 1) included a behavioral effect for females

(*Behavior-F*) and indicated a significant positive behavioral response for females ($\beta = 0.98$, 95% CI = 0.59–1.38). Individual covariate *CapFreq* was well supported and appeared in the 7 highest-ranked models either on its own, as part of a gender interaction (*CapFreq*g*), for males only (*CapFreq-M*), or for females only (*CapFreq-F*). *CapFreq* was a good predictor of capture probability ($\beta = 3.59$, 95% CI = 0.91 – 6.27) for the highest ranked model. Inclusion of the *CapFreq*g* interaction term in the highest-ranked model was also supported ($\Delta\text{AIC}_c = 1.38$). The covariate *JDate* was not supported in any of the models ($w < 0.002$, $\Delta\text{AIC}_c = 11.3$) nor were models with different capture probabilities in the first primary period compared with the other 2 primary periods.

Parameter Estimates.—Model-averaged estimates of apparent survival for males and females across both survival periods was 0.91 (SE = 0.08). The proportion of male bears in the first capture heterogeneity mixture was 0.87 (SE = 0.06) and remained constant across primary periods (Table 3). The proportion of female bears in the first mixture increased across primary periods ($\pi = 0.82$ [SE = 0.06], 0.94 [SE = 0.03], and >0.99 [SE < 0.01] for 2006, 2007, and 2008, respectively). The mean weekly capture probabilities across all 24 secondary periods for both mixtures was 0.05 (SE = 0.01) for males and 0.10 (SE = 0.01) for females. Respective annual estimates of *N* for 2006–2008 were 198 (SE = 59), 116 (SE = 34), and 185 (SE = 51) for males, and 143 (SE = 22), 106 (SE = 17), and 133 (SE = 23) for females (Fig. 7). Combining estimates for males and females and averaging across primary periods, *N* was 294 (SE = 31). The overall density estimate was 0.66 bears/km² (SE = 0.07) based on an effective sampling area of 44,300 ha. Population growth varied by annual interval and gender. The pooled growth rate for both genders and annual intervals was 1.04% (SE = 0.18).

V. DISCUSSION

My estimate of apparent survival ($\phi = 0.91$) is plausible given that black bears in the Tensas River Basin are not hunted, are protected by the Endangered Species Act, reside primarily on public lands managed for wildlife. Clark et al. (2010) reported that bears on the Lower White River in Arkansas, prior to establishment of a bear hunting season and initiation of a repatriation project that removed females with cubs from the population, had similarly high apparent survival. My analysis also showed exclusive support for models with no temporary emigration. Given the discrete nature of the bear habitat where my study took place it is also reasonable to expect very limited temporary emigration. Consequently, permanent emigration is probably also low which helps explain my high estimate of ϕ .

Direct comparison of my abundance estimate ($N = 294$) and those of Boersen (2001; $N = 119$) and Beausoleil (1999; $N = 50$) is difficult. First, the area sampled by Boersen (2001) and Beausoleil (1999), differs from the area that I sampled and populations exposed to sampling also may have differed. Additionally, CMR models available at the time of Boersen (2001) and Beausoleil (1999) could not account for capture heterogeneity as well as the CMR models I used. Unaccounted-for capture heterogeneity causes negative bias (Pollock et al. 1990); thus, their abundance estimates are potentially biased low. Regardless of these issues, the increase in abundance is too high to be due only to unaccounted biases in the previous studies. Therefore, I conclude that the population of bears in the Tensas River Basin has increased in abundance since 1997–1999.

The density estimate I report (0.66 bears/km^2) is in the upper-range for reported densities of black bear populations in the southeastern US (Table 4). However, there is variability among these estimates due to the different estimation methods used. The estimate of Boersen (2001) is

most comparable to the estimate of this study. Boersen (2001) used the same methods I used for estimating density and his study area is roughly 75% of my study area. Beausoleil (1999) reported an extreme density of 1.43 bears/ km² in the Tensas River Basin. The area for which Beausoleil (1999) estimated density (i.e., the Deltic Tracts) is only 6% of my study area.

Estimation of population abundance and other demographic parameters is an ever-evolving process. The earliest methods relied on assumptions that often were violated for wildlife populations. For example, I was able to reduce much of the concern regarding population closure with the robust design. My abundance estimates were based on data collected during time periods when demographic gains and losses were unlikely (i.e., secondary periods). By making a concerted effort to sample from almost all available bear habitat in the Tensas River Basin, I was able to approximate geographic closure as well. Furthermore, I was able to estimate apparent survival across primary periods when the population is expected to be open to gains and losses and documented and accounted for temporary emigration (Nichols and Pollock 1990).

Despite the strengths of the methods I used, there are limitations. For example, capture probabilities must be sufficient to reliably estimate capture biases. Boulanger et al. (2004) recommended capture probabilities ≥ 0.2 to estimate capture heterogeneity for bears. My capture probabilities were lower than this recommendation, particularly for males (mean $p = 0.05$). Possible reasons for those low probabilities include sparse trap layout relative to the number of bears being sampled, avoidance of sampling hair snares by bears, ineffective bait, poor hair-collection technique, poor genotyping technique, or insufficient subsampling. To ensure that all bears in the Tensas River Basin bear population had a chance of being captured, I placed hair snares so that females had multiple opportunities for capture. Male bears had the opportunity to encounter even more hair snares due to their larger home range. Given that capture probabilities

were much lower for males than females, it seems unlikely that site availability was an issue. Likewise, genotyping success was high ($\approx 90\%$) which suggests that laboratory protocols were adequate. I collected more hair samples than I analyzed, which suggests that the design of the hair snares and bait was adequate. Subsampling may have affected my capture probabilities. However, increasing the number of samples during 2006 only marginally increased capture probabilities for females (0.223 to 0.295) and the increase was even less so for males (0.102 to 0.122) based on a non-mixture model with no differences in apparent survival by sex.

Those modest increases in capture probabilities, especially for males, could have been the result of a behavioral avoidance of traps after initial capture as the additional genotypes were mostly comprised of new animals that were only capture once. However, avoidance of the barbed wire after initial capture is also a possibility. In 2008, I used a remote digital camera (Cuddeback[®], Non Typical Inc., Green Bay, Wisconsin, USA) to document bear activity at some hair snares. I obtained 24 videos and still photos of bears of both genders and various sizes ranging from a cub to large, adult males (as determined by evidence of male genitalia). Of the roughly 20 cases when I could demonstrate that a bear had visited a site and crossed the barbed wire, only 2 resulted in a collectable sample. On 5 occasions I obtained video of large male bears stepping on or over the barbed wire. This could have resulted in a behavioral effect if this tendency increased after initial capture. A posteriori analysis revealed a negative, additive behavioral effect for males, although the slope did not statistically differ from zero ($\beta = -0.20$, 95% CI = -0.93–0.53). Finally, capture heterogeneity among males may have been caused by large males in the Tensas River Basin losing fur along their underside and hind quarters during summer, sometimes to the point of near baldness. In all cases in which I obtained video of large male bears entering a hair snare, the bears crossed over the barbed wire exposing their abdomen

and lower rear legs to the barbs. Such baldness could have reduced the capture probability of those individuals. Moreover, any samples from these male bears may have been comprised of fewer hairs or underfur so my field protocol for culling samples and the laboratory's protocol for sample selection could have exacerbated this type of heterogeneity.

Another segment of the population that may have been less available for capture was family groups consisting of mothers with cubs. The timing of my primary periods coincided with the period during which cubs were limited in their ability to travel. These family groups likely were restricted to a fewer number of hair snares than other bears in the population. Furthermore, based on video I collected of a cub walking under the barbed wire without making contact, the height of the barbed wire probably excluded cubs from capture. Consequently, my annual abundance estimates are valid only for the population of bears >1 year old.

Continued CMR sampling in the Tensas River Basin should concentrate on improving precision of male estimates by decreasing potential capture heterogeneity. One option is to redesign the hair collection snares to include a second perimeter wire. Lowering the existing strand of barbed-wire (e.g., 35–40 cm from the ground) and adding a second wire approximately 55–60 cm from the ground would likely force more bears of different sizes (e.g., yearlings, adult males) to contact at least one wire while entering or exiting the hair snares. For example, this method was effective in increasing the number of bear hair samples in a coastal South Carolina study (Drewry 2010).

In the presence of finite project funds, increasing the number of samples collected will increase the need for an appropriate subsampling strategy. For example, using a set proportion of samples rather than a number of samples per secondary period would be a more efficient way to allocate resources (Tredick et al. 2007). Evaluating the potential for gender bias in the

subsampling strategy I employed should also be considered. Whereas genotyping a multi-locus genotype with gender is expensive, determining gender of a sample is relatively inexpensive. Samples normally culled in the field (i.e., ≤ 5 hairs) and those culled in the lab (i.e., too little root material to ensure a reliable genotype) could be identified to the level of gender and used to determine if there is a significant gender bias in the sample culling criteria.

Another possibility to increase capture probabilities and further define capture heterogeneity is the addition of a second sampling method unrelated to hair snares. The secondary capture method does not have to be as intensive as the primary capture method and it can be biased as long as the bias is not the same as the bias of the primary capture method (K. Kendall, U.S. Geological Survey, personal communication). Boulanger et al. (2008) used hair collected from hair snares and from bear rub trees to estimate abundance of grizzly bears (*Ursus arctos*). Trees upon which bears had rubbed or marked were a common sight along roads and trails in my study area. It was also common to see utility poles and wooden sign posts that had been rubbed and bitten by bears. Karamanlidis et al. (2010) found power poles to be an effective source of brown bear (*Ursus arctos*) hair.

Another factor which could have contributed to capture heterogeneity was use of non-forested land adjacent to my sampling grid by males. Some tracts of land surrounding my study area were agricultural lands enrolled in the Wetlands Reserve Program (WRP), and were in the early stages of being reforested. Additionally, one of the primary crops grown on lands adjacent to my study area was corn, which is a potential food source and provides protective cover. Although males and females used WRP lands and corn fields, I suspect that males spend more time in corn fields. This was not a direct violation of the assumption of closure as these bears were still a part of the sampled population but it may have been a factor in lowering male capture

probabilities. Because capture probabilities for males were low, heterogeneity and other biases were probably poorly accounted for, as evidenced by the wide confidence intervals for abundance. In contrast, capture probabilities for females were higher and confidence intervals were narrower. I could not include additional samples from 2007 and 2008 but these additional data should yield more precise and accurate estimates of all parameters.

Estimating density can be challenging because it is difficult to measure the effective sampling area. A variety of methods have been proposed to alleviate this problem, from techniques for estimating boundary strip widths (Dice 1938), web-sampling designs (Anderson et al. 1983), to spatially explicit methods (Efford 2004). In contrast to the homogeneous habitats where those methods are usually applied, bear habitat in the Tensas River Basin largely consists of distinct forest tracts surrounded by agriculture or CRP or WRP land. Therefore, rather than relying on complex statistical techniques, I used the area of forested land cover to estimate density. Although agricultural and forest regeneration areas provide valuable bear habitat at certain times, I did not include those areas in my density estimates because bears are not commonly found there. Once those non-forested areas were eliminated, application of a boundary strip around the hair snares resulted in only a small addition to the effective sampling area.

VI. MANAGEMENT AND RESEARCH IMPLICATIONS

This study indicates that the Tensas River Basin bear population has increased in size and has extended its range since the late-1990s. Documentation of these increases, while important, is only a preliminary step in meeting the recovery criteria as listed in the Louisiana Black Bear Recovery Plan. To fully meet the recovery criteria it must be demonstrated that the Tensas River Basin bear population is viable and will be perpetuated into the future. A population viability analysis (PVA) is needed. The results of this study should be used as base values for a PVA.

Since the conclusion of my analysis, WGI has completed additional genotypic analysis of hair samples I collected in 2007 and 2008. The resulting genotypes and concomitant capture information should be pooled with the capture histories from this analysis. The resulting data should be analyzed with focus directed toward the effect the additional samples have on capture probability and parameter precision.

Finally, although population abundance is a parameter of popular interest, it is one of the most difficult population parameters to estimate and is not always necessary for effective population management. Estimating and monitoring population growth (λ) may suffice because that parameter is generally more robust to capture heterogeneity biases than population size (Schwarz 2001). Pradel (1996) and Schwarz and Arnason (1996) developed maximum likelihood methods for estimating population growth, apparent survival (ϕ), and recruitment (f) for open populations, which have since been added as modules in Program MARK (White and Burnham 1999). Given the robustness to heterogeneity, lower capture probabilities than those needed for estimating N might suffice. Thus, monitoring changes in λ over time may be a more cost effective method to monitor the status of this bear population.

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APPENDECIES

APPENDIX A: TABLES

Table 1. Number of alleles and heterozygosity of 22 loci evaluated for efficacy in distinguishing between individual Louisiana black bears from the Tensas River Basin, Louisiana, USA, 2006–2008.

Locus	n^a	A^b	A_e^c	H_o^d	H_e^e	UHe^f
MU23	202	5	2.99	0.59	0.67	0.67
MU50	202	6	2.76	0.60	0.64	0.64
G10M	202	3	2.60	0.63	0.61	0.62
MSUT2	202	4	2.96	0.63	0.66	0.66
G1D	202	4	2.63	0.64	0.62	0.62
G10P	202	6	3.15	0.75	0.68	0.68
MU26	202	6	4.55	0.79	0.78	0.78
G10X	93	3	2.18	0.60	0.54	0.54
A06	79	5	2.32	0.48	0.57	0.57
G10B	68	4	2.39	0.62	0.58	0.59
G10J	29	2	1.23	0.21	0.19	0.19
MU59	29	2	1.31	0.21	0.24	0.24
CXX110	29	3	1.43	0.24	0.30	0.30
G10U	29	2	1.27	0.24	0.21	0.22
CPH9	29	2	1.62	0.31	0.38	0.39
G1A	29	3	1.43	0.34	0.30	0.31
G10L	29	3	1.52	0.41	0.34	0.35
G10C	29	2	1.58	0.41	0.37	0.37
P07	29	2	1.86	0.45	0.46	0.47
G10H	29	2	1.86	0.52	0.46	0.47
CXX20	29	3	2.28	0.59	0.56	0.57
MU51	17	1	1.00	0.00	0.00	0.00

^a Number of bears identified using given locus.

^b Number of observed alleles.

^c Number of expected alleles.

^d Observed heterozygosity.

^e Expected heterozygosity.

^f Unbiased expected heterozygosity.

Table 2. Summary of model selection procedures based on second-order Akaike's Information Criteria (AIC_c) to determine the parameterization of Huggins full heterogeneity models to estimate Louisiana black bear population parameters in the Tensas River Basin, Louisiana, USA, 2006–2008. Apparent survival (ϕ) was modeled as constant ($\cdot$) or as a function of gender (g). Temporary emigration was modeled as a random ($\gamma'' = \gamma'$) or no-movement model ($\gamma'' = \gamma' = 0$). Temporary emigration under the random-movement model was modeled as a function of gender and time (t). The proportion of animals in 1 of 2 finite mixtures within genders (π) was modeled as a function of gender, time, time for females only (t -F), or fixed at 1 (last $\pi = 1$; i.e., no mixture). Capture probability (p) was modeled as a function of gender, time, finite mixtures within gender (mix), individual covariate *CapFreq*, a *CapFreq* gender interaction (*CapFreq* * g), *CapFreq* for females only (*CapFreq*-F), *CapFreq* for males only (*CapFreq*-M), group covariate *JDate*, a *JDate* gender interaction (*JDate* * g), or as a function of the first primary period differing from the second 2 primary periods (*FirstPP*). *CapFreq* was the frequency at which a bear was captured during a previous primary period. *JDate* was the Julian date of the onset of sampling each primary period. Probability of recapture was modeled as a behavioral effect (*Behavior*), a behavioral effect gender interaction (*Behavior* * g), a behavioral effect for females only (*Behavior*-F), or as no behavioral effect (*No Behavior*).

Model Number	Model	AIC_c	ΔAIC_c^a	w_i^b	K^c
1	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F}[\text{last } \pi = 1])$, $p(\text{mix}, g, \text{CapFreq}, \text{CapFreq} * g)$, <i>Behavior</i> -F }	2793.83	0.00	0.49	10
2	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F}[\text{last } \pi = 1])$, $p(\text{mix}, g, \text{CapFreq})$, <i>Behavior</i> -F }	2795.21	1.38	0.24	9
3	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F}[\text{last } \pi = 1])$, $p(\text{mix}, g, \text{CapFreq}, \text{CapFreq} * g)$, <i>Behavior</i> , <i>Behavior</i> * g }	2795.87	2.04	0.18	11
4	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F}[\text{last } \pi = 1])$, $p(\text{mix}, g, \text{CapFreq}, \text{CapFreq} * g)$, <i>Behavior</i> }	2798.49	4.66	0.05	10
5	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g, \text{CapFreq-M})$, <i>Behavior</i> }	2799.38	5.55	0.03	9
6	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g, \text{CapFreq})$, <i>Behavior</i> }	2801.65	7.82	0.01	9
7	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g, \text{CapFreq-F})$, <i>Behavior</i> }	2804.57	10.74	<0.01	9
8	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g, \text{JDate})$, <i>Behavior</i> }	2805.12	11.29	<0.01	9
9	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g, \text{JDate}, \text{JDate} * g)$, <i>Behavior</i> }	2805.16	11.33	<0.01	10
10	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t\text{-F})$, $p(\text{mix}, g+t)$, <i>Behavior</i> }	2807.02	13.18	<0.01	10
11	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g + t)$, $p(\text{mix}, g+t)$, <i>Behavior</i> }	2811.54	17.71	<0.01	11
12	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g)$, $p(\text{mix}, g)$, <i>Behavior</i> }	2821.68	27.85	0	7
13	{ $\phi(\cdot)$, $\gamma'' = \gamma' = 0$, $\pi(g)$, $p(\text{mix}, g+t)$, <i>Behavior</i> }	2822.44	28.61	0	9
14	{ $\phi(\cdot)$, $\gamma'' = \gamma'$, $\pi(g + t\text{-F})$, $p(\text{mix}, g)$, <i>Behavior</i> }	2822.64	28.81	0	8
15	{ $\phi(\cdot)$, $\gamma''(g + t) = \gamma'(g)$, $\pi(g)$, $p(\text{mix}, g, \text{FirstPP})$, <i>Behavior</i> }	2823.89	30.06	0	10
16	{ $\phi(\cdot)$, $\gamma'' = \gamma'$, $\pi(g + t)$, $p(\text{mix}, g)$, <i>Behavior</i> }	2833.85	40.02	0	9
17	{ $\phi(\cdot)$, $\gamma'' = \gamma'$, $\pi(g)$, $p(\text{mix}, g)$, <i>Behavior</i> }	2838.09	44.26	0	7

Table 2 (Continued).

Model Number	Model	AIC _c	ΔAIC_c^a	w_i^b	K^c
18	$\{ \varphi(\cdot), \gamma'' = \gamma' = 0.185\text{-F}, 0.646\text{-M}, \pi(g + t\text{-F}), p(\text{mix}, g, \cdot), \text{Behavior} \}$	2851.76	57.93	0	7
19	$\{ \varphi(\cdot), \gamma''(g + t) = \gamma'(g), p(g, \text{FirstPP}), \text{Behavior} \}$	2859.16	65.32	0	7
20	$\{ \varphi(\cdot), \gamma''(g + t) = \gamma'(g), p(g+t), \text{Behavior} \}$	2860.17	66.34	0	8
21	$\{ \varphi(\cdot), \gamma''(g + t) = \gamma'(g), p(g), \text{Behavior} \}$	2872.58	78.75	0	6
22	$\{ \varphi(\cdot), \gamma''(g + t) = \gamma'(g), p(\cdot), \text{Behavior} \}$	2930.67	136.84	0	6
23	$\{ \varphi(\cdot), \gamma''(g + t) = \gamma'(g), p(\cdot), \text{No Behavior} \}$	2939.76	145.93	0	5
24	$\{ \varphi(\cdot), \gamma''(g) = \gamma'(g), p(\cdot), \text{No Behavior} \}$	2941.40	147.57	0	4
25	$\{ \varphi(g), \gamma''(g) = \gamma'(g), p(\cdot), \text{No Behavior} \}$	2943.43	149.60	0	5
26	$\{ \varphi(\cdot), \gamma'' = \gamma' = 0, p(\cdot), \text{Behavior} \}$	2946.71	152.88	0	3
27	$\{ \varphi(\cdot), \gamma'' = \gamma', p(\cdot), \text{No Behavior} \}$	2958.73	164.90	0	3
28	$\{ \varphi(\cdot), \gamma'' = \gamma' = 0, p(\cdot), \text{No Behavior} \}$	2969.75	175.92	0	2

^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 3. Model-averaged estimates of the proportion of bears in each of 2 finite mixtures and capture probability for each mixture by gender and year, Tensas River Basin, Louisiana, USA, 2006–2008.

	π (SE) ^a	p Mix ₁ (SE) ^b	p Mix ₂ (SE) ^c	p Mean (SE) ^d
Male				
2006	0.87 (0.06)	0.02 (0.01)	0.15 (0.05)	0.04 (0.01)
2007	0.87 (0.06)	0.03 (0.01)	0.22 (0.05)	0.05 (0.01)
2008	0.87 (0.06)	0.02 (0.01)	0.19 (0.05)	0.05 (0.01)
Female				
2006	0.82 (0.06)	0.07 (0.02)	0.41 (0.06)	0.13 (0.03)
2007	0.94 (0.03)	0.08 (0.02)	0.44 (0.06)	0.10 (0.02)
2008	>0.99 (<0.00) ^e	0.08 (0.02)	0.43 (0.06)	0.08 (0.01)

^a Proportion of bears in first finite mixture with standard error.

^b Capture probability for bears in first finite mixture with standard error.

^c Capture probability for bears in second finite mixture with standard error.

^d Mean capture probability with standard error.

^e Average includes models whereby π was fixed at 1 with SE = 0.

Table 4. Population densities of black bears in the southeastern United States.

Locality	Bears/ km ²	Reference
Camp Lejeune, North Carolina	0.02	Brandenburg 1996
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	0.14 – 0.26	Clark et al. 2010
White River National Wildlife Refuge, Arkansas	0.29	Smith 1985
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	This study
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

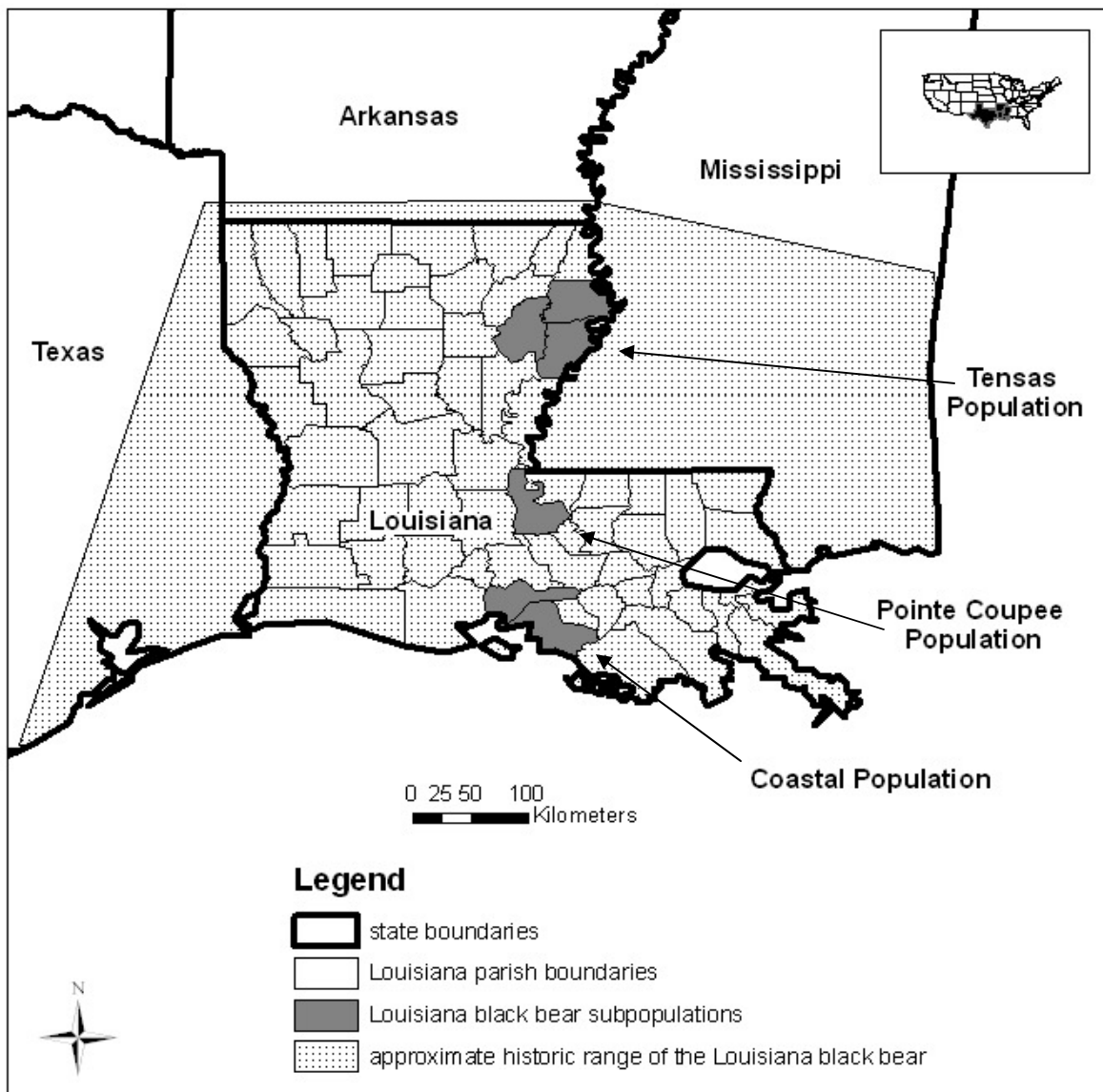


Fig.1. Approximate historic range of the Louisiana black bear and general location of 3 bear subpopulations within Louisiana, USA.

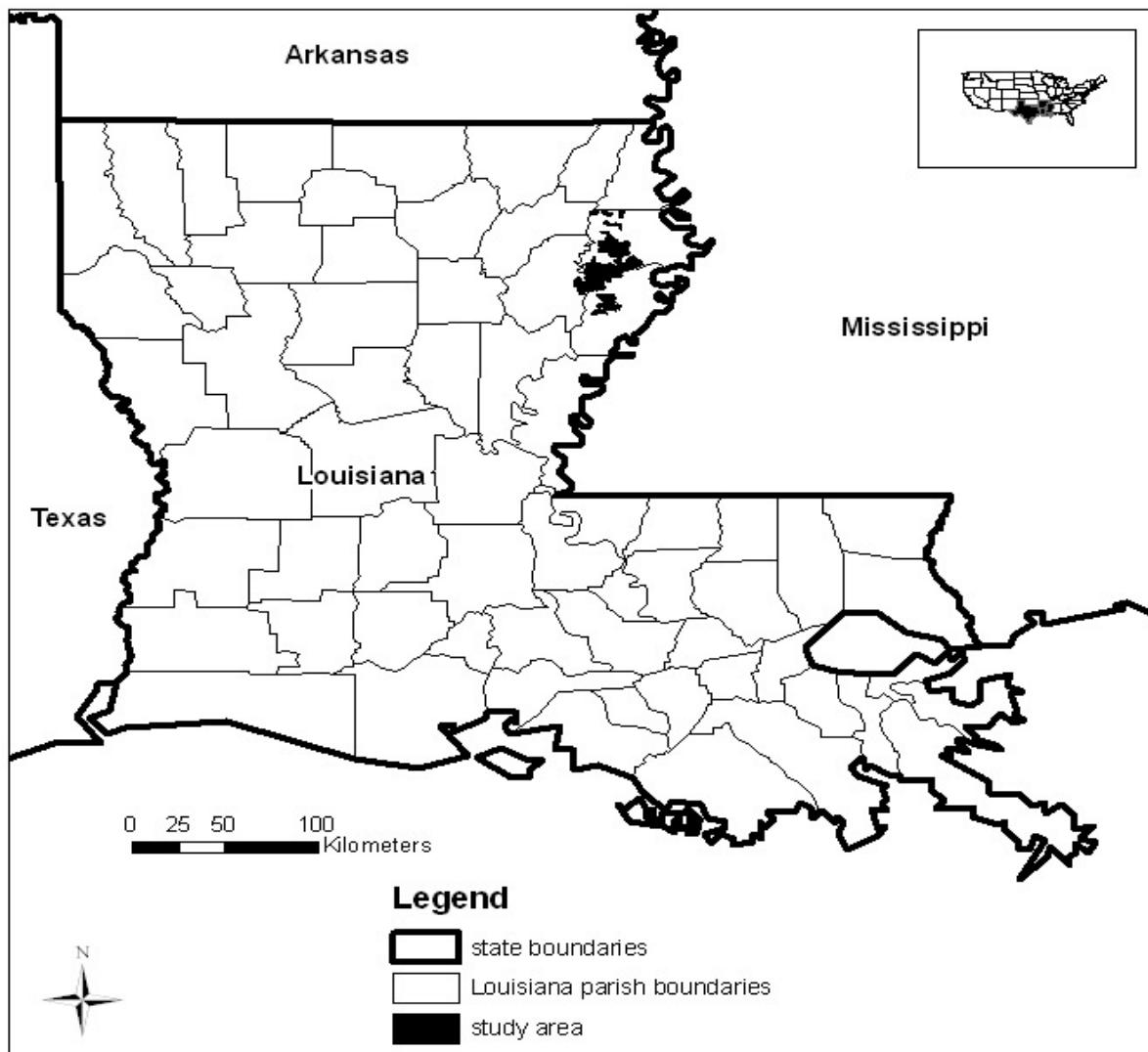


Fig. 2. Study area used to estimate population parameters of the Louisiana black bear in the Tensas River Basin, Louisiana, USA, 2006–2008.

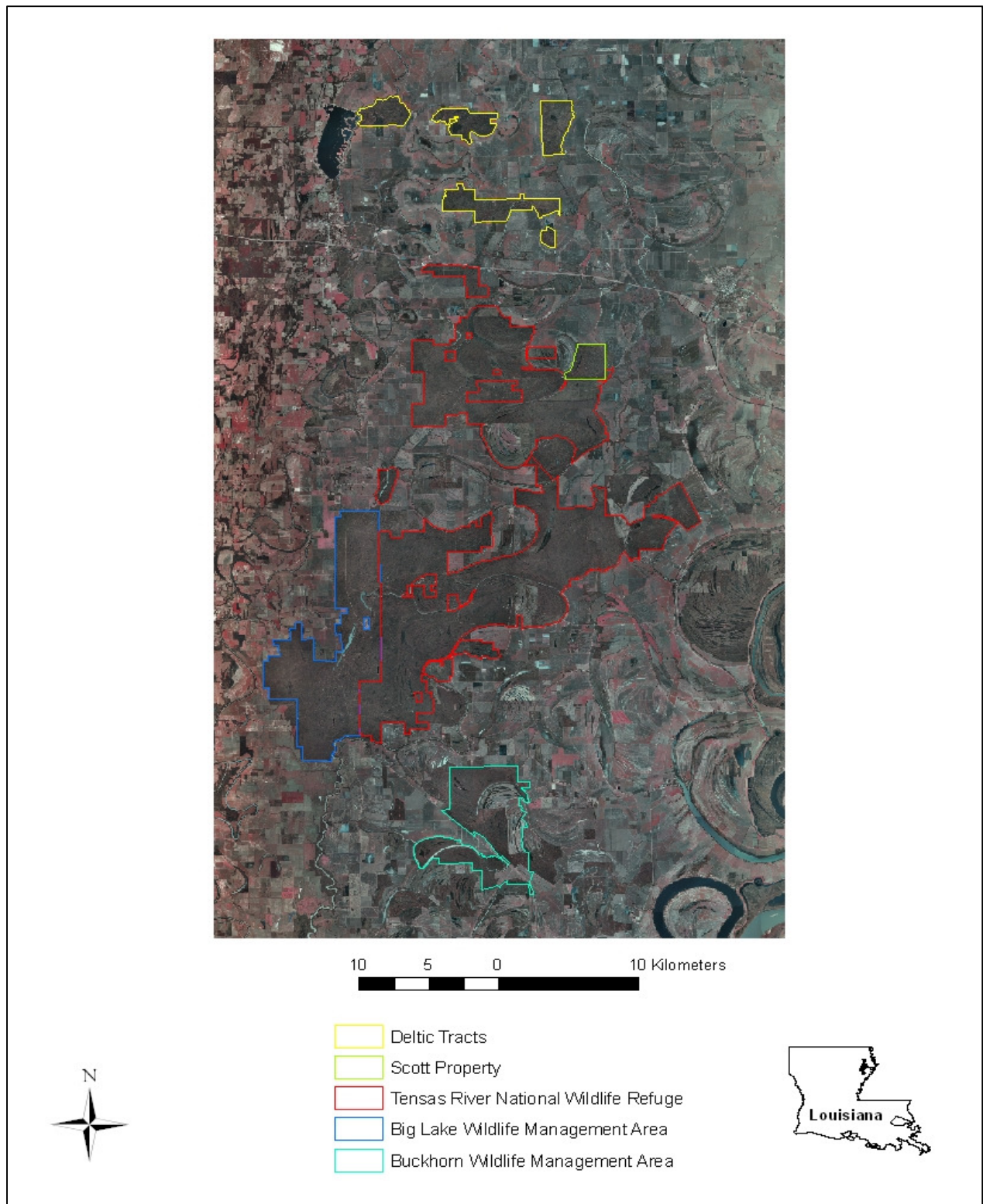


Fig. 3. Property boundaries of large tracts of bottomland hardwood forest in the Tensas River Basin, Louisiana, USA, 2006–2008.

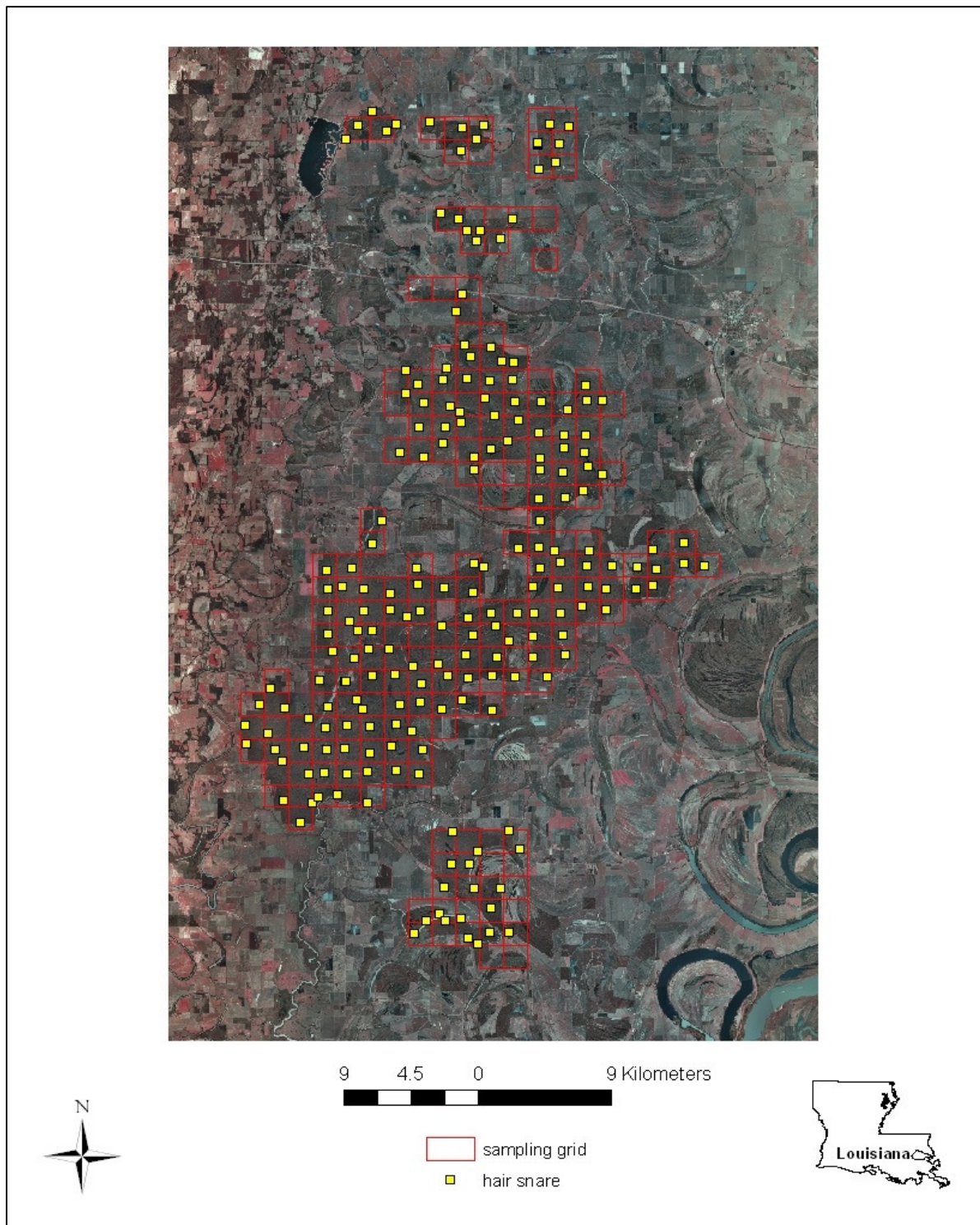


Fig. 4. Sampling grid with 2.6-km² cell size and locations of 209 hair snares used to collect hair from Louisiana black bear in the Tensas River Basin, Louisiana, USA, 2006–2008.

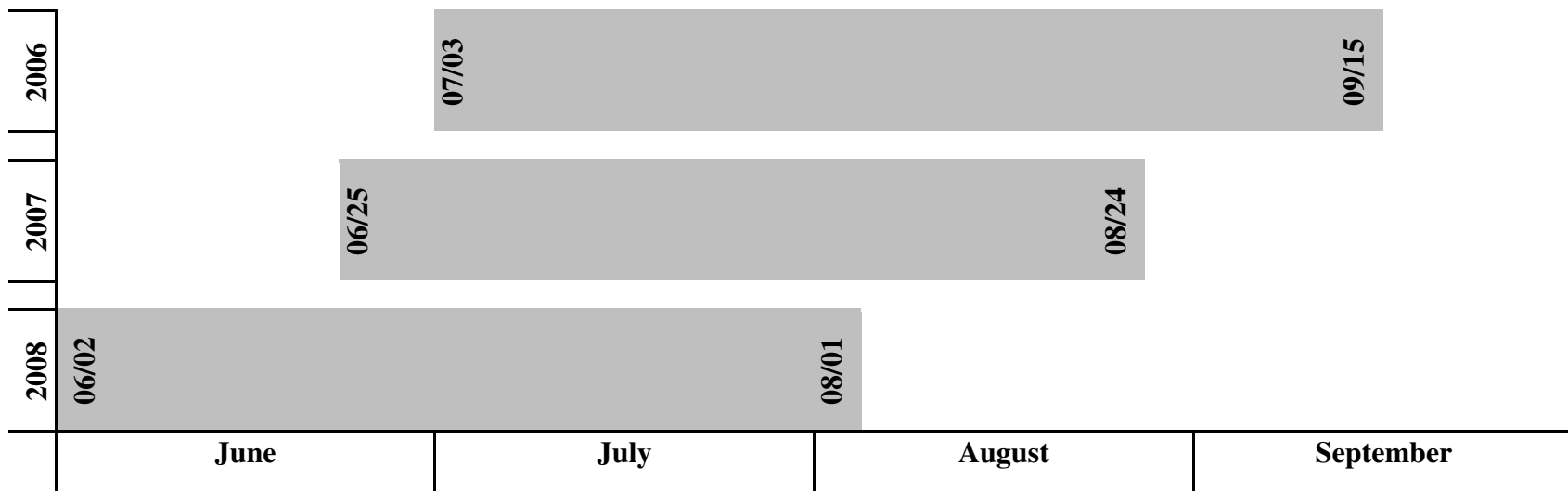


Fig. 5. Sampling schedule with start and end date of annual sampling periods for 3-year robust design study of Louisiana black bears in the Tensas River Basin, Louisiana, USA, 2006–2008.

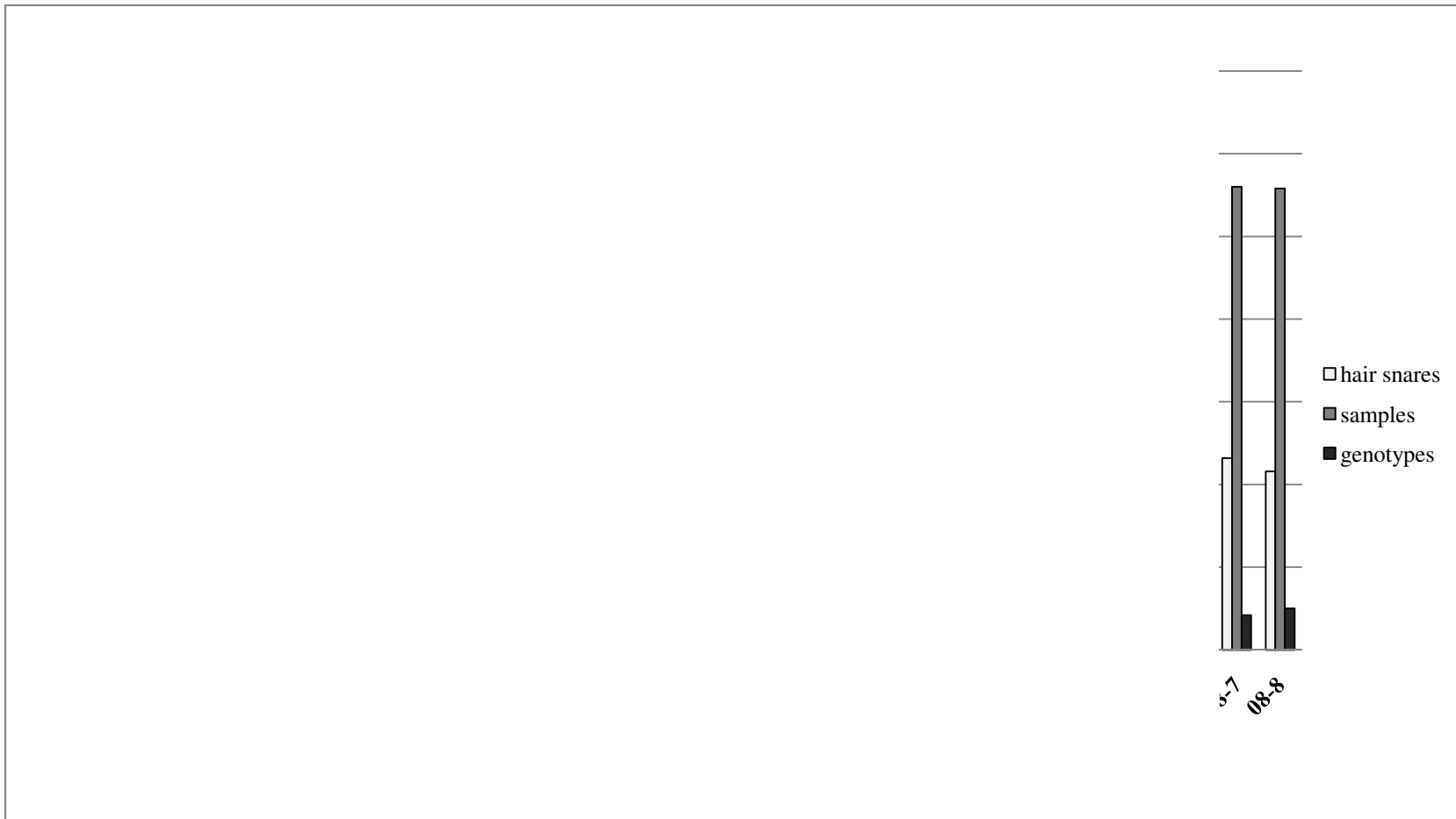


Fig. 6. Number of hair snares producing samples, total number of hair samples collected, and number of individual genotypes by period for 3-year robust design study of Louisiana black bear in the Tensas River Basin, Louisiana, USA, 2006–2008.

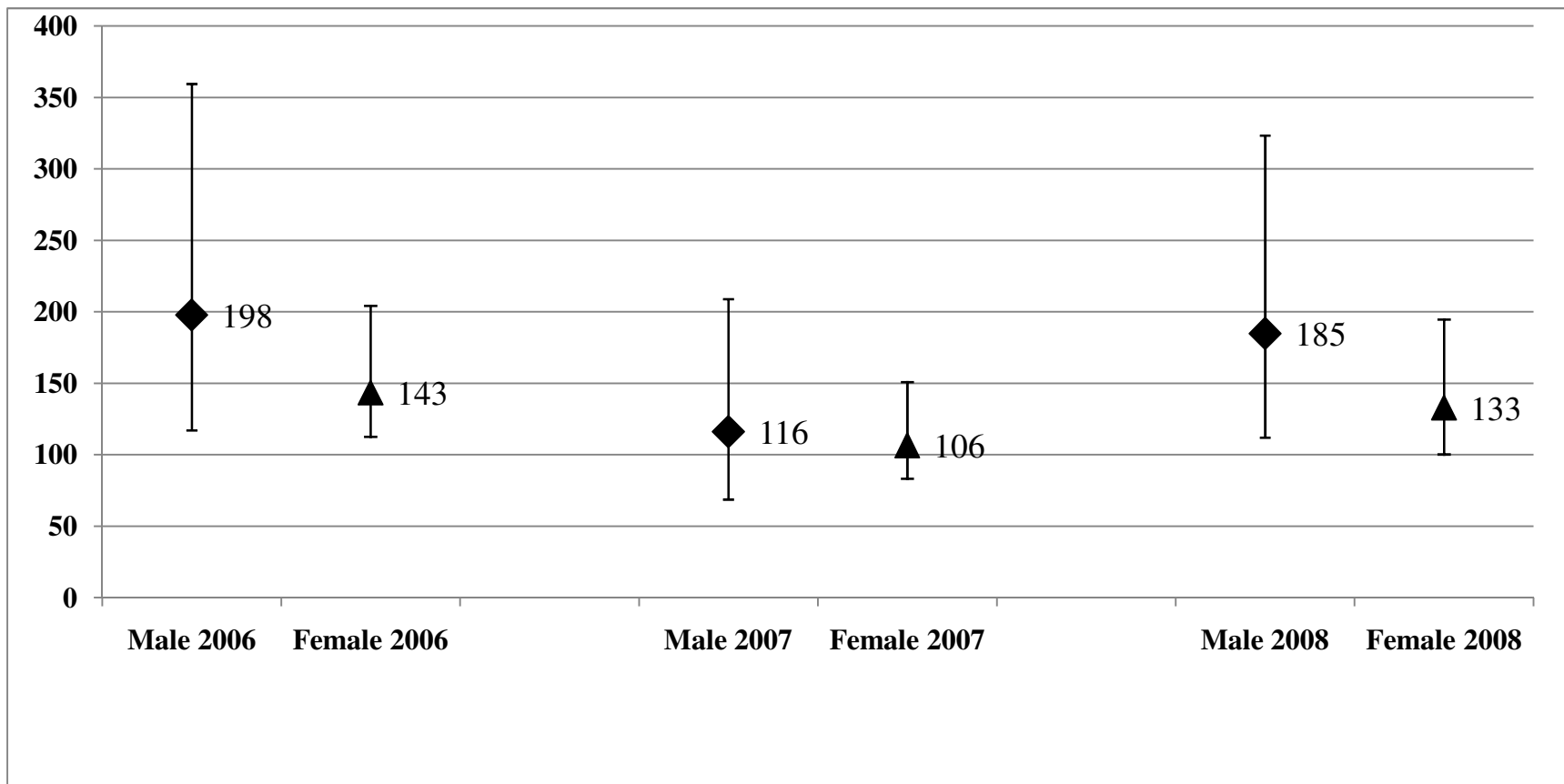


Fig. 7. Model-averaged annual abundance estimates by gender with 95% confidence intervals for the Louisiana black bear in the Tensas River Basin, Louisiana, USA, as estimated by robust design capture-mark-recapture, 2006–2008.

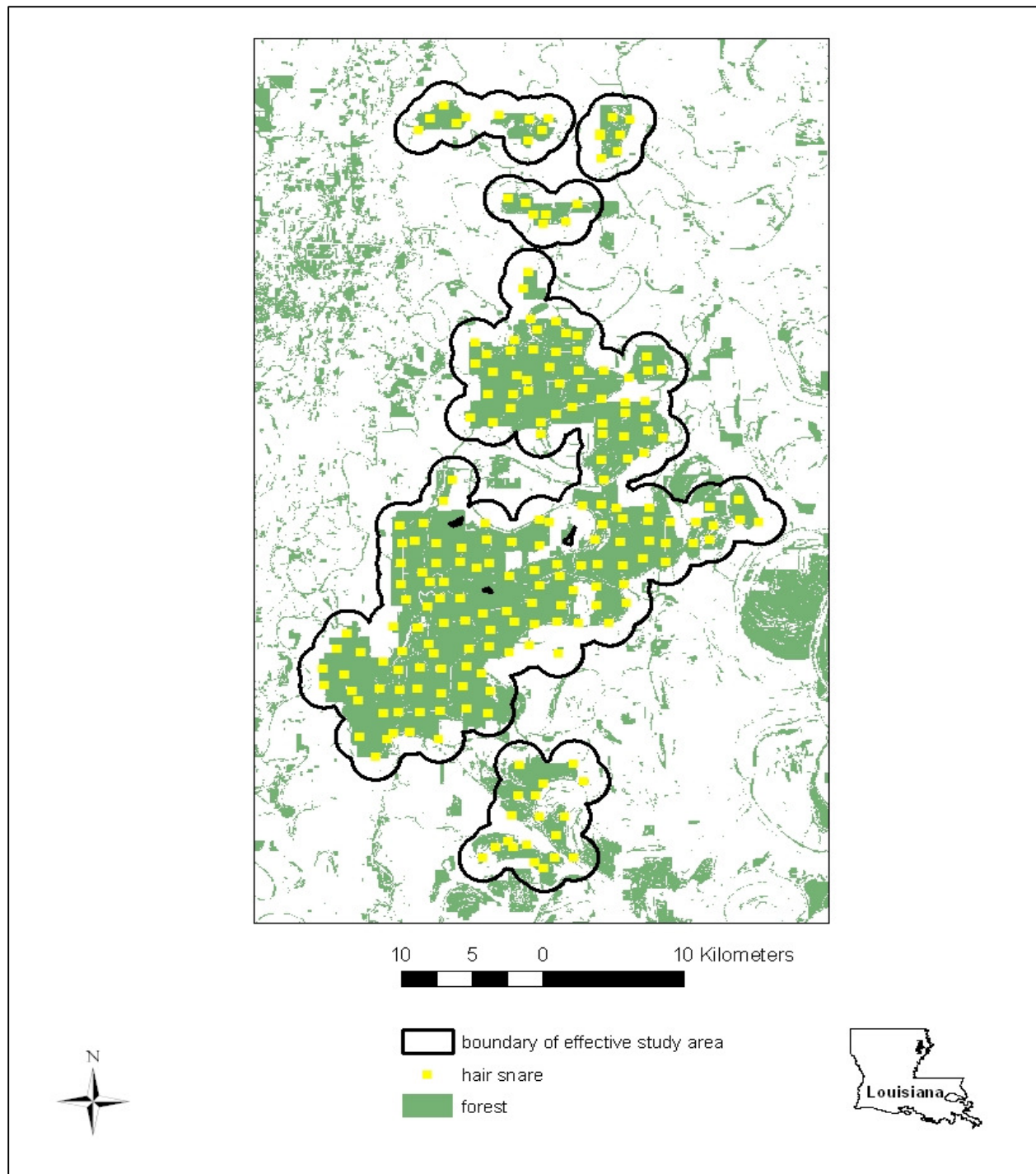


Fig.. 8. Effective study area used to estimate density of the Louisiana black bear population in the Tensas River Basin, Louisiana, USA, 2006-2008.

VITA

Michael J. Hooker was born in Olean, New York on 20 August 1967. He spent his childhood and teenage years among the hills and hollows of South Bolivar, New York. His fascination with wildlife led him to obtain an Associate of Applied Science Degree in Fisheries and Wildlife Technology from the State University of New York at Cobleskill, and a Bachelor of Science Degree in Wildlife Biology from Colorado State University. After his 1989 graduation from Colorado State University, he spent many years in the western United States conducting wildlife research projects for the University of Wyoming. In May 2000 he obtained a Biologist position with the Wyoming Game and Fish Department which he held for four years. In May of 2004 he accepted a position with the University of Tennessee which eventually led to his pursuit of a graduate degree. He received his Master of Science degree in Wildlife and Fisheries Science from the University of Tennessee in December 2010.