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Abundance and density of Louisiana black bears on the Tensas River National Wildlife Refuge

Mark Ryan Boersen

To the Graduate Council:

I am submitting herewith a thesis written by Mark Ryan Boersen entitled "Abundance and density of Louisiana black bears on the Tensas River National Wildlife Refuge." 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.

Joseph D. Clark, Major Professor

We have read this thesis and recommend its acceptance:

Michael Pelton, Frank van Manen, Mary Sue Younger

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Mary Sue Younger

Accepted for the Council:

Interim Vice Provost and
Dean of the Graduate School

ABUNDANCE AND DENSITY OF LOUISIANA BLACK BEARS ON THE TENSAS RIVER NATIONAL WILDLIFE REFUGE

A Thesis

Presented for the

Master of Science Degree

The University of Tennessee, Knoxville

Mark R. Boersen

May 2001

DEDICATION

This thesis is dedicated to my parents:

Sherwin and Norma Boersen.

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ABSTRACT

Extensive habitat loss throughout the historic range of the Louisiana black bear (*Ursus americanus luteolus*) has resulted in small remaining isolated populations existing primarily on publicly owned lands. The U.S. Fish and Wildlife Service provided federal protection to the Louisiana bear by granting it "threatened" status on the Endangered Species List in 1992. Accordingly, the Louisiana Black Bear Recovery Plan mandated research efforts to determine the current status of the remaining bear populations within the historic range.

I sampled the bear population at the Tensas River National Wildlife Refuge, the adjacent Big Lake State Game Management Area, and adjoining privately owned forested lands (these areas together are hereafter referred to as the Tensas River Tract) to estimate population size from 1998–99. Because the Tensas River Tract is entirely surrounded by agricultural lands, it represents an "island" situation permitting use of models that assume geographic population closure. The study area for the Tensas complex encompassed nearly all-available black bear habitat.

Two approaches were used to sample the bear population at Tensas. Livetrapping resulted in 50 captures of 42 bears during 2 years of study. However, the live-trapping sample seemed to be affected by unequal capture probabilities among bears. Therefore, a non-invasive sampling technique was employed to provide population estimates. This method was based on microsatellite DNA analysis of hair samples collected from hair-trapping stations to allow use of mark-resight population models. Hair traps were

constructed throughout the study area to simultaneously sample the population. During 14 weeks of hairtrapping, project personnel collected 1,939 hair samples. A subsample of 116 hair samples was randomly chosen for analysis. All samples were analyzed at 8 microsatellite loci to individually identify bears. Matching samples were reanalyzed at 4 additional loci to improve identification power. Complete multilocus genotypes from 58 bears were obtained from 114 hair samples. Model Chao M_{th} produced an estimate for the Tensas bear population size of 115 (95% CI = 85–182), averaging 0.35 bears/km^2. My study provided the first estimate of population size for the Tensas bear population based on rigorous statistical sampling. The bear population at Tensas appears to have increased based on former guesses of population size by the U.S. Fish and Wildlife Service.

This study represents the first black bear population estimate in the Southeast based on non-invasive sampling techniques. The hair-trapping approach provided several advantages over livetrapping including increased sample sizes, low bias, and improved precision. Additionally, the genetic data can be used to assess genetic variability within and between populations. Inbreeding and genetic drift may have already impacted the isolated Tensas population. Tensas bears were found to have 1–2 fewer alleles per locus than populations in northwest Arkansas and east-central Louisiana.

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CHAPTER I

INTRODUCTION

General Problem Statement

The bottomland hardwood forests of the lower Mississippi valley support a high diversity of wildlife species including the Louisiana black bear (*Ursus americanus luteolus*). Although once a common resident throughout its historic range of eastern Texas, Louisiana, and southern Mississippi (Hall 1981), the Louisiana bear persists today only in small isolated populations. In the southeastern United States, where habitat loss has been most extensive, bears now occupy only 20% of their former range (Fig. 1; Pelton and van Manen 1997).

The primary cause of this decline has been the conversion of forested lands to agricultural uses. Beginning with the arrival of settlers in the early 1800s, nearly half of the bottomland hardwood forests were cleared by 1937 (Spencer 1981) and by 1980, less than 20% of the original bottomland hardwoods remained (Neal 1992). More than 80% of the land cleared since 1937 was planted into soybeans (Spencer 1981). Within the Tensas River Basin (TRB) in northeast Louisiana, approximately 10,000 ha of forestland have been cleared each year since 1937. Today, forests cover only about 15% of the original forested area in the TRB (Gosselink et al. 1989), all of which have been cut at some point in the past (Burdick et al. 1989). Species that now are locally extinct in the TRB include the red wolf (*Canis rufus*), Florida panther (*Puma concolor coryi*), ivory-

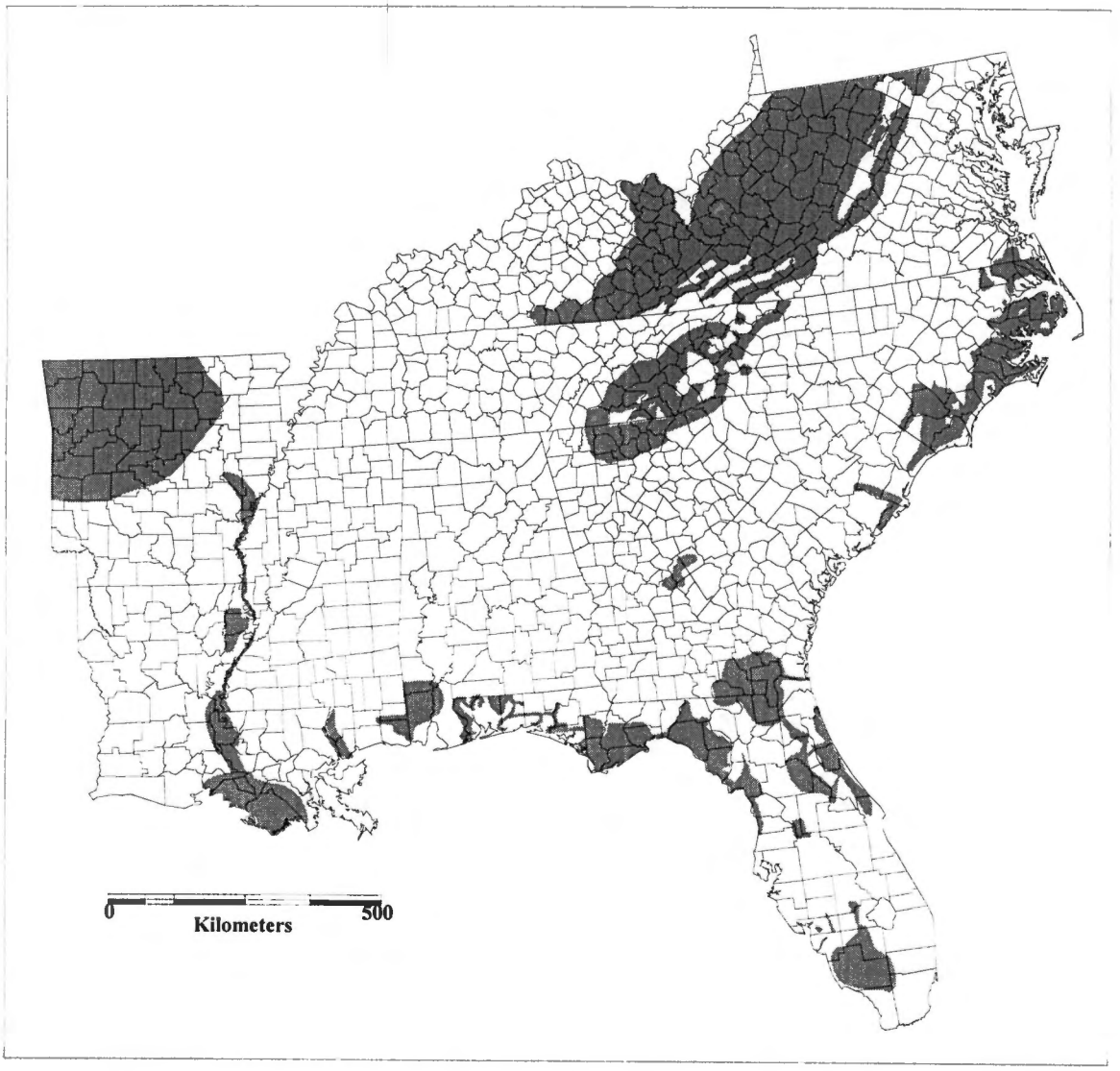

Fig. 1. Current distribution of black bears in the southeastern United States (Pelton and van Manen 1997).

billed woodpecker (*Campephilus principalis*; Burdick et al. 1989), and Bachman's warbler (*Vermivora bachmanii*; Gosselink et al. 1989).

Although the "yellow bear" of the Southeast was first described by Shaw in 1800 (Merriam 1893), it was first officially recognized by Edward Griffith in 1821, who compared the "yellow bear, *Ursus luteolus*" to the American black bear as "...smaller; the forehead more convex; the nose more conical than in the black species; the ears also stand farther back; the physiognomy may be said to be more fox-like, and the hair is not so long or thick" (Griffith 1821 as cited by Merriam 1893:148). Based upon the features of 5 skulls from Morehouse parish, Merriam (1893) later gave the Louisiana bear a more thorough description and classified it as a subspecies, *Ursus americanus luteolus*.

Within the last 2 decades, the validity of the Louisiana black bear as a subspecies has been questioned (Pelton 1990, Neal 1992). In the mid-1960's, the Louisiana Department of Wildlife and Fisheries translocated 161 American black bears (*U. a. americanus*) from Cook County, Minnesota to augment local native bear populations in Louisiana (Lowery 1974). Pointe Coupeé Parish was the release site for 130 bears, whereas the remaining 31 bears were set free along the Tensas River near Somerset (Taylor 1971). Those translocations may have resulted in cross breeding of the Louisiana black bear with the American black bear. While tracking 3 of the original Minnesota females, Taylor (1971) reported that reproduction had occurred in Pointe Coupeé Parish. However, based on the apparent dispersal and recoveries of several bears that were released in the TRB, some authorities believed the releases did not impact the native population in northeast Louisiana (Nowak 1986). A study to address this issue funded by

the U.S. Fish and Wildlife Service did not detect any significant genetic differences between the Louisiana bear and the American black bear (M. R. Pelton, University of Tennessee, unpublished report). However, further genetic research by Miller (1995) suggested that *U. a. luteolus* is different from *U. a. americanus*. Aside from the genetic questions, morphological differences between the subspecies were evident (Nowak 1986, M. L. Kennedy, University of Memphis, unpublished report).

Because of extensive loss of habitat and declining numbers, the Louisiana black bear was listed in the U.S. Fish and Wildlife Service notices of review in 1982, 1985, and 1989 as a category 2 listing. This category included taxa that may warrant listing, but for which there is presently a lack of information (Neal 1990). The U.S. Fish and Wildlife Service was petitioned to list *U. a. luteolus* as an endangered species on 6 March 1987. On 21 June 1990, the Louisiana bear was first proposed for "threatened" status on the Endangered Species List (Neal 1990). Based on the loss of suitable habitat, the final rule granting "threatened" status to the Louisiana bear was passed on 7 January 1992 (Neal 1992). Because of the difficultly in distinguishing Louisiana black bears from American black bears (which may have immigrated from outside of the Louisiana bear's historical range or are descendants of the Minnesota bears), all black bears within the historic range of *U. a. luteolus* were protected by similarity of appearance (Neal 1992). Since that time, critical habitat has been proposed by the U.S. Fish and Wildlife Service to protect bottomland hardwoods in areas deemed critical to the conservation of the subspecies. Approximately 5,060 km^2 (1.25 million ac) within an area of 12,100 km^2 (3 million ac) of the TRB and Atchafalaya River Basin (ARB) would be affected. The rule was first

proposed on 2 December 1993 (Neal 1993) but has been delayed, first by a moratorium, and more recently by a restructuring of listing priorities (Pace et al. 1997).

Three core black bear populations remain within Louisiana. One population is located primarily in Point Coupeé Parish, within the upper ARB, whereas another population inhabits coastal St. Mary and Iberia parishes, in the lower ARB (Fig. 2). The remaining population resides in northeast Louisiana within the TRB, which includes approximately 405 km^2 (100,000 ac) of bottomland hardwood forests (Neal 1992). The majority of habitat in the TRB is in public ownership consisting of the Tensas River National Wildlife Refuge (Tensas Refuge) and Big Lake State Game Management Area (Big Lake). Numerous other small, scattered blocks of bottomland hardwoods can be found throughout the historic range of the Louisiana bear. Many of these areas, although inhabited by bears, lack suitable travel corridors to core populations and are isolated by roads and other human development. These smaller populations are especially vulnerable to extinction because of demographic and environmental stochasticity (Shaffer 1981). Therefore, the remaining 3 core populations are of paramount importance to the survival of the subspecies. The U.S. Fish and Wildlife Service has developed a Recovery Plan for the Louisiana black bear (U.S. Fish and Wildlife Service 1995), which details the criteria necessary to achieve the goal of delisting. These criteria include the preservation and protection of at least 2 subpopulations connected by travel corridors (Chapter II, section A). Recovery actions in the Plan include determination of the current status of the bear populations in Louisiana (Chapter II, section B, part 3.5), which include estimates of

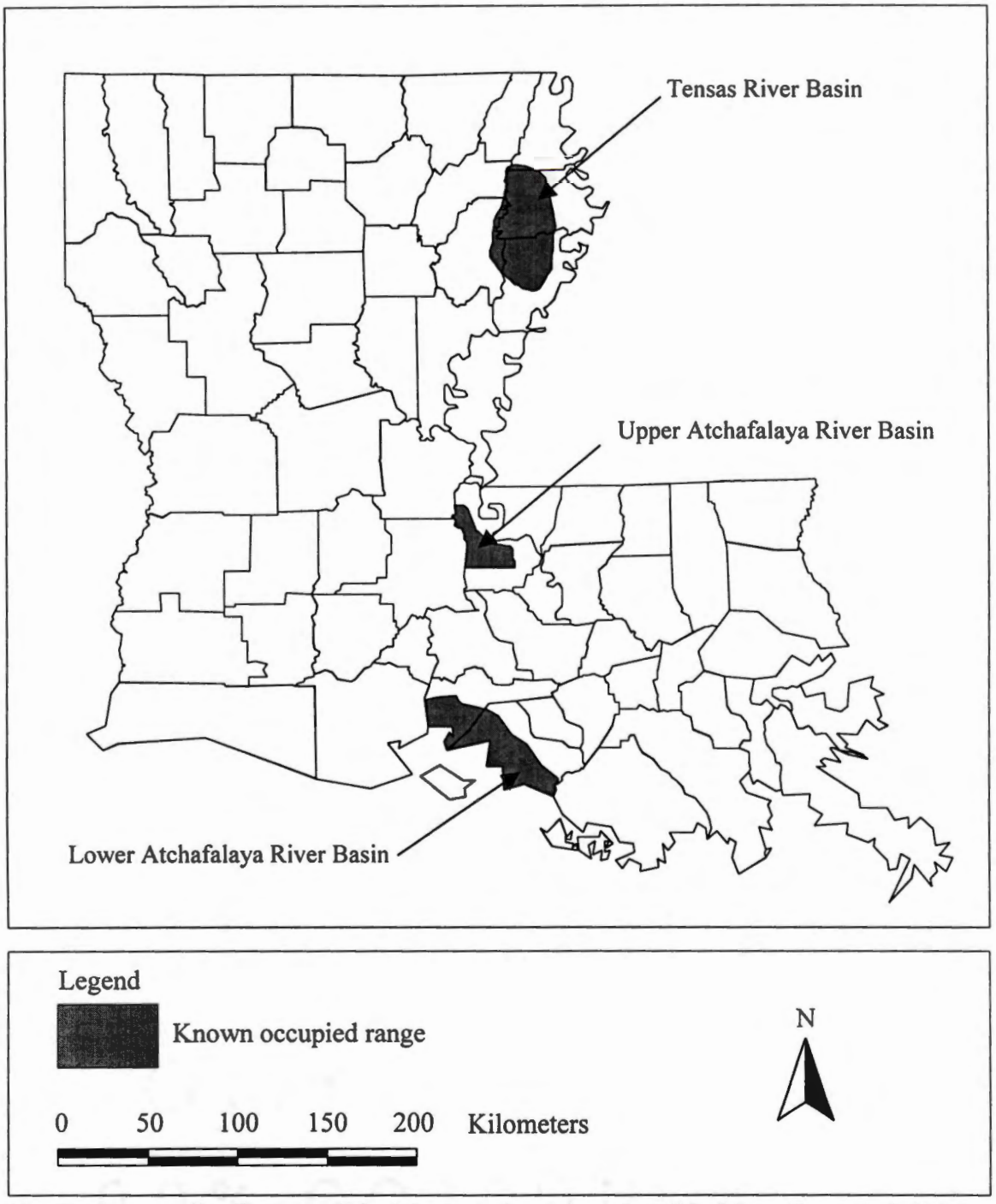

Fig. 2. Current distribution of black bears in Louisiana (modified from Pace et al. 1994).

abundance. Additionally, the development of population indicies is called for (Chapter II, section B, part 4.1).

Justification

Data on population abundance are important for evaluating habitat management practices, tracking changes in population levels, and determining possible source populations for bear reintroductions. The small size of remaining populations may subject the subspecies to reduced overall genetic variation and higher probabilities of local extinction (Gilpin and Soulé 1986, Hellgren and Maehr 1992). Other factors such as habitat fragmentation and inbreeding can affect the likelihood that a population will exist for a given amount of time into the future. Inbreeding, or breeding between closely related individuals in a population, decreases levels of heterozygosity, which may result in inbreeding depression (Ralls et al. 1986). A consequence of inbreeding depression may be an increase in the expression of harmful recessive genes because of the presence of more homozygote alleles (Allendorf and Leary 1985). Genetic drift is the loss of alleles from a population due to random changes in the frequencies of alleles. Small isolated populations seem to be particularly vulnerable to inbreeding depression and loss of genetic variation because of bottlenecks and associated random genetic drift (Allendorf 1986, Frankham 1998). Within small fragmented habitats, however, natural mechanisms that minimize inbreeding, such as dispersal (Ralls et al. 1986), are likely to be less effective. A decline in size of an already small population such as the one at Tensas, may magnify the deleterious effects of such impacts (Gilpin and Soulé 1986).

Therefore, when considering small populations that are threatened with extinction such as with the Louisiana bear, evaluation and monitoring of existing populations are particularly imperative.

Previous Research

Intensive black bear research in the TRB began in the late 1980s when the U.S. Fish and Wildlife Service was first petitioned to list the Louisiana black bear as an endangered species. Subsequently, Weaver et al. (1990) developed management guidelines for black bears in bottomland hardwood habitats and Weaver and Pelton (1994) investigated the denning ecology of bears in the TRB. Three studies were conducted on 4 forested tracts owned by the Deltic Farm and Timber Company located approximately 12 km north of the Tensas River Tract. Marchinton (1995) examined black bear movement ecology and habitat use within these 4 fragmented forests. Anderson (1997) evaluated corridor use between forested tracts, habitat use, and diet of Deltic bears. Most recently, Beausoleil (1999) assessed home range size and overlap, reexamined bear movements and corridor use, and provided an estimate of bear population size for the Deltic tracts.

The TRB black bear study was initiated in 1987 to examine the ecology and life history of *U. a. luteolus* by monitoring 25 radiocollared bears on the Tensas and Deltic lands (Weaver 1999). A population estimate of 48 individuals was projected for the forested areas of Tensas from 17 bears identified from 1988 to 1991 within a subsection

of the area (Weaver 1999). However, no statistical estimates of population size have previously been produced for the Tensas River Tract.

My study is one part of a larger effort to assess the status of the Louisiana black bear. Currently, biologists estimate there are 200–300 bears residing in Louisiana (Pace et al., Louisiana State University, unpublished report). However, those estimates were not based on rigorous statistical sampling. A robust estimate of population size at the Tensas River Tract, the estimate for the Deltic lands provided by Beausoleil (1999), and the results of an ongoing abundance study in the Upper and Lower Atchafalaya River Basins (D. Triant, Louisiana State University, personal communication) will aid the U.S. Fish and Wildlife Service in implementing management programs designed to support the recovery of the Louisiana bear.

Objectives

The remaining fragmented populations of the Louisiana black bear, coupled with its current "threatened" status on the Endangered Species List and mandates set by the Louisiana Black Bear Recovery Plan, identify the need for a reliable population estimate for the Tensas River Tract. Therefore, the objectives of my study were to:

1) Provide a robust estimate of the number of black bears on the Tensas River Tract, with a coefficient of variation $\leq 25\%$ and,
2) Estimate the density of black bears on the Tensas River Tract.

CHAPTER II

STUDY AREA

General

The study area for my investigation was located in the 620-km^2 TRB in northeast Louisiana. The center of the study area was located at approximately 32° 16' north latitude, 91° 21' west longitude. All forested areas of the Tensas Refuge, excluding the isolated Moore woods unit, were included in the study. Additionally, the north and east portions of Big Lake, numerous private inholdings, and several private forested lands adjacent to the Tensas Refuge were included (Fig. 3). As such, the study area comprised approximately 329 km^2 of contiguous bottomland hardwoods and was contained within Madison, Tensas, and Franklin parishes. The center of the study area was located approximately 46 km west of Vicksburg, Mississippi and 74 km east-southeast of Monroe, Louisiana. The nearest major roadways were Interstate 20 to the north, Highway 65 to the east, Highway 4 to the south, and Highways 577 and 578 to the west. Nearby population centers were the city of Tallulah (population 8,911) to the northeast, the town of Delhi (population 3,158) to the northwest, and the town of Winnsboro (population 5,729) to the southwest (U.S. Census Bureau 1998).

The Tensas Refuge was created in 1980 when Congress took action to save one of the largest remaining bottomland hardwood forests in the lower Mississippi River Valley (Fontenot and Ziegler 1987). The acquisition of the Refuge was a cooperative effort involving the U.S. Fish and Wildlife Service and the U.S. Army Corps of Engineers to

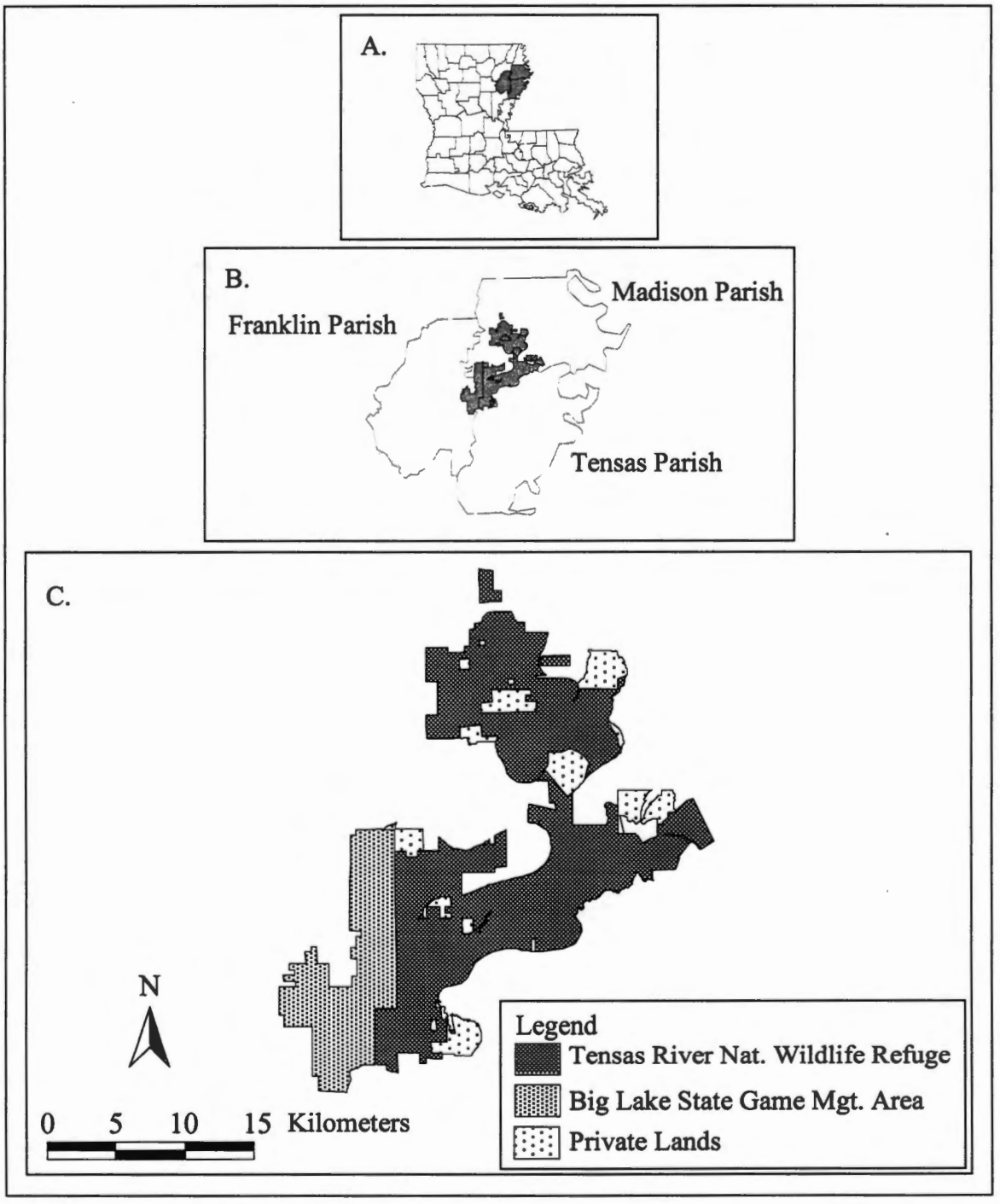

Fig. 3. Location of the 3-parish region containing the Tensas River Tract study area, (B) distribution of the study area with the parishes, and (C) division of forested lands enclosing the study area, Tensas River Basin, northeast Louisiana.

mitigate loss of fish and wildlife resources related to 6 flood control projects proposed or under construction in northeast Louisiana (U.S. Fish and Wildlife Service, unpublished report). Approximately 24,000 ha of forest were purchased from the Chicago Mill and Lumber Company for $50 million (Fontenot and Ziegler 1987). Subsequent land acquisitions have increased the size of the Refuge to 26,618 ha.

Habitat on the Tensas River Tract was characterized by bottomland hardwood forests, surrounded entirely by agricultural lands. The study area was interspersed by several gravel and hard surface roads, all terrain vehicle (ATV) trails, and foot trails. Major drainages on the area were the Tensas and Fool rivers. Numerous bayous, cypress sloughs, natural lakes, oil wells, and reforested former agricultural lands in early successional stages were scattered throughout the study area.

Geology and Soils

The Tensas River winds through the center of the study area in a north-south direction. About 5,000 years ago the Tensas River was formed as a result of a decrease in the gradient of the Mississippi River caused by post-glacial rising of sea levels (Weems et al. 1982). This event resulted in several meandering river courses of the Mississippi. The Tensas River is recognized as one of the earliest of these river courses (Weems et al. 1982).

Soils on the study area are primarily in the Sharkey, Tensas-Sharkey, or Sharkey-Alligator-Tunica associations (Weems et al. 1982). These associations are characterized by level or gently undulating, poorly drained, clayey soils (Weems et al. 1968, 1982).

Although natural fertility is high, slow runoff and low permeability make the wet winter months unsuitable for growing crops. The topography of the area is flat with elevations ranging from 18 to 24 m (Weems et al. 1982).

Land Use

Agriculture was the primary land use in Madison, Tensas, and Franklin parishes with 57, 48, and 54% of the area in crop production in each parish, respectively (U.S. Department of Agriculture 1997). Major crops for the area included soybeans, corn, cotton, wheat, sorghum, and rice. Irrigation of farmlands was common. Aerial application of fertilizers and pesticides was widely used for agriculture, especially cotton.

Timber products were the chief crop in Louisiana. In 1998, landowner forestry income for the entire state totaled $1.3 billion (Louisiana Cooperative Extension Service 1998). Timber harvest operations were scattered throughout Madison, Tensas, and Franklin parishes. Timber sales for these parishes totaled $9.2 million in 1998 (Louisiana Cooperative Extension Service 1998).

During my study, several forest stands on the northern portion of the study area were selection cut for hardwoods. Additional forest stands were marked for future timber harvests. Forests at the Tensas Refuge were managed with selection cuts on a 100-year rotation schedule (Weaver 1990). Objectives of forest management included preservation of old-age stands and habitat corridors, and maintenance of forest openings. In addition, all bald cypress (*Taxodium distichum*) and other cavity containing trees, which were important for bear den sites, were preserved (Weaver 1990).

Climate

The climate for northeast Louisiana is affected by both the sub-tropical humid Gulf of Mexico air masses and drier air masses from the north and west (J. Grymes, Louisiana Office of State Climatology, unpublished report). Summers were hot and humid and winters were mild. The average minimum and maximum winter temperatures in 1998 were 4.6°C and 14.7°C, respectively, compared with average minimum and maximum temperatures of 22.9°C and 33.7°C in summer, respectively (National Climatic Data Center 1998). In 1999, the mean low and high winter temperatures were 5.0°C and 17.1°C, respectively, whereas those for summer were 21.5°C and 33.5°C, respectively (National Climatic Data Center 1999). Temperatures below freezing were recorded on 21 days in 1998 and 29 days in 1999.

Summer and fall typically are the driest seasons in northeast Louisiana. Measurable rainfall was recorded on about 100 days annually (J. Grymes, Louisiana Office of State Climatology, unpublished report). In 1998, rainfall totaled 159.3 cm, whereas in 1999, 108.8 cm of precipitation were recorded (National Climatic Data Center 1998, 1999). Seasonal flooding was common due to abundant winter and spring rainfall. All weather data were recorded in Tallulah, Louisiana.

Flora

The bottomland forests of the study area were comprised of second- and third-growth stands in 40- to 80-year age classes. Rich and Thomas (1981) identified 717 species of vascular plants in Madison Parish. Overstory species on the study area

included sweetgum (*Liquidambar styraciflua*), cherrybark oak (*Quercus falcata* var. *pagodaefolia*), willow oak (*Q. phellos*), water oak (*Q. nigra*), Nuttall oak (*Q. nuttallii*), overcup oak (*Q. lyrata*), sweet pecan (*Carya illinoensis*), sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), elm (*Ulmus* spp.), and bald cypress. Understory species included saw palmetto (*Sabal minor*), switchcane (*Arundinaria gigantea*), greenbriar (*Smilax* spp.), blackberry (*Rubus* spp.), elderberry (*Sambucus canadensis*), and poison ivy (*Rhus radicans*).

Fauna

The forests of the TRB support a high number of wildlife species. Within the Basin, 227 bird, 78 fish, 45 reptile, 40 mammal, and 19 amphibian species are found. Hunting is a popular activity in northeast Louisiana. Game species commonly harvested include white-tailed deer (*Odocoileus virginianus*), gray squirrel (*Sciurus carolinensis*), fox squirrel (*Sciurus niger*), cottontail rabbit (*Sylvilagus floridanus*), swamp rabbit (*Sylvilagus aquaticus*), raccoon (*Procyon lotor*), eastern wild turkey (*Meleagris gallopavo*), American woodcock (*Philohela minor*), mourning dove (*Zenaida macroura*), and several species of waterfowl. Hunting seasons on the study area occured from October through January.

CHAPTER III

METHODS

Study Design

Originally, 3 years of livetrapping were planned to permit use of open and closed mark-recapture models to estimate population size at Tensas. Livetrapping took place throughout the study area during the 1998 field season. However, early in the 1999 trapping period, it became apparent that the capture sample was affected by low capture and recapture rates. Had I continued livetrapping, sample size problems would likely have resulted in biased and imprecise estimates of population size (see Discussion). Therefore, I was forced to consider other alternatives.

Recent advances in molecular biology have resulted in increased use of genetic markers to estimate population size (Taberlet et al. 1997, Woods et al. 1999, Mowat and Strobeck 2000). Small quantities of tissue, scat, or hair can provide sufficient quantities of DNA to identify individuals of a free-ranging species (Morin and Woodruff 1996). Non-invasive sampling techniques are particularly attractive for mark-recapture analysis because such methods often are more efficient and less biased than live-trapping approaches. Microsatellite analysis of collected hair root samples can provide multilocus genotypes, which allow for individual identification of bears (T. L. King, U.S. Geological Survey, personal communication; Taberlet and Luikart 1999), providing a "resight" history for each bear observed. Traditional mark-recapture models can then be used to provide estimates of population size (Woods et al. 1996, 1999, Mills et al. 2000).

I used barbed-wire hair traps as first described by Woods et al. (1996) to obtain hair samples from free-ranging bears at Tensas. Such non-invasive sampling techniques offer several advantages over livetrapping. These advantages include:

1) low impact on the study population because bears do not have to be captured (Morin and Woodruff 1996, Parker et al. 1998),
2) reduced bias due to "trap shyness" because there is no apparent disturbance to bears (Woods et al. 1996),
3) genetic "tags" can never be lost (Woods et al. 1999) and are available from birth,
4) simultaneous sampling of the entire study area can be accomplished,
5) no special expertise is needed to capture hair samples,
6) increased sample sizes, and
7) improved public acceptance.

Therefore, my approach was to use traditional mark-recapture estimators with hair samples collected at barbed-wire hair traps distributed across the study area and over several recapture periods.

Study Area Delineation

The sampling grid defined by the locations of the live traps during the 1998 field season included all forested areas of the Tensas Refuge and Big Lake, and nearly all privately owned forested lands adjacent to the public areas. The 1999 field season primarily consisted of hair sample collection from barbed-wire hair traps. All areas sampled with the live traps in 1998 also were sampled with the hair traps in 1999, except

for the southwest portion of Big Lake. That area was excluded because of time and logistical constraints.

I delineated my study area by circumscribing each of the 1999 hair-trap locations with a circle, the area of which was equivalent to the smallest home range estimate (100% minimum convex polygon estimate; Weaver 1999) for Tensas females (Fig. 4). The area delineated by the outermost borders of these circles, excluding agricultural fields, was counted as the study area, which totaled 32,939 ha (Fig. 5).

Trapping and Handling

Black bears were trapped using modified Aldrich spring-activated snares (Aldrich Animal Trap Company, Clallam Bay, Washington). Project personnel anchored snares to trees or mobile home earth anchors. Traps were baited with bakery products, meat scraps, or sardines. Artificial raspberry or honey flavoring (Medallion International Incorporated, North Haledon, New Jersey; Mother Murphy's, Greensboro, North Carolina) was used as a scent attractant to lure bears into trap sites.

Access to the area was by roads, ATV trails, and foot trails. I placed traps about 0.8 km apart, near trails to permit access. Universal Transverse Mercator (UTM) coordinates (North American Datum 1927, Zone 15) were recorded for each trap using global positioning system (GPS) receivers (Garmin GPS II Plus, Olathe, Kansas). Each morning 20–30 traps were checked, baits were replenished, and scent lures were refreshed. Trap appearance or placement was changed after 3 bear visits without a capture. Each bear trap was set for approximately 21 days during 1998. During 1999,

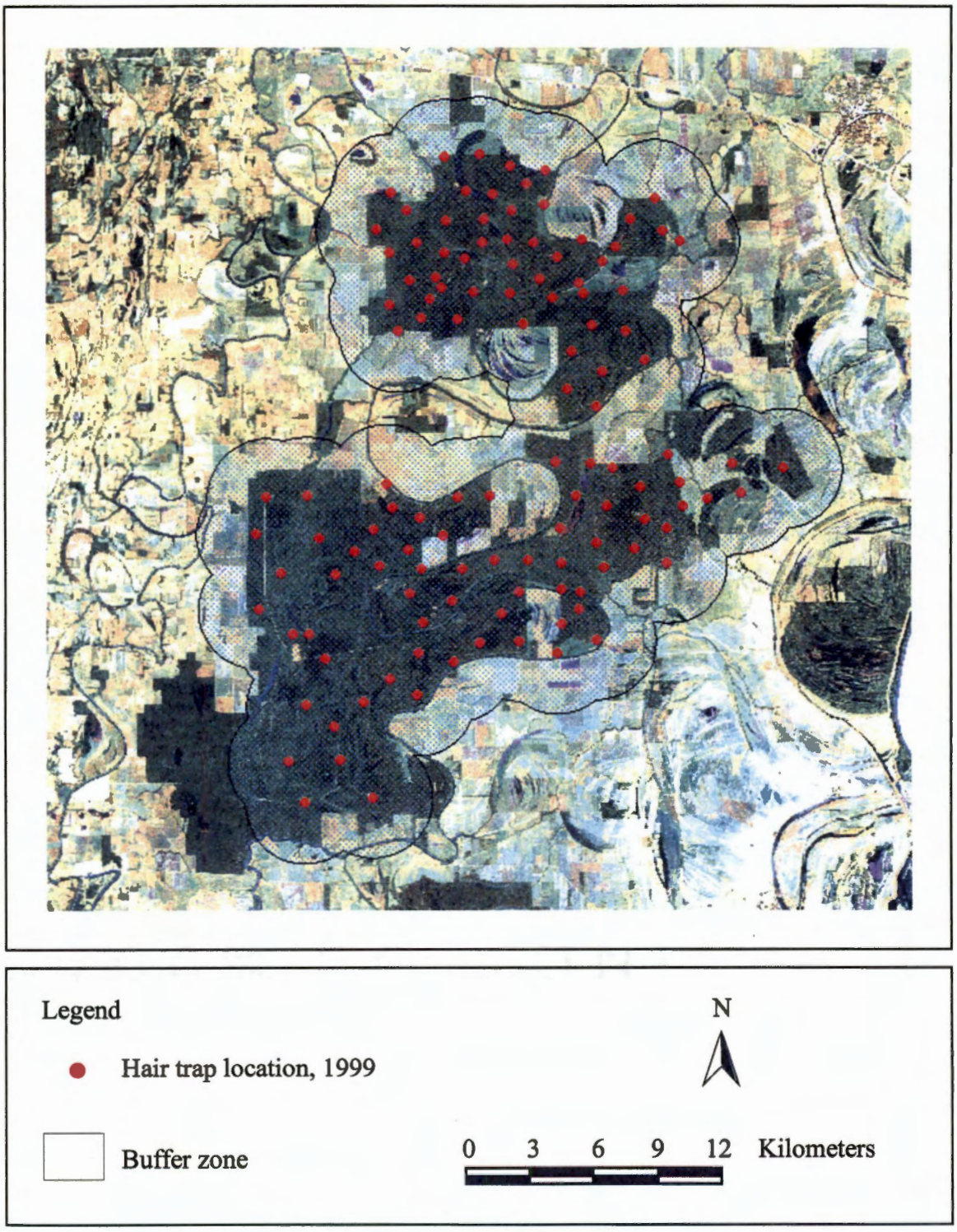

Fig. 4. Delineation of the Tensas River Tract study area from the 1999 hair-trap locations, northeast Louisiana.

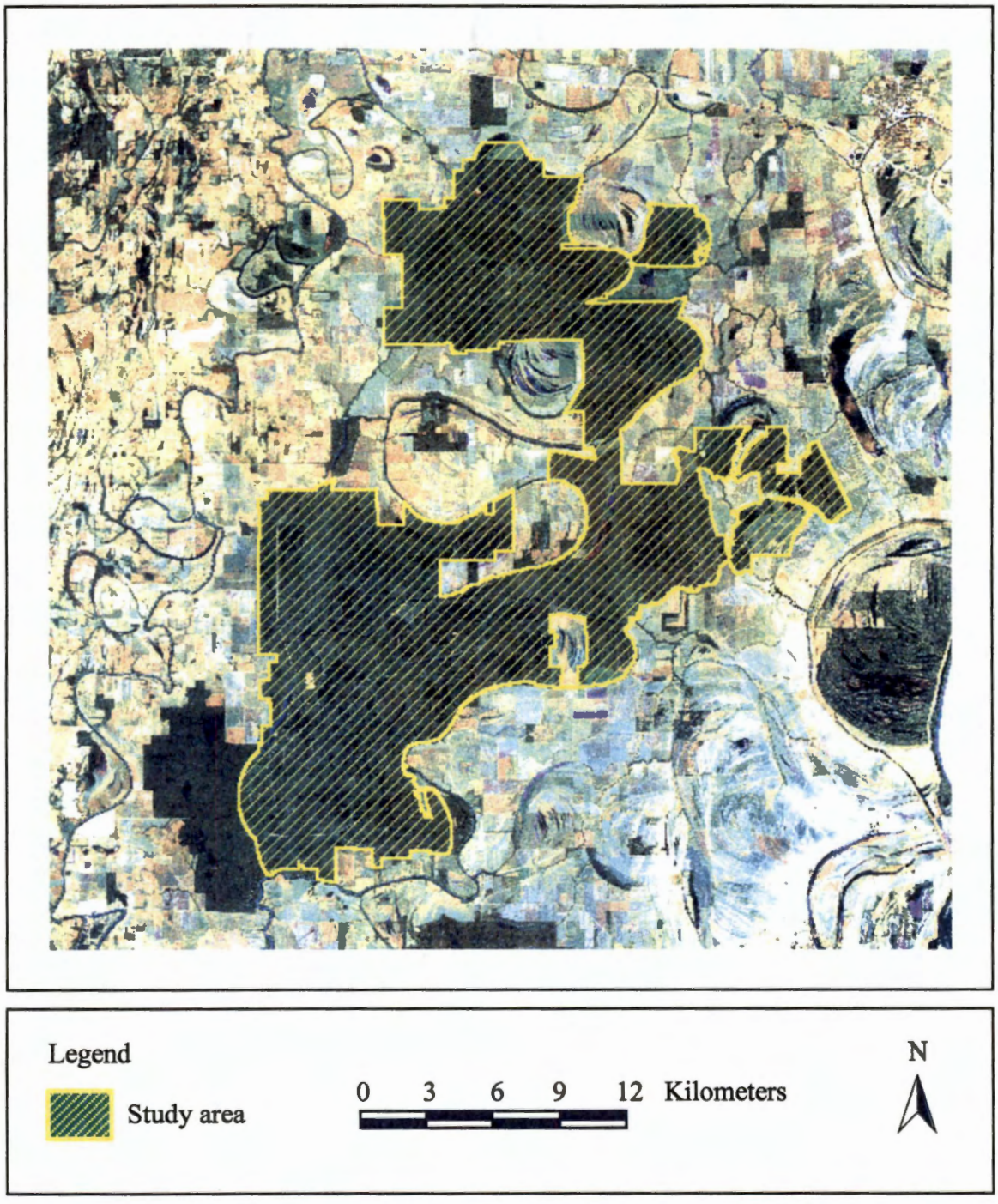

Fig. 5. The Tensas River Tract study area, northeast Louisiana, 1998–99.

each trap was set for an average of 14 days to provide more time to increase study area coverage.

Project personnel immobilized bears with an intramuscular injection of ketamine hydrochloride (Ketaset®, Fort Dodge Animal Health, Fort Dodge, Iowa) and xylazine hydrochloride (Rompun®, Bayer Corporation, Shawnee Mission, Kansas) at 8.8 mg/kg and 4.4 mg/kg estimated body mass, respectively. We used a blowgun (Pneu Dart, Williamsport, Pennsylvania) or jab stick to deliver immobilization drugs. After immobilization, a wetting agent (Akwa Tears, Akorn Incorporated, Abita Springs, Louisiana) was applied to the bear's eyes to prevent desiccation. A blindfold was used to protect the eyes of captured bears from debris and insects. We gave all bears an intramuscular injection of oxytetracycline antibiotic (LA-200®, Pfizer Animal Health, New York, New York) at 8.8 mg/kg body mass. Temperature and respiration were monitored throughout the handling procedures. We cooled all captured bears with ice packs and water to alleviate the effects of heat and humidity. Each bear was given a uniquely numbered ear tag and a corresponding lip tattoo number. In 1998, metal color-coded cattle ear tags were used. In 1999, small plastic hog tags (Fearing Corporation, South St. Paul, Minnesota) were used because of improved retention (R. Eastridge, University of Tennessee, personal communication).

We collected hair samples from each captured bear for microsatellite analysis. A first upper premolar tooth was extracted for aging by cementum annuli analysis (Willey 1974). Sectioning, staining, and aging of teeth was conducted by Mattson Laboratories (Milltown, Montana). Project personnel measured bear mass with a spring scale and took

measurements of a number of other morphological features. Those included: total body length, head length, head width, zygomatic circumference, neck circumference, chest circumference, shoulder height, forearm circumference, front pad length and width, hind pad length and width, teat length range for females, and baculum length for males. Upon completion of the data collection, yohimbine hydrochloride (Spectrum Laboratory Products, New Brunswick, New Jersey), an antagonist for xylazine hydrochloride, was administered through the sublingual vein or the femoral vein at a dosage of 0.2 mg/kg body mass.

Hairtrapping

Project personnel began large-scale hairtrapping following the conclusion of the live-trapping period in 1999. One-hundred twenty two hair-trapping stations were constructed throughout the Tensas River Tract, and adjacent forested private lands, averaging 1 hair trap per 270 ha of study area, or 9 hair traps per average female home range. Otis et al. (1978) suggested that population studies should be designed so that animals have ≥4 traps in their estimated home range; this implies that traps be spaced $\leq\sqrt{2}$ x W (W = average home range radius; White et al. 1982). Therefore, based on the most conservative estimate of home range radius of 2,779 m (100% minimum convex polygon home range estimate for females; Weaver 1999), traps were placed ≤3,930 m apart throughout the study area.

Hair traps were spaced ≤1,600 m apart in areas having relatively high bear densities to increase opportunities for hair capture and decrease effects of trap clogging.

White et al. (1982) recommend a systematic grid layout that provides equal spacing between adjacent hair traps. Because of limited access to several locations on the study area, however, systematic sampling was not possible at Tensas. Therefore, to provide adequate coverage, we placed hair traps adjacent to inaccessible areas. Hair traps were maintained for an average of 13.3 weeks (mode = 14).

Project personnel constructed hair traps by wrapping a single strand of barbed wire around 3–5 trees to form an enclosure (Fig. 6). Barbed-wire height above the ground was 40–50 cm, allowing bears to step over or crawl under the wire. Hair traps were constructed of 15½-gauge barbed wire. Barb spacing was 12.7 cm with 4 points per barb. The barbed wire was pulled tight between each tree with standard fencing tools. The wire was attached to trees with 3.8-cm fencing staples. Enclosures generally were 10–30 m^2 in size, depending on distances between trees. Irregularities in terrain, which caused the wire to be too high or too low, were blocked with debris.

Baits were hung inside the perimeter of each trap station with string tied between 2 or 3 anchor trees. Bears were not able to reach the baits without entering the enclosure. Traps were baited with bakery products, sardines, and meat scraps. Scent lures and cane syrup (Norris Syrup Company, Monroe, Louisiana) also were used to entice bears.

UTM coordinates were recorded for each hair trap with GPS receivers. Each strand of barbed wire was marked with brightly colored flagging for public safety. Prior to the start of the hunting seasons, reflective warning signs were added at each hair-trap site to further alert hunters. Additionally, signs were placed at each entrance to the study area to explain the research and alert the public to the presence of the hair traps.

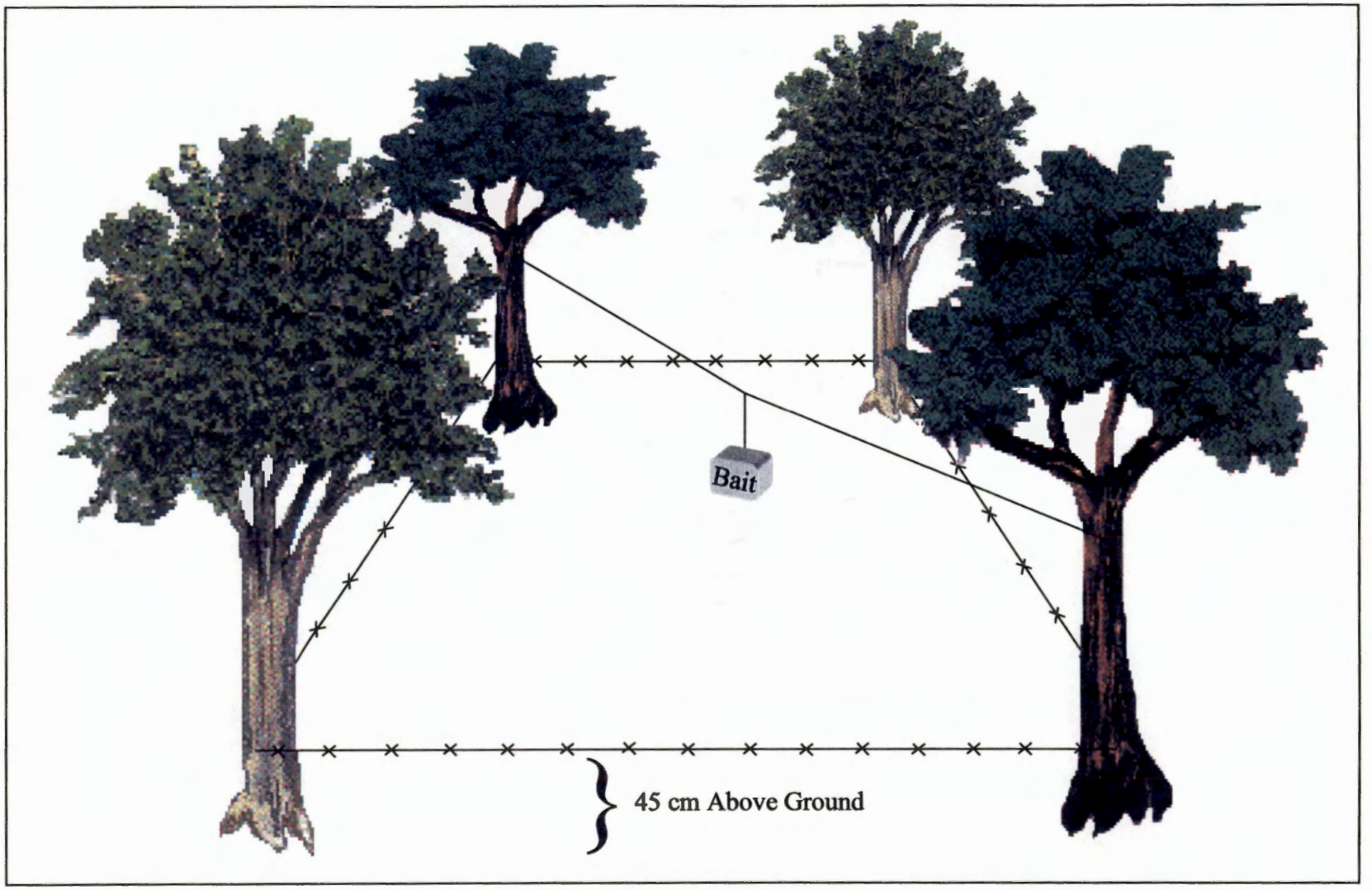

Fig. 6. Barbed wire hair trap enclosure used for the Tensas River Tract population study, Louisiana, 1998–99.

Hair traps were checked about every 7 days at which time hair samples were collected, baits were replenished, scent lures refreshed, and the barbed wire was tightened as needed. Hair collected from each barb was considered a separate sample and stored in individual coin envelopes. After removal of each hair sample, a cigarette lighter was used to burn off any remaining hair, preventing cross-contamination of future samples. All hair samples were frozen in a household freezer to prevent degradation of DNA. Frozen hair samples were stored in airtight, re-sealable plastic bags with color-indicating desiccant (Drierite®, W.A. Hammond Drierite Company Ltd., Xenia, Ohio).

Each week could be treated individually as a sampling occasion, or data from sequential weeks could be pooled to reduce the overall number of occasions. I chose not to make the hair-trapping sessions longer than 7 days because of concern over the increased chance of sampling multiple bears and the risk of DNA degradation in the hot and humid environment at Tensas (K. Kendall, U.S. Geological Survey, personal communication). As a measure of hair-trapping success, I used the number of bear visits resulting in a hair capture divided by the number of sampling sessions during the sampling period. I defined hair-trap sessions as the number of active hair traps times the number of weeks the hair traps were activated.

Subsampling and Microsatellite Analysis

When bears visited the hair traps, hair samples were often collected on >1 barbs. In those cases, a single sample was randomly subsampled for analysis from those collected from each bear visit from 27 July to 9 September 1999. However, there was a

large increase in the number of samples collected after 10 September 1999. Consequently, I chose for analysis only 1 sample from every 4 bear visits resulting in hair capture subsequent to that date. Of all the samples, only those with ≥10 hairs were considered for analysis to reduce the probability of genotyping errors (Goossens et al. 1998).

Preparation of hair samples was conducted at The University of Tennessee. Samples were thawed and visually inspected for attached roots. I clipped approximately 0.6 cm of the root end of each hair and placed all roots from each sample into a 1.5-ml centrifuge tube. All cut hair samples were shipped to the U.S. Geological Survey Aquatic Ecology Laboratory at the Leetown Science Center, Kearneysville, West Virginia for microsatellite analysis.

A suite of 8 microsatellite loci were analyzed for all hair samples selected for analysis. Those loci were described by Paetkau and Strobeck (1994; G1A, G1D, G10B and G10L); and by Paetkau et al. (1995; G10C, G10M, G10P, and G10X). All samples with matching genotypes were further analyzed at 4 additional loci ([UarMU10, UarMU23, UarMU50; Taberlet et al. 1997]; [G10J; Paetkau et al. 1998]) to improve the probability of identity.

Probability of Identity

Correct identification of individuals is essential for mark-resight experiments (Pollock et al. 1990). Hair samples with identical genotypes were assumed to come from

the same individual, although it is possible for ≥2 bears in a population to have identical genotypes based on the loci examined (Woods et al. 1999).

The probability that multiple animals share the same observed genotype can be estimated from the multilocus allele frequency distribution of the bears identified during the hair-sampling period. That parameter is known as the probability of identity (PI) and was first estimated for each locus by:

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

where p_i and p_j are the frequencies of the ith and jth alleles (Paetkau and Strobeck 1994). Calculation of $PI_{\text{single locus}}$ assumes the allele genotypes are in Hardy-Weinberg proportions (Taberlet and Luikart 1999). The Hardy-Weinberg law is based on the following requirements (Wessells and Hopson 1988):

1) random mating within the population,
2) large population size,
3) no genetic mutations,
4) isolation of the population prohibiting gene flow, and
5) no natural selection of alleles.

Consequently, the assortment of alleles at each locus must be independent.

A PI across all loci can then be calculated as (Paetkau et al. 1995, Parker et al. 1998):

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

The calculation of $PI_{overall}$ assumes independence between alleles at different loci (Taberlet and Luikart 1999, Mills et al. 2000); the presence of linkage disequilibrium may cause bias in this estimate.

Few, if any, natural populations could completely satisfy all of these assumptions, including the black bear population at Tensas. Tensas bears are isolated and the microsatellite markers used for identification may not be subject to natural selection (Wright 1993). However, the population size is relatively small, random mating among bears is not typical with dominant males making the largest contribution to breeding (Rogers 1987), and microsatellites are subject to mutation (Schug et al. 1997). This calculation for PI tends to be biased low when the underlying assumptions are not met. Populations containing many closely related individuals can have substantially low biased estimates of PI (Taberlet and Luikart 1999). This bias is most severe where large numbers of siblings are present in the population (Donnelly 1995). Consequently, the above estimate represents a lower limit in the range of possible PIs for a population.

An alternative computation for PI, which estimates the identity probability among randomly sampled siblings is (Taberlet and Luikart 1999):

$$PIsibs_{\text{single locus}} = 0.25 + \left(0.5\sum p_i^{\,2}\right) + \left[0.5\left(\sum p_i^{\,2}\right)^2\right] - \left(0.25\sum p_i^{\,4}\right).$$

Calculation of PI*sibs* requires the same assumptions as $PI_{overall}$ and is also calculated as the product of the $PIsibs_{\text{single locus}}$ values across all loci. However, PI*sibs* represents the upper limit for the theoretical range of PI values thus producing a more conservative estimate (Taberlet and Luikart 1999).

$PI_{overall}$ and PI*sibs* estimate average probability of identity over all observed genotypes. Multilocus genotypes comprised of many common alleles are more likely to be present in >1 animal over a given set of loci than genotypes containing rare alleles (Woods et al. 1999). Woods et al. (1999) described 3 match tests, which provide PI estimates for each observed genotype identified from the barbed-wire trapping sample. The sibling match test, the most conservative of these tests, calculates the probability that a given individual will have the same observed genotype as its sibling and is estimated by:

$$P_{sib} = \left(1 + 2p_i + p_i^2\right)/4, \text{ for homozygotes, and}$$

$$P_{sib} = \left(1 + p_i + p_j + 2p_i p_j\right)/4, \text{ for heterozygotes (Woods et al. 1999).}$$

Thus, I used the sibling match test to identify 8 loci genotypes that may not be unique to an individual. Multilocus genotypes with P_{sib}<0.05 were considered to be distinct. Hair samples that did not satisfy this condition were not used to estimate population size (Woods et al. 1999, Mowat and Strobeck 2000).

Hardy-Weinberg and Linkage Disequilibrium Tests

Null alleles are the result of a mutation or deletion in the DNA sequence flanking the microsatellite, inhibiting the primer from binding to its complementary site (Paetkau and Strobeck 1995, Pemberton et al. 1995). Consequently, heterozygous individuals that have 2 different alleles at the locus in question will be mistakenly scored as homozygotes due to the observation of only 1 allele (Bruford and Wayne 1993).

I tested for evidence of inbreeding in the population, null alleles in the genetic data and, therefore, violations to the assumptions for calculation of $PI_{single\ locus}$, by use of the Hardy-Weinberg probability test in Program GENEPOP 3.1 (Raymond and Rousset 1995). This analysis tests the null hypothesis that the union of gametes is random and homozygote genotypes occur at a frequency expected from the overall allele frequency distribution (T. L. King, U.S. Geological Survey, personal communication). I examined individual tests for each locus (Paetkau et al. 1998) for all genotypes analyzed at 8 loci, and the subset of samples analyzed at 12 loci (T. L. King, U.S. Geological Survey, personal communication).

Gametic phase (or linkage) disequilibrium is defined as the non-random association between alleles of different microsatellite loci (Waples 1991, Avise 1994). This condition may arise after a population bottleneck because of associated random genetic drift (Allendorf 1986, Waples 1991). I used the linkage disequilibrium test in Program GENEPOP 3.1 (Raymond and Rousset 1995) to test for allele associations between all pairs of loci. This test evaluates the underlying assumption of random gametic association between alleles at the different microsatellite loci analyzed for the calculations of $PI_{overall}$ and $PI\mathit{sibs}_{overall}$. The original 8 microsatellite markers used in my study have been found to be independent (Paetkau and Strobeck 1994, Paetkau et al. 1995). Therefore, the presence of significant linkage among loci pairs within my dataset may indicate sampling bias, non-random mating within the population, or stochastic processes (i.e. genetic drift) which act upon small populations (T. L. King, U.S. Geological Survey, personal communication).

Population Size Estimation

General. All capture-recapture or mark-resight models fall into 2 categories. Closed models assume the population size is constant through the duration of the study (White et al. 1982, Pollock et al. 1990); there can be neither births or deaths (demographic closure) nor immigration or emigration (geographic closure) between sampling occasions. These models are appropriate for relatively short periods of time (Pollock et al. 1990) during non-breeding seasons (Otis et al. 1978). Open models are typically used for estimating population size, survival, and recruitment rates over longer time periods (Otis et al 1978). Therefore, additions to the population through births and immigration and permanent deletions from deaths and emigration are allowed (Pollock et al. 1990). Because open models contain more variables than closed models, more data are usually required to produce estimates with similar precision (Otis et al. 1978).

I used a combination of several closed population models to estimate the black bear population size on the Tensas River Tract. The modified Lincoln-Petersen model was used to estimate population size with data from the first and second halves of the 1999 hair-trapping season (Fig. 7). Additionally, I used the closed multiple mark-recapture models described by Otis et al. (1978) and White et al. (1982) for within-year estimates using the 1999 hair-trap data. Otis et al. (1978) detailed several models that allow relaxation of ≥ 1 of the standard mark-recapture assumptions required by the most restrictive model, M_o. I examined the entire set of models and selected the most reasonable model that best fit the data according to criteria described by Otis et al. (1978).

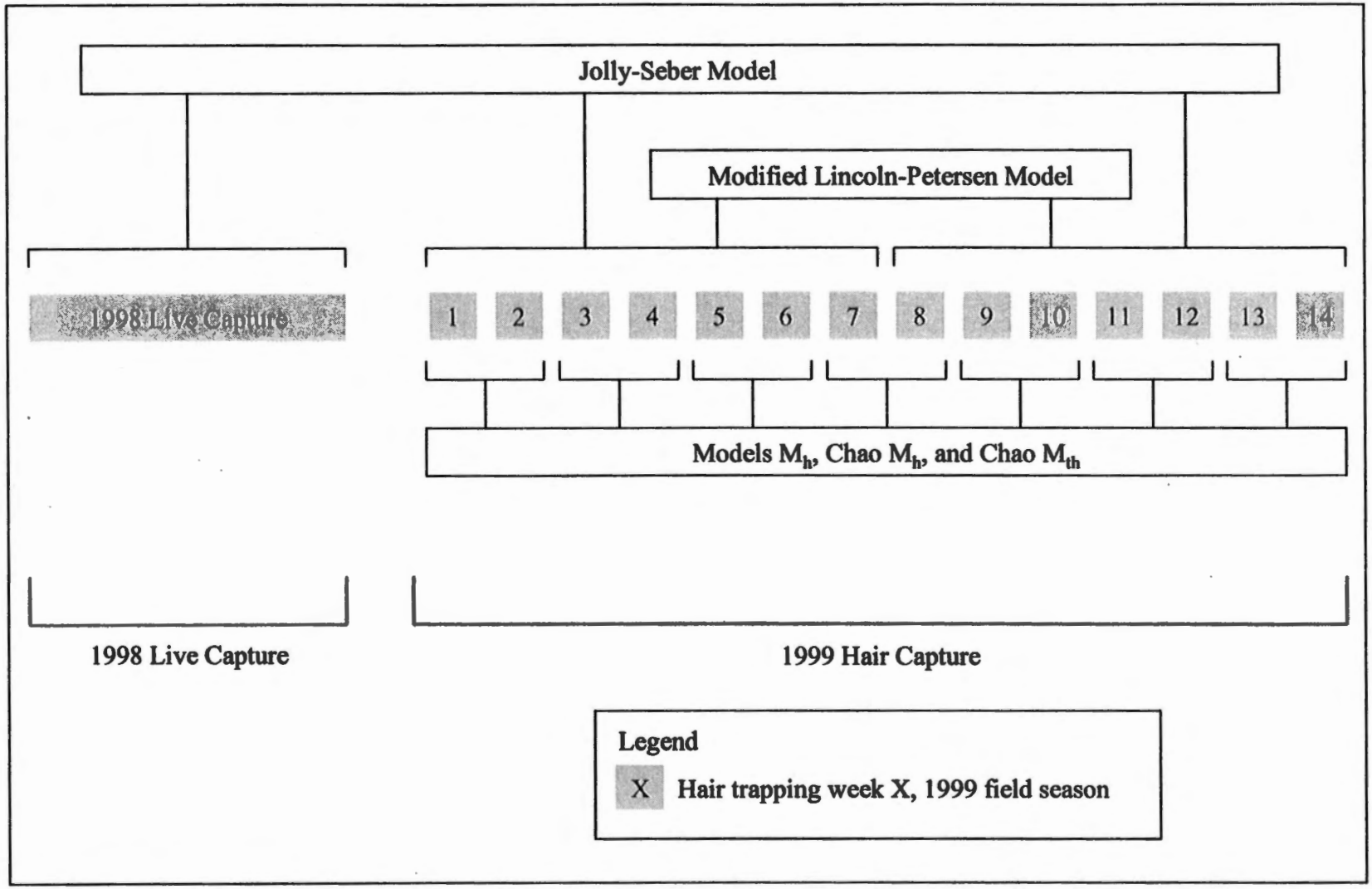

Fig. 7. Mark-resight models used to estimate black bear population size at the Tensas River Tract, northeast Louisiana, 1998–99.

The Jolly-Seber model, an open model, was also used to estimate population size with the live-capture data from 1998 and the hair-trap resight data from 1999 (Jolly 1965, Seber 1965, Pollock et al. 1990). Special cases of the general Jolly-Seber model require stricter assumptions, resulting in estimation of fewer parameters, but with a concomitant increase in precision (Pollock et al. 1990). These models also were evaluated for improved model fit. For all models, several pooling configurations of the 1999 hair-trap data were considered to maximize capture probabilities while minimizing data loss (Fig. 8). Capture histories were pooled by combining data from sequential hair-trapping weeks and counting the number of unique individuals in each lengthened sampling occasion (Menkins and Anderson 1988).

The multiple mark-recapture and Jolly-Seber models require the complete capture histories of the animals sampled during the study. A SAS program (SAS Institute, Inc. 1988) was written to generate the full capture histories for the 1999 hair-capture data. All resight histories and, therefore, estimates of population size, were derived from resight data based entirely on microsatellite genetic markers. Accordingly, the requirement of permanent marks for each animal was met.

Modified Lincoln-Petersen Model. The modified Lincoln-Petersen model provides an estimate of population size based on 2 periods of sampling. Population size is estimated by (Chapman 1951)

$$\hat{N}_C = \left[\frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} \right] - 1,$$

with an approximately unbiased estimate of variance (Seber 1970, 1982:60) calculated as

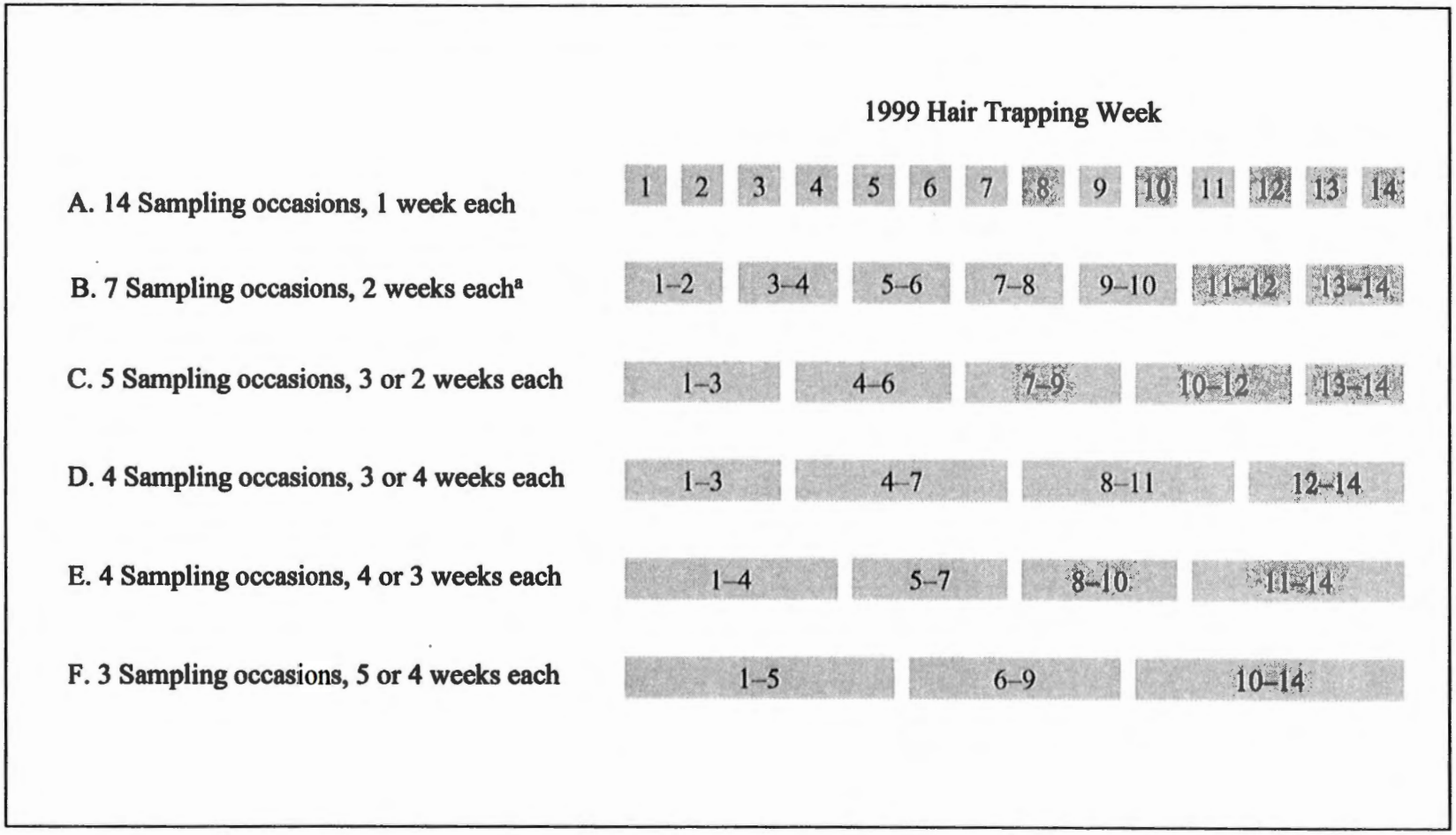

Fig. 8. Sampling occasion configurations considered for multiple mark-recapture models to estimate population size at the Tensas River Tract, northeast Louisiana, 1999 ([a] indicates chosen configuration).

$$\operatorname{var}\hat{N}_C = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)},$$

where $\hat{N}$ = population size, n_1 = the number of animals marked in capture period i, n_2 = the number of marked animals captured in period $i + 1$, and m_2 = the number of animals captured in period $i + 1$. The modified Lincoln-Petersen model is based on the assumptions that:

1) the population is geographically and demographically closed,
2) all animals have an equal probability of being captured in each sample,
3) marks are not lost and are recorded correctly upon capture, and
4) marks do not affect probability of future capture.

For the hair-trap data collected in 1999, the marking period was from late July to mid-September (1st half), whereas the resight period was from mid-September to early November (2nd half).

Multiple Mark-Recapture Models. Otis et al. (1978) described a set of 8 closed models appropriate for mark-recapture data when >2 periods are sampled. Assumptions of the equal catchability model (M_o) are:

1) the population is closed to additions and deletions,
2) all animals have an equal probability of being captured in each sample,
3) marks are not lost and are correctly recorded upon capture, and
4) marks do not affect probability of future capture.

This model is the most restrictive of the multiple mark-recapture models. Assumption (2) is not met in most studies of natural populations (Carothers 1973*a*, White et al. 1982) and

several models have been developed that allow its relaxation (Otis et al. 1978, Chao 1987, Chao et al. 1992). I evaluated all the specialized models, including model M_o described by Otis et al. (1978), for the hair-trap resight data in this study.

Model M_h, the heterogeneity model, allows the capture probability to vary for each animal. The time variation model, model M_t, allows capture probabilities to vary only by time. The behavioral response model (M_b) accounts for the influence of trap response on the probability of capture (Otis et al. 1978, White et al. 1982). Three other models that I considered were M_{bh}, M_{bt}, and M_{tbh}; these allow combinations of the above forms of capture heterogeneity.

I also considered 3 additional multiple mark-recapture models described by Chao (1987, 1988, 1989) and Chao et al. (1992). Two of these models are intended to provide reliable estimates of population size when average capture probabilities are low. These models are characterized by alternative calculations for the heterogeneity and time variation models (M_h, M_t) presented by Otis et al. (1978). Population size is estimated strictly from the first 2 or 3 capture frequency counts. Assumptions for the Chao M_h and Chao M_t models are the same as those of their M_h, and M_t counterparts. In the presence of both time and individual heterogeneity effects, population size is estimated by model Chao M_{th}.

I used Program CAPTURE to compute estimates of population size and associated standard errors for the multiple mark-recapture models (Rexstad and Burnham 1992). This computer program provides estimates for all models previously discussed, except model M_{thb} for which no estimator has been derived (White et al. 1982). A model

selection procedure within Program CAPTURE uses chi-square goodness-of-fit tests to suggest the most appropriate model for a particular set of data. These tests identify various types of capture heterogeneity, which may result in biased estimates under inappropriate models. As an additional test for heterogeneity, I used a test described by Caughley (1977) that compares observed capture frequencies to a zero-truncated Poisson distribution.

Program CAPTURE provides a procedure to test the assumption of population closure. The closure test examines the alternative hypothesis that some bears captured ≥ 2 times were not available for capture during the initial or late periods of the study (Otis et al. 1978). Although the test is not adversely affected by individual heterogeneity of capture probabilities (Otis et al. 1978), in the presence of time and behavior effects, the test is unreliable (White et al. 1982). Therefore, I used the closure test only to aid in selecting between different data pooling configurations where individual heterogeneity models were considered.

Many of the multiple mark-recapture models used within Program CAPTURE do not have "closed form" estimators for population size. That is, it is impossible to express population size in a simple formula in which all terms are equated to N alone (Otis et al. 1978). Such algorithms for producing the maximum likelihood estimates for models M_o, M_t, M_b, M_{bh}, and the jackknife estimate for model M_h are detailed in Otis et al. (1978) with associated variance formulas. The original calculation for variance for model M_h, which led to poor confidence interval coverage (Otis et al. 1978), was changed in the version of Program CAPTURE that I used (version 16 May 1994). Rexstad and

Burnham (1992) described the improved calculation method, which enhanced coverage of the confidence interval.

The heterogeneity model developed by Chao (1987, 1988), Chao M_h, has a closed form estimator. This model estimates population size as:

$$\text{Chao } \hat{N}_h = S + \frac{f_1^2}{2f_2},$$

or,

$$\text{Chao } \tilde{N}_h = S + \left[\frac{f_1^2}{2f_2}\right]\left\{\left[1 - \frac{2f_2}{tf_1}\right] \Big/ \left[\frac{(1-3f_3)}{tf_2}\right]\right\} \text{ if } tf_1 > 2f_2,\ tf_2 > 3f_3, \text{ and } 3f_1f_3 > 2f_2^2,$$

where S = the number of individuals captured in the experiment, f_k = the number of animals captured exactly k times, and t = the number of sampling occasions (Chao 1988). Estimates of variance are calculated as:

$$\text{var}\left(\text{Chao } \hat{N}_h\right) = f_2\left[0.25\left(\frac{f_1}{f_2}\right)^4 + \left(\frac{f_1}{f_2}\right)^3 + 0.5\left(\frac{f_1}{f_2}\right)^2\right],$$

and,

$$\text{var}\left(\text{Chao } \tilde{N}_h\right) = f_2\left[0.25A^2\left(\frac{f_1}{f_2}\right)^4 + A^2\left(\frac{f_1}{f_2}\right)^3 + 0.5A\left(\frac{f_1}{f_2}\right)^2\right],$$

where

$$A = \left[\frac{(1-2f_2)}{tf_1}\right] \Big/ \left[\frac{(1-3f_3)}{tf_2}\right] \text{ (Chao 1988).}$$

Closed form estimators for model Chao M_t are described by Chao (1989). Model Chao M_{th} estimates population size based on the sample capture probability coverage

(Chao et al. 1992). Sample coverage C is defined as the proportion of the total individual capture probabilities of the bears captured in the experiment (Chao et al. 1992). Three estimates of Chao $\hat{N}_{th}$ are computed; each estimate is appropriate for a different range of coefficients of variation (CV) of the capture probabilities. Population size is estimated by:

$$\text{Chao } \hat{N}_{ith} = \frac{S}{\hat{C}_i} + \frac{f_1}{\hat{C}_i}\hat{\bar{\gamma}}_i^2, \qquad i = 1, 2, 3,$$

where,

$$\hat{C}_1 = 1 - \frac{f_1}{\sum_{k=1}^{t} k f_k}, \quad \hat{C}_2 = 1 - \frac{(f_1 - 2f_2)/(t-1)}{\sum_{k=1}^{t} k f_k}, \quad \hat{C}_3 = 1 - \frac{(f_1 - 2f_2)/(t-1) + 6f_3/[(t-1)(t-2)]}{\sum_{k=1}^{t} k f_k},$$

$$\hat{\bar{\gamma}}_i^2 = \max\left\{ \hat{N}_{0,i} \sum_k k(k-1) f_k \Big/ \left[2 \sum_j \sum_{k>j} n_j n_k \right] - 1, 0 \right\}, \quad i = 1, 2, 3,$$

$$\hat{N}_{0,i} = S / \hat{C}_i, \qquad i = 1, 2, 3,$$

k = the number of times an animal was captured, n_i = the number of animals captured in sample i, j = the sampling occasion, and $\bar{\gamma}$ = the CV of the capture probabilities (Chao et al. 1992). In general, Chao $\hat{N}_{1th}$ is appropriate when $\bar{\gamma} \geq 0.8$ and Chao $\hat{N}_{2th}$ or Chao $\hat{N}_{3th}$ are suitable when $0.4 \leq \bar{\gamma} < 0.8$ (Chao et al. 1992). The procedures for estimating variance for Chao M_{th} are described by Chao et al. (1992).

Program CAPTURE produces asymmetrical confidence intervals for all multiple mark-recapture models. These intervals are based on the assumption that all the individuals in the population that were not sampled in the experiment are log-normally

distributed (Rexstad and Burnham 1992). The lower and upper bounds of the confidence interval (95%) are estimated as:

$$\left[S+\frac{f_0}{C},\quad S+f_0\cdot C\right],$$

where f_0 = the number of individuals in the population that were not sampled during the experiment, and

$$C=\exp\left(1.96\sqrt{\log\left[1+\frac{\mathrm{var}\left(\hat{N}\right)}{f_0^{\,2}}\right]}\right)\text{(Chao 1989).}$$

These calculations of confidence intervals produce lower bounds that cannot be smaller than S. The upper bounds of the intervals also tend to be larger than those calculated in the more general approach outlined by Otis et al. (1978; Rexstad and Burnham 1992).

Jolly-Seber Model. I used Program JOLLY to compute estimates of population size using the open Jolly-Seber model (Pollock et al. 1990). The assumptions of model A, the most general Jolly-Seber model in terms of underlying assumptions, are:

1) the population is open to additions from births and immigration, and deletions from deaths and permanent emigration,
2) every animal has an equal probability of capture within each sampling occasion,
3) every animal within the population after sample i has an equal survival probability until sample $i + 1$,
4) marks are not lost and are correctly recorded, and
5) all samples are instantaneous.

Model A', the deaths only model, allows deletions to the population, but prohibits additions. Model B is the constant survival model and requires that survival probabilities do not vary throughout the duration of study. Model D is for cases where both survival and capture probabilities are constant during the investigation. Model 2 is the temporary trap response model, which allows for a short-term effect of capture on the survival and capture probabilities.

Program JOLLY provides goodness-of-fit tests to aid in the selection of appropriate models. The 2 components of those tests require expected cell counts ≥ 2 (Pollock et al. 1990). The Jolly-Seber model estimates population size by:

$$\hat{N}_i = \frac{n_i M_i}{m_i}$$

and,

$$\hat{M}_i = m_i + \frac{n_i z_i}{r_i} \qquad \text{or} \qquad \hat{M}_i = m_i + \frac{R_i z_i}{r_i} \qquad \text{if } R_i < n_i$$

where n_i = the number of individuals captured (or observed) in sample i; $\hat{M}_i$ = the number of marked animals in the population at the time the i^{th} sample is taken; m_i = the number of marked animals captured in sample i; z_i = the number of animals observed before i, that are not observed in sample i, but observed again in a later sample; R_i = the number of animals released after sample i; and r_i = the number of animals released from i that are subsequently captured (Pollock et al. 1990).

The sampling periods for the Jolly-Seber estimates consisted of the 1998 live-trapping season, coupled with the 6 different pooling configurations considered for the

multiple mark-recapture models. Additionally, I calculated estimates based on the capture data from 1998, together with the 1999 hair-sampling session split into 2 7-week periods. Bears captured outside the study area and known mortalities were not included in the Jolly-Seber estimate.

Population Density

I compared the bear population at Tensas to populations elsewhere by computing an average density estimate for the entire Tensas River Tract. To provide an average density estimate, I divided the estimate of population size by the size of the study area delineated by the 1999 hair-trap locations. Confidence intervals of the density estimate were calculated by dividing the upper and lower bounds of the population estimate by the size of the study area.

CHAPTER IV

RESULTS

Trapping

In 1998, 141 traps were set for 2,816 trapnights. Thirty-two bears were captured 38 times (16M:16F) resulting in trap success of 1.3%, or 74 trapnights per capture. U.S. Fish and Wildlife Service personnel had previously captured 12 of these bears. Project personnel radio collared 6 females to allow monitoring by Refuge staff. One collared bear (#442) was poached during the 1998 fall deer hunting season and recovered by law enforcement personnel (D. R. Anderson, U.S. Fish and Wildlife Service, personal communication).

In 1999, 1,322 trapnights were recorded at 84 trap sites. Project personnel captured 11 bears on 12 occasions (3M:8F). Trapping success during 1999 was 0.9% and averaged 110 trapnights per capture. One bear (#414) was a recapture from the 1998 field season. Additionally, 1 other bear captured in 1999 had been previously handled by U.S. Fish and Wildlife Service employees.

Over the 2 years of trapping, traps were placed in 225 locations on the area with trapping success averaging 1.2%, or 83 trapnights per capture. The sex ratio of captured bears (18M:24F) did not differ from 1:1 ($\chi^2_{0.05} = 0.857$, 1 df, $P = 0.355$).

Hairtrapping

Overall, 1,627 hair-trap sessions were recorded in 1999, resulting in 688 bear visits, of which 568 (82.6%) produced ≥1 hair sample. A total of 1,939 hair samples were collected during 1999. Twelve bears (3M:9F) livecaptured in 1998 were detected at hair traps during the 1999 hair-trapping season. Success of hair-trapping was higher on the Jud Brake and East Fool River units than on the West Fool River and Big Lake units (Fig. 9). Overall, hair-trapping success was 34.9%, averaging 2.9 trapsessions per hair-capture event.

Microsatellite Analysis

Multilocus microsatellite genotypes were obtained from hair samples for 41 of 42 (98%) live-captured bears. All individuals had unique genotypes based on 8 loci.

From the 1999 hair-trapping season, 116 hair samples were chosen for microsatellite analysis, of which complete multilocus genotypes were obtained for 110 (of 114 or 95%). Additional samples for 4 that were not successful were resubmitted using samples from those same 4 hair traps. That increased the hair-sample total to 114, from which 58 bears were identified. Further analysis at the 4 additional loci was completed on 92 samples representing 36 individuals to confirm genetic matches, including 19 bears that were livecaptured in 1998 and 1999, and visited the hair-trap stations in 1999. One hair sample, obtained from a live-captured bear (#442) in 1998, was identical to other barbed-wire hair samples based on the first 8 loci, but was found to be unique using the additional loci. At each locus, 2–6 alleles were observed (Tables 1

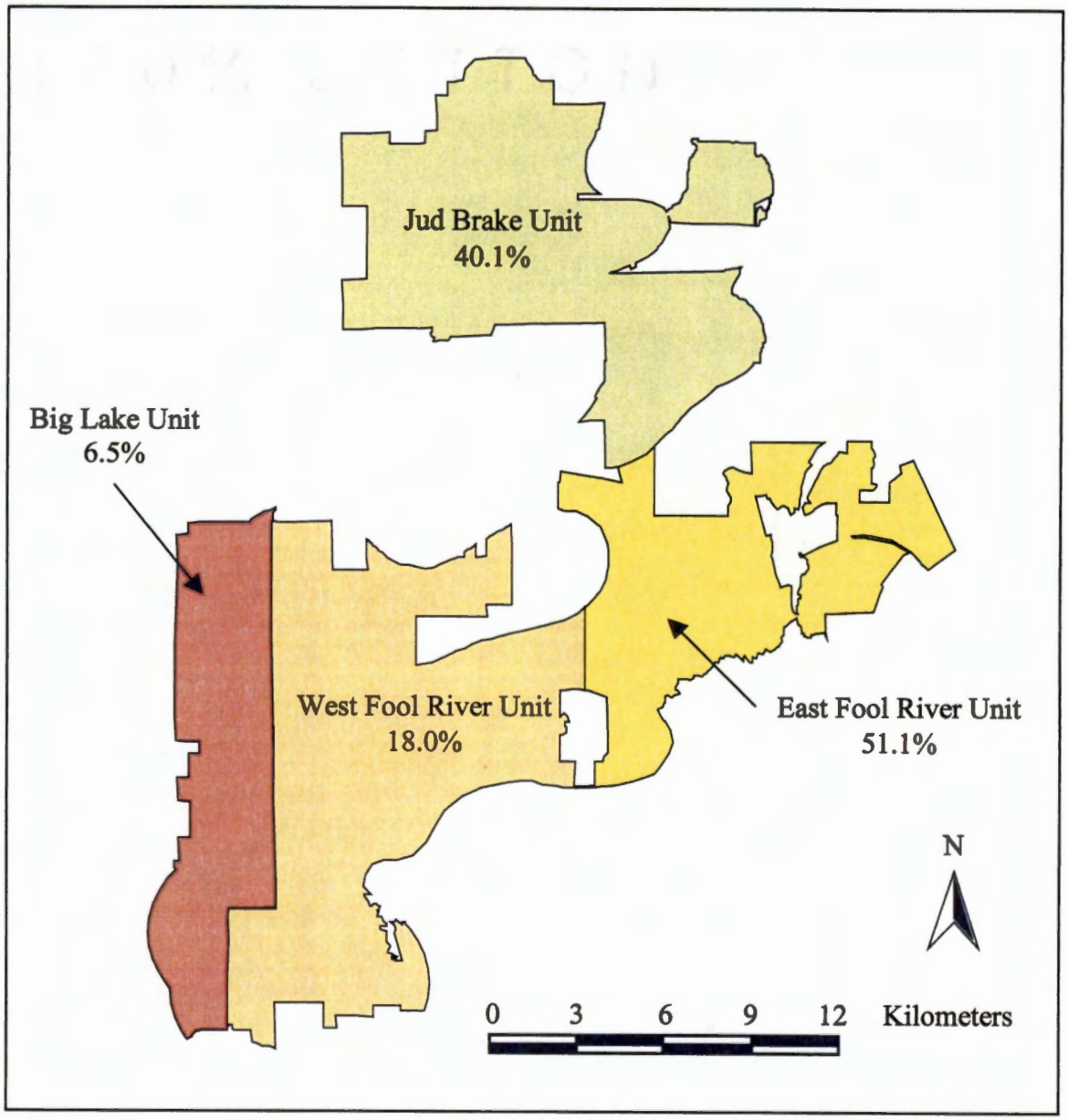

Fig. 9. Study area units and associated success rates of hairtrapping on the Tensas River Tract, northeast Louisiana, 1999.

Table 1. Observed alleles and frequencies for 58 black bears identified from barbed-wire hair traps for the Tensas River Tract, northeast Louisiana, 1999.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1A	183	5	0.043	G1D	176	62	0.534
	187	108	0.931		186	39	0.336
	189	1	0.009		190	15	0.129
	191	2	0.017				
G10B	157	57	0.491	G10C	112	90	0.776
	163	26	0.224		114	26	0.224
	165	33	0.284				
G10L	133	99	0.853	G10M	211	14	0.121
	153	13	0.112		213	53	0.457
	157	3	0.026		215	47	0.405
	159	1	0.009		217	2	0.017
G10P	148	33	0.284	G10X	144	21	0.181
	152	52	0.448		152	78	0.672
	158	9	0.078		158	17	0.147
	160	5	0.043				
	166	17	0.147				

and 2). Average heterozygosity was 47.4% (n = 58) for the original 8 loci, whereas heterozygosity for the additional 4 loci was 57.6% (n = 36). Twelve of 32 (37.5%) captured bears from 1998 were detected at hair traps during 1999, whereas 7 of 11 (63.6%) bears captured in 1999 were later detected at hair traps. Seven of the 114 (6%) samples from hair traps were obtained from bears that visited traps more than once within a sampling session and, therefore, were excluded from the hair-capture histories.

Hardy Weinberg and Linkage Disequilibrium

The probability test for Hardy-Weinberg equilibrium was used to check for evidence of non-random mating in the population and the presence of null alleles. For the 58 individuals identified from the 1999 hair traps, evidence of non-random mating was detected for 2 loci (G1A, P = 0.023; G10M, P = 0.018) at the 5% level, but not when applying the Bonferroni experimentwise error rate (Rice 1989, Sokal and Rohlf 1995). Non-random mating was detected for 3 loci (G1A, P = 0.033; G10J, P = 0.031; UarMU50, P = 0.023) when testing the 36-individual subset over 12 loci; however, no tests were significant after Bonferroni correction.

Linkage disequilibrium tests were used to examine possible associations between pairs of alleles at different loci. No associations were detected taking into consideration the number of comparisons (28 tests) of 8 loci for 58 bears identified during the 1999 hair-trapping session. Two loci pairs (G1D vs. G10M, P = 0.002; G1A vs. G10X, P = 0.002), however, had P-values only slightly greater than the comparison-wise significance level of 0.0018. Pairwise tests comparing the 36-individual subset analyzed

Table 2. Observed alleles and frequencies for 36 black bears identified from barbed-wire hair traps for the Tensas River Tract, northeast Louisiana, 1999.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G1A	183	5	0.069	G10M	211	8	0.111
	187	65	0.903		213	29	0.403
	191	2	0.028		215	33	0.458
					217	2	0.028
G10B	157	37	0.514	G10X	144	17	0.236
	163	15	0.208		152	44	0.611
	165	20	0.278		158	11	0.153
G10L	133	63	0.875	G10J	101	62	0.861
	153	7	0.097		103	2	0.028
	157	1	0.014		117	8	0.111
	159	1	0.014				
G10P	148	18	0.250	UarMU10	101	9	0.125
	152	35	0.486		109	1	0.014
	158	6	0.083		111	40	0.556
	160	2	0.028		117	22	0.306
	166	11	0.153				
G1D	176	34	0.472	UarMU23	153	26	0.361
	186	28	0.389		157	34	0.472
	190	10	0.139		167	8	0.111
					171	3	0.042
					175	1	0.014
G10C	112	56	0.778	UarMU50	206	37	0.514
	114	16	0.222		208	6	0.083
					222	2	0.028
					224	22	0.306
					226	1	0.014
					230	4	0.056

over 12 loci also showed no associations after adjustment for the number of tests examined (66 tests). Nevertheless, 3 pairs of loci (G10L vs. G1D, $P = 0.004$; G1A vs. G10X, $P = 0.004$; G1A vs. G10J, $P = 0.006$) had relatively low probability values.

Probability of Identity

The theoretical PI based on the distribution of alleles at the original 8 microsatellite loci for 58 individuals sampled with hair traps was 1.14×10^{-4} corresponding to 1 chance in 8,750 of having identical genotypes in the population. This estimate was similar to the 8-loci PI estimate of 1.01×10^{-4} for the subset of 36 individuals analyzed at all 12 loci. Microsatellite analysis of the 4 additional loci increased overall PI to 5.70×10^{-7} (Table 3), approximating a 1 in 1.75 million ($n = 36$) chance of finding 2 identical genotypes in the Tensas bear population. Individual locus PI estimates ranged from 0.157 to 0.683.

Probability of identity for siblings based on the first 8 loci was estimated at 1.52×10^{-2} ($n = 58$), analogous to a 1 in 66 chance of encountering identical genotypes. A comparable PI*sibs* estimate of 1.42×10^{-2} was obtained for the 36 individual subset over the same loci. The addition of 4 microsatellite loci changed the estimate of PI*sibs* to 1.34×10^{-3} (Table 3), representing a 1 in 745 chance of observing 2 identical genotypes. Therefore, there was a high probability that identical genotypes were obtained from the same individual sampled on separate occasions (i.e., this represented a recapture) if 2 or more samples exhibited the same multilocus genotype after analysis of 12 loci. PI*sibs* estimates for individual loci ranged from 0.454 to 0.831. The sibling match test

Table 3. Probability of identity estimates for black bears at the Tensas River Tract, northeast Louisiana, 1999 (n = 36).

Locus	Number of Alleles	Probability of Identity	Probability of Identity (siblings)
G1A	3	0.683	0.831
G1D	3	0.237	0.506
G10B	3	0.218	0.497
G10C	2	0.488	0.699
G10L	4	0.616	0.792
G10M	4	0.226	0.499
G10P	5	0.157	0.454
G10X	3	0.266	0.543
G10J	3	0.589	0.775
UarMU10	4	0.245	0.520
UarMU23	5	0.203	0.485
UarMU50	6	0.193	0.482
Overall	3.75[a]	5.70×10^{-7} [b]	1.34×10^{-3} [b]

[a] Average number of alleles
[b] Product of individual values

for each 8-locus genotype was $P_{sib} < 0.04$. Therefore all genotypes identified from the barbed-wire hair traps met the criteria for inclusion ($P_{sib} \leq 0.05$) in the capture history data.

Population Size and Density

Modified Lincoln-Petersen Model. Hairtrapping results were pooled for the first and second halves of the 1999 hair-sampling period. The modified Lincoln-Petersen model produced a population size estimate of 94 bears during 1999, averaging 0.29 bears/km^2 (Table 4).

Multiple Mark-Recapture Models. The test for heterogeneity of capture probabilities (Caughley 1977) indicated that the observed capture frequencies differed from the expected zero-truncated Poisson distribution when all 14 hair-sampling occasions from 1999 were considered ($\chi^2_{0.05} = 5.431$, 1 df, $P = 0.012$), but did not differ when capture histories were pooled into 7 sampling occasions ($\chi^2_{0.05} = 2.838$, 1 df, $P = 0.092$). However, Program CAPTURE's model selection procedure consistently detected individual heterogeneity of capture probabilities for 6 different pooling configurations of the hair-trapping data. Time variation in capture probabilities also was detected in the presence of individual variation among animals for some pooling configurations of ≤5 occasions. Behavioral response was not detected as an important influence on capture probabilities in any of the data pooling configurations.

In an effort to select the best pooling configuration for my analysis, I wanted to make sure the closure assumption was upheld while minimizing the number of samples

Table 4. Estimates of population size for the Tensas River Tract, northeast Louisiana, 1998–99.

Model	Sampling Period	Population Estimate	Coefficient of Variation (%)	95% Confidence Interval	Density (Bears/km^2)	95% Confidence Interval
Mod. Lincoln-Petersen	1999	94	16	65–124	0.29	0.20–0.38
M_h	1999	118	15	93–164	0.36	0.28–0.50
Chao M_h	1999	112	22	81–185	0.34	0.25–0.56
Chao M_{th}[a]	1999	115	21	85–182	0.35	0.26–0.55
Jolly-Seber A	1998–99	145	46	14–276	0.44	0.04–0.84
Jolly-Seber A'	1998–99	117	14	85–149	0.36	0.26–0.45

[a] Indicates chosen model

lost through pooling. The test for population closure detected lack of closure (Z = -2.192, P = 0.014) when the full capture histories were considered. The population closure test, however, did not detect a lack of closure (Z = 0.351, P = 0.637) for the 7-occasion data arrangement, nor any arrangement of <7 sampling occasions (P > 0.09). Only 8% of the 107 samples in the full capture history matrix were excluded in the 7-sampling occasion pooling configuration. Therefore, I selected the pooling configuration that collapsed capture histories into 7 sampling occasions of 2 weeks each (Fig. 8). Hair samples that were excluded or "lost" in the pooling process were duplicate samples from bears that were detected in both weeks of the 2-week sampling occasion.

The jackknife heterogeneity model M_h produced a population size estimate of 118 bears during 1999, averaging 0.36 bears/km^2 (Table 4). Model Chao M_h estimated population size at Tensas at 112 bears, averaging 0.34 bears/km^2. I also examined model Chao M_{th} to account for possible effects of time variation in capture probabilities, which estimated population size at 115 bears, averaging 0.35 bears/km^2. The goodness-of-fit test for the individual heterogeneity models did not indicate a poor fit ($\chi^2_{0.05}$ = 10.50, 6 df, P = 0.105).

Jolly-Seber Model. Models A and A' consistently produced population size estimates for all data pooling configurations including both 1998 live-capture data and 1999 hair-trapping data. Models B, D, and 2 failed to produce estimates for most data pooling arrangements and standard errors were large for the remainder. Therefore, only models A and A' were given further consideration. Program JOLLY did not provide goodness-of-fit tests for model A because expected cell values in the contingency table

frequently were <2. Similarly, the first component of the goodness-of-fit test for model A', the deaths only model, was not computed because of small expected counts.

The Jolly-Seber estimates based on 3 sampling occasions provided the best fit to the data (Fig. 7). Model A estimated population size at 145 bears, averaging 0.44 bears/km^2 (Table 4). Model A' produced an average population estimate of 117 bears, averaging 0.36 bears/km^2 (Table 4). Component 2 of the goodness-of-fit test did not detect a lack-of-fit for model A' ($\chi^2_{0.05} = 2.675$, 1 df, $P = 0.102$).

CHAPTER V

DISCUSSION

Population size

My original plan for the Tensas River Tract study included 3 years of intensive livetrapping, followed by estimation of population size using the Jolly-Seber mark-recapture model. A camera resight period also was proposed to provide within-year estimates of population size; this was to be undertaken near the conclusion of each field season. Livetrapping was conducted as originally planned during the first field season from May through October 1998. However, because of time constraints and the large size of my study area, I decided to abandon the camera resight sampling period to achieve satisfactory coverage with the live traps.

The second field season commenced in May 1999, also with livetrapping. By July, project personnel had captured only 10 bears, compared to 20 captures at the same time the previous year, although the sampling effort was greater than the effort achieved by the same date in 1998. More importantly, only 1 of the bears was a recapture from 1998. Clearly, this recapture rate was not sufficient to produce a population estimate with a coefficient of variation of <25% as planned. Pollock et al. (1990) demonstrated that such precision required a recapture rate of about 30%, based on an approximate 90% survival rate and a population size around 100. It became apparent that this was not going to be possible at Tensas.

More significant than the low recapture rates, the capture sample during 1999 seemed to be biased. Project personnel recorded 67 bear visits to live traps during 1999 when bears took baits but avoided traps. The Jolly-Seber and modified Lincoln-Peterson models require that all animals have equal capture probabilities in each sampling occasion (Pollock et al. 1990); trapping results strongly suggested this was not the case for my study area. The specific causes of bias in my capture sample are difficult to identify with certainty, but trap avoidance because of previous capture experience likely was a principal influence. If I had continued trapping and used the above models to produce an estimate of population size for the Tensas bear population, my estimate would not only have been imprecise, but would likely have been biased high.

When it became apparent that livetrapping was not the best approach to sample the population, trapping was suspended. Hair traps were immediately constructed in the area livetrapped in 1998. A 2,900-ha portion of the southwest section of Big Lake was excluded from sampling because of time and logistical constraints, and limited access. However, based on low live-trapping success there, exclusion of that area from the hair-trap grid should not have significantly affected the assumption of closure.

The Tensas River Tract is entirely surrounded by agricultural lands and an extensive road system. Bears tend to avoid crossing busy roads (Brody and Pelton 1989) and use forested corridors for travel when available (Weaver et al. 1990, Anderson 1997). Few corridors remain on the study area; those that do exist are usually intersected by roadways. In 11 years of bear research in the TRB, only 4 instances of immigration or emigration at the Tensas Refuge have been documented (Anderson 1997, Weaver 1999;

D. R. Anderson, U.S. Fish and Wildlife Service, unpublished data). As such, the Tensas study area can be considered geographically closed to dispersals from, and additions to, the resident bear population and exemplifies an island situation with agricultural lands representing ecological boundaries. Because I sampled almost all the available habitat for black bears within the Tensas River Tract, the assumption of closure for the modified Lincoln-Petersen and multiple mark-recapture models probably was not violated.

Demographic closure also is an assumption of the closed models. The hair-sampling period in 1999 was conducted in late summer and fall. Obviously, no births occurred during that time. Because the sampling duration was short, any effects of mortality on population size should have been minimal. Therefore, the requirements of demographic closure generally were upheld for within-year estimates.

The hair-trapping technique provided an advantage over livetrapping because the entire bear population had concurrent access to the hair traps. By comparison, the live-trapping approach used in 1998 sampled only a small portion of the study area at a time. Bears that temporarily moved out of the live-trapping grid in a particular area, and returned at a later time, may never have had the opportunity to be captured.

All the mark-recapture and mark-resight models that I used to estimate population size are based on the assumption that marked individuals are correctly identified when sampled. The original 8 microsatellite loci that were first examined for the Tensas bear population seemed to contain sufficient variation to resolve individual bears. However, 1 multilocus genotype identified from the 1999 hair-trapping session was matched to bear #442, a bear that had been killed in late 1998. This anomaly was not surprising because

58 bears were identified from the barbed-wire sampling period and PI*sibs* estimated the probability of >1 animals sharing a single observed multilocus genotype at 1 in 66. However, to ensure that the condition was not common throughout the dataset, I conducted a reanalysis with 4 additional microsatellite loci. The additional markers allowed distinction between the genotypes in question, and provided a substantial improvement in the overall probability of identity for all samples (i.e., PI*sibs* = 1.52×10^{-2} for 8 loci vs. 1.34×10^{-3} for 12 loci). Consequently, based on the large number of genetic markers used to identify bears in my study and the resulting low average probability of identity, it is highly unlikely that each observed genotype represented >1 bear within the population.

It is well recognized that the assumption of equal catchability is rarely met in natural populations (Carothers 1973*a*, Burnham and Overton 1979, Seber 1982, White et al. 1982, Koper and Brooks 1998). Otis et al. (1978) described 3 types of variation that can influence probabilities of capture. First, capture probabilities can vary by time. This variation may be result of a seasonal change or the start of a hunting season resulting in a change in bear behavior. Second, probabilities of capture may be influenced by a previous history of capture. Bears previously captured may avoid traps ("trap-shy") or become more prone to trapping ("trap-happy"). Finally, capture probabilities can vary between individuals (trap heterogeneity); this may be caused by differences in sex, age, social status (White et al. 1982), and fitness. Furthermore, bears may have different numbers of traps within their home range, giving each differing opportunities for capture (Otis et al. 1978, White et al. 1982).

Several aspects of my study design allowed reduction of potential biases in the estimates of population size. The hair-trapping session in 1999 was shorter in duration than the live-trapping session in 1998 (≈3 months versus ≈5 months), possibly reducing temporal biases. By selecting only 25% of hair samples of sufficient size collected after 10 September 1999, I may have diminished capture probability variation over time caused by the large increase in samples collected after that date. Additionally, the hair-trapping approach likely reduced bias due to "trap shyness", because there is no apparent disturbance to bears using this technique. Furthermore, large sample sizes and high average capture probabilities, however, can diminish the effects of heterogeneity on population size estimates (Carothers 1973*b*, Gilbert 1973, Otis et al. 1978). Because of the improvement in sample size with the hair-trapping approach, catchability biases were reduced.

Studies of populations of known size have shown that the model selection procedure in program CAPTURE does not always select the most appropriate model for estimation of population size (Menkins and Anderson 1988, Manning et al. 1995). Instead of depending on the selection algorithm to choose the best model for my data, I used the procedure to identify consistent sources of heterogeneity that may have resulted in biased estimates using unsuitable models (K. H. Pollock, North Carolina State University, personal communication; Manning et al. 1995; Menkins and Anderson 1998).

The amount of data pooling needed to achieve the optimal number of sampling occasions for the multiple mark-recapture models is difficult to determine. Otis et al. (1978) suggested a minimum of 5 trapping occasions, but recommended 7–10. The

pooling configuration composed of 7 2-week sampling occasions that I chose falls within this guideline and had acceptable results for both the closure test and goodness-of-fit test for the individual heterogeneity model. Additionally, only 8% of the samples were "lost" through pooling.

Variation in capture probabilities was detected by Program CAPTURE in the full capture history matrix from the 1999 hair-sampling session as was a lack of population closure. The empirical evidence supporting population closure for within-year data at Tensas was substantial. Therefore, I concluded that the significant closure test results for this data arrangement were probably a result of heterogeneity caused by a time influence (White et al. 1982) and low capture probabilities for some bears.

Using the model selection procedure, I was able to identify patterns of heterogeneity in many of the various data pooling configurations I considered. Individual capture heterogeneity was apparent throughout all data arrangements. Therefore, only the multiple mark-recapture models designed for this type of variation (models M_h, Chao M_h, and Chao M_{th}) were given further consideration. Sex was not determined for the bears sampled at hair traps; therefore, stratification of the sample by gender to reduce individual heterogeneity was not possible. Because males have home ranges several times larger than those of females at Tensas (Weaver 1999), higher probabilities of capture would seem likely for males because of increased opportunity. Twelve of the bears detected at the hair traps in 1999 had been captured in 1998. Of these, however, only 3 were males, despite an even sex ratio within the 1998 capture sample.

Consequently, it seems that capture probability was not directly related to home range size.

Capture probabilities also may have varied over time, although this influence likely was small. Time variation was only detected in the presence of individual heterogeneity when sampling occasions were ≤5. As a result, consideration of model Chao M_{th} also was justified. Behavioral response was not identified as a significant influence upon any data arrangement, despite evidence that it significantly affected livetrapping in 1999.

The modified Lincoln-Petersen estimate of 94 bears was computed from the pooled 1999 hair-trap resight histories into 1 mark and 1 resight period (Fig. 7). Lack of population closure was not evident because all data pooling configurations of ≤7 occasions had non-significant closure test results. Relative to estimates based on the multiple mark-recapture models, the modified Lincoln-Petersen estimate was low. This can be caused by heterogeneity of individual capture probabilities (Otis et al. 1978, Pollock et al. 1990). Program CAPTURE consistently detected this type of variation across all data pooling configurations. The increase in sample size within each sampling occasion and higher probabilities of capture because of data pooling may not have been sufficient to eliminate the heterogeneity effects on the modified Lincoln-Petersen estimate.

The multiple mark-recapture models M_h, Chao M_h, and Chao M_{th} estimated population sizes of 118, 112, and 115 respectively. Although those point estimates were consistent, the precision of the Chao models was distinctly lower than that of the

jackknife model M_h. That is not surprising because model Chao M_h used only the first 2 or 3 capture frequency counts (Chao 1989). Wide confidence intervals can likewise be expected for these estimates because time variation was also considered by model Chao M_{th}. Although the jackknife model M_h produced the most precise estimate, Otis et al. (1978) found that this model performed best when many animals are caught a large number of times. This was not the case within my dataset of selected hair samples as 83% of the bears were sampled ≤ 2 times. The confidence interval associated with the model M_h estimate may, therefore, be deceptively narrow. Although the Chao M_h and M_h models are fairly robust to some levels of time-influenced variation (Otis et al. 1978, Chao 1989), they do not directly allow capture probabilities to vary over time. Program CAPTURE only detected time variation in pooling configurations consisting of ≤ 5 sampling occasions. So, the possibility of a time influence cannot be ignored. Consequently, I selected model Chao M_{th}, which allows both individual and time influences on capture probabilities for within-year hair-trap data. This is further supported by the guidelines provided by Chao et al. (1992) for adequate sample coverage of the capture probabilities.

The Jolly-Seber model A estimated population size as 145 based on 2 years of data. This estimate was considerably higher than the estimate produced by model Chao M_{th}. Although the estimate of 117 bears computed by the Jolly-Seber model A' across 2 years was consistent with the model Chao M_{th} estimate, this model did not consider additions from births. Therefore, the deaths only model, A', also would have produced an estimate distinctly higher than model Chao M_{th}, had reproduction been considered.

Trap avoidance was evident in the live-capture sample in 1999. That avoidance behavior may have resulted in some bears avoiding hair traps because of an association of baits and human scent with a previous capture experience. Trap-shy behavior always results in overestimation of population size (Pollock et al. 1990). I suggest that the Jolly-Seber estimates were likely biased high because of avoidance behavior initiated by the live-trapping period. This effect, however, would not have influenced the estimates based on closed models because the trap response (or decrease in the probability of future capture) occurred before initiation of the hair-trapping period.

Based on the above, I conclude that the estimate produced by model Chao M_{th} of 115 bears (95% CI = 85–182), is the most appropriate for this study. I selected this estimate because it was based on within-year data permitting the use of a closed model that required fewer assumptions than the open Jolly-Seber model. Model Chao M_{th} was the most appropriate of the multiple mark-recapture models because it is robust when capture probabilities vary due to both time and differences among individual bears.

Population Density

The estimated density of black bears at the Tensas River Tract was 0.35 bears per km^2, based on my population estimate of 115. Variation between this and other population estimates in the Southeast may be attributed to the sampling techniques used and delineation of the study areas, and actual differences between populations and habitats (Table 5). However, the bear density at Tensas was lower than the estimate of 1.43 bears per km^2 reported for the neighboring Deltic population (Beausoleil

Table 5. Population densities of black bears in the southeastern United States.

Locality	Bears / km^2	Reference
Tensas River Tract, Louisiana	0.35	This study
Deltic, Tensas River Basin, Louisiana	1.43	Beausoleil 1999
Great Smoky Mountains NP, Tennessee	0.87	J. McNutt, University of Tennessee, unpublished report
Alligator River NWR, North Carolina	0.86	Allen 1999
Gum Swamp, North Carolina	1.35	Martorello 1998
Big Pocosin, North Carolina	0.53	Martorello 1998
Camp Lejeune MCB, North Carolina	0.02	Brandenburg 1996
White Rock, Arkansas	0.08	Clark 1991
Dry Creek, Arkansas	0.09	Clark 1991
Great Dismal Swamp, North Carolina-Virginia	0.47–0.68	Hellgren and Vaughan 1989

1999). The underlying reasons for the 4-fold difference in density are difficult to determine. Both areas are characterized by bottomland hardwood habitats surrounded by agricultural lands. The Deltic bear population is distributed among 4 small, fragmented tracts held in private ownership. Conversely, the Tensas population is located within the largest contiguous forest remaining in the TRB. The large size of the Tensas habitat would seemingly offer superior habitat quality in terms of the large space requirements of black bears. In reality, the fragmented nature of the Deltic lands may actually improve the availability of food for bears compared with Tensas (Weaver 1999) resulting in a relatively greater population carrying capacity. The high ratio of forest edge to interior area may make agricultural lands more accessible to bears and provide abundant food sources. Past forest management practices also may account for differences. Mast producing trees were regularly removed from the Tensas lands before establishment of public ownership (Weaver 1999). Today, intensive timber management on the Deltic tracts promotes a dense understory, providing abundant food sources (Beausoleil 1999). Although forests are actively managed at Tensas, timber harvests are concentrated within the northern Jud Brake Unit, where hair-trapping success was relatively high. Finally, unrestricted public access to many areas of the Tensas River Tract may provide greater opportunities for poaching of black bears compared with the Deltic lands (Weaver 1999).

Inbreeding and Genetic Drift

The genetic data acquired by using the hair-trapping technique allow an assessment of possible inbreeding and genetic drift within the Tensas bear population.

Four microsatellite loci (G1A, G10M, G10J, UarMU50) had significant heterozygote deficiencies when given independent consideration. The combinations of alleles at those loci indicated that inbreeding cannot be ruled out at Tensas. Consequently, inbreeding and the resulting increase in the proportion of homozygote loci among offspring could lead to inbreeding depression (Ralls et al. 1986) within the population. Linkage disequilibrium, or the non-random association of alleles at different gene loci, may be the result of genetic drift after a population bottleneck (Allendorf 1986, Waples 1991). Significant linkage disequilibrium was detected within the genetic data set between 4 allele pairs (G1D vs. G10M; G1A vs. G10X; G10L vs. G1D; and G1A vs. G10J) by the individual tests. Those results were not significant after consideration of the total number of pairwise tests within the analysis; however, given the large number of tests, the significance levels ($\alpha = 0.00179$ for 8 loci and $\alpha = 0.00076$ for 12 loci) were extremely conservative. The Louisiana Department of Wildlife and Fisheries estimated that there may have been as few as 30 bears within the entire TRB in 1981 (State Survey, 1981, Louisiana Department of Wildlife and Fisheries, cited in M. R. Pelton, University of Tennessee, unpublished report), perhaps constituting a population bottleneck. The genetic data from the hair samples is consistent with that possibility. The relatively few numbers of alleles at the observed microsatellite loci also support the possibility that genetic drift has affected the Tensas population. For example, Tensas bears seem to have 1–2 fewer alleles per microsatellite locus than do bears from the upper ARB, and northwest Arkansas populations (J. D. Clark, U.S. Geological Survey, personal communication).

CHAPTER VI

MANAGEMENT IMPLICATIONS

General

The Louisiana Black Bear Recovery Plan (U.S. Fish and Wildlife Service 1995) identified the need for determination of the current status of the remaining bear populations in Louisiana. My study provided the first estimate of bear population size and density for the Tensas Refuge, Big Lake, and adjacent private lands based on statistical sampling. Because of the lack of earlier estimates, it was not possible to determine rates of increase for the population. However, based upon past guesses of abundance for the TRB, the population seems to have increased. This trend may be related to several factors that affect Louisiana bears and their habitats. First, the granting of legal protection under the U.S. Endangered Species Act for the Louisiana bear and the bottomland hardwoods where it resides may have been beneficial. Also, bottomland hardwood forest management at Tensas is designed to provide for the life requisites of bears. Current habitat management practices seem to benefit black bears. Additionally, the listing, and the efforts of organizations such as the Black Bear Conservation Committee, have increased public awareness to save the Louisiana bear.

Nevertheless, the threat of future extinction remains for the Louisiana bear. The Tensas population remains isolated from other bear populations because of the lack of adequate travel corridors. One consequence of this isolation may be inbreeding and the loss of genetic variation due to genetic drift. Those factors have been linked to higher

extinction rates for isolated populations (Frankham 1998). The genetic data from my study indicate genetic drift may have already affected the Tensas population. Low genetic variation as indicated by low levels of heterozygosity will result in the genetic effective size of a population being smaller than the actual population size. Genetic effective size is defined as the size of an ideal population that undergoes the same amount of genetic change as the actual population (Waples 1991). Although I estimated that 115 bears reside at Tensas, the effective population size may be as few as 32 individuals (based on mutation rate of 10^{-2} [DeWoody and Avise 2000]). Consequently, population monitoring should continue within the TRB. Additional research may be warranted to help identify reasons for the apparent lower use of the southern portion of the study area.

Black bear populations are particularly difficult to enumerate because of their large home ranges, relatively low densities and reclusive behavior (Pelton 1982, Miller et al. 1987). The hair-trapping technique that I used provided a robust estimate of population size for the Tensas River Tract that would not have been possible with the live-trapping approach. Hair traps can be constructed and maintained by relatively few people over large geographic areas. Additionally, the low impact on the population is particularly appealing for studies of threatened bear populations. The hair-trapping technique may be used in the future to provide the most accurate and precise population parameter estimates. However, live-trapping approaches will continue to be essential for assessing home range dynamics, den site selection, reproductive status, habitat use, and physiological factors.

This study represents the first effort in the Southeast to provide population estimates of black bears based exclusively on a non-invasive genetic approach. Genetic approaches have other advantages because the data can be used to examine genetic variability within and between fragmented populations subdivided by human development. Questions regarding lineage, gene flow between populations, or historical events, such as bottlenecks, also can be addressed. However, there is room for improvement with these genetic approaches. Genetic techniques have high laboratory costs, that may be prohibitive for some studies. Populations comprised of a small effective number, such as that at Tensas, tend to have lower genetic diversity, and consequently fewer alleles per locus. In this study I was forced to examine a substantial number of loci to differentiate between individuals. The development of improved genetic markers with higher levels of variability could greatly reduce the number of loci required to separate individuals and, consequently, reduce analysis costs. Additionally, standardization between laboratories is needed to minimize differences in interpretation and comparison of microsatellite data.

LITERATURE CITED

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Allen, T. G. 1999. Black bear population size and habitat use on Alligator River National Wildlife Refuge, North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology 5:181–190.

_____, and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57–76 *in* M. E. Soulé, editor. Conservation biology - the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Anderson, D. R. 1997. Corridor use, feeding ecology, and habitat relationships of black bears in a fragmented landscape in Louisiana. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, New York, 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, Tennessee, USA.

Brandenburg, D. M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5–10.

Bruford M. W., and R. K. Wayne. 1993. Microsatellites and their application to population genetic studies. Current Opinion in Genetics and Development 3:939–943.

Burdick, D. M., D. Cushman, R. Hamilton, and J. G. Gossselink. 1989. Faunal changes and bottomland hardwood forest loss in the Tensas watershed, Louisiana. Conservation Biology 3:282–292.

Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60:927–936.

Carothers, A. D. 1973*a*. Capture-recapture methods applied to a population with known parameters. Journal of Animal Ecology 42:125–146.

_____. 1973*b*. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons. New York, New York, USA.

Chao, A. 1987. Estimating population size for capture-recapture data with unequal catchability. Biometrics 43:783–791.

_____. 1988. Estimating animal abundance with capture frequency data. Journal of Wildlife Management 52:295–300.

_____. 1989. Estimating population size for sparse data in capture-recapture experiments. Biometrics 45:427–438.

_____, S. M. Lee, and S. L. Jeng. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. Biometrics 48:201–216.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1:131–160.

Clark, J. D. 1991. Ecology of two black bear (*Ursus americanus*) populations in the Interior Highlands of Arkansas. Dissertation, University of Arkansas, Fayetteville, Arkansas, USA.

DeWoody, J. A., and J. C. Avise. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. Journal of Fish Biology 56:461–473.

Donnelly, P. 1995. Non-independence of matches at different loci in DNA profiles: quantifying the effect of close relatives on the match probability. Heredity 75:26–34.

Fontenot, M. A. and Ziegler, E. 1987. The Tensas Story. Moran Colorgraphic. Baton Rouge, Louisiana, USA.

Frankham, R. 1998. Inbreeding and extinction: island populations. Conservation Biology 12:665–675.

Gilbert, R. O. 1973. Approximations of the bias in the Jolly-Seber capture-recapture model. Biometrics 29:501–526.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in* M. E. Soulé, editor. Conservation biology - the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Goossens, B., L. P. Waits, and P. Taberlet. 1998. Plucked hair samples as a source of DNA: reliability of dinucleotide microsatellite genotyping. Molecular Ecology 7:1237–1241.

Gosselink, J. G., G. P. Shaffer, L. C. Lee, D. M. Burdick, D. L. Childers, N. Taylor, S. Hamilton, R. Boumans, D. Cushman, S. Fields, M. Koch, and J. Visser. 1989. Cumulative impact assessment and management in a forested wetland watershed in the Mississippi River floodplain. Marine Sciences Department, Louisiana State University, Baton Rouge, Louisiana, USA. LSU-CEI-89-02.

Hall, E. R. 1981. The mammals of North America. Vol. 2. John Wiley and Sons, New York, New York, USA.

Hellgren, E. C., and D. S. Maehr. 1992. Habitat fragmentation and black bears in the eastern United States. Eastern Workshop for Black Bear Research and Management 11:154–165.

_____, and M. R. Vaughan. 1989. Demographic analysis of a black bear population in the Great Dismal Swamp. Journal of Wildlife Management 49:668–674.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Koper, N., and R. J. Brooks. 1998. Population-size estimators and unequal catchability in painted turtles. Canadian Journal of Zoology 76:458–465.

Louisiana Cooperative Extension Service. 1998. Louisiana summary, agriculture and natural resources. Louisiana State University. Baton Rouge, Louisiana, USA.

Lowry, G. H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge, Louisiana, USA.

Manning, T., W. D. Edge, and J. O. Wolf. 1995. Evaluating population-size estimators: an empirical approach. Journal of Mammalogy 76:1149–1158.

Marchinton, F. B. 1995. Movement ecology of black bears in a fragmented bottomland hardwood habitat in Louisiana. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Martorello, D. A. 1998. Ecology of black bears in coastal North Carolina. Thesis, University of Tennessee, Knoxville, Tennessee, USA.

Menkens, G. E., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69:1952–1959.

Merriam, C. H. 1893. The yellow bear of Louisiana, *Ursus luteolus* Griffith. Proceedings of the Biological Society of Washington 3:147–152.

Miller, D. A. 1995. Systematic classification of black bears in the Southeastern United States. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Miller, S. D., E. F. Becker, W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. International Conference on Bear Research and Management 7:23–35.

Mills, L. S., J. J. Cita, K. P. Lair, M. K. Schwartz, and D. A. Tallmon. 2000. Estimating animal abundance using non-invasive DNA sampling: promise and pitfalls. Ecological Applications 10:283–294.

Morin, P. A., and D. S. Woodruff. 1996. Non-invasive genotyping for vertebrate conservation. Pages 298–313 *in* T. B. Smith and R. K. Wayne, editors. Molecular genetic approaches in conservation. Oxford Press, New York, New York, USA.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183–193.

National Climatic Data Center. 1998. Daily Surface Data. National Oceanic and Atmospheric Administration, United States Department of Commerce, Washington, D.C., USA.

National Climatic Data Center. 1999. Daily Surface Data. National Oceanic and Atmospheric Administration, United States Department of Commerce, Washington, D.C., USA.

Neal, W. A. 1990. Proposed threatened status for the Louisiana black bear. Federal Register 55(120):25341–25345.

_____. 1992. Threatened status for the Louisiana black bear and related rules. Federal Register 57(4):588–595.

_____. 1993. Proposed designation of critical habitat for the Louisiana black bear. Federal Register 58(230):63560–63569.

Nowak, R. M. 1986. Status of the Louisiana black bear. Office of Endangered Species, U.S. Fish and Wildlife Service, Washington D.C., USA. Mimeograph.

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, D. R. Anderson, and T. E. Rabot. 1997. Louisiana status report. Eastern Workshop for Black Bear Research and Management 14:5–7.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

_____, G. F. Shields, and C. Strobeck. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7:1283–1292.

_____, and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489–495.

_____, and _____. 1995. The molecular basis and evolutionary history of a microsatellite null allele in bears. Molecular Ecology 4:519–520.

Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: choosing and using a molecular marker. Ecology 79:361–382.

Pelton, M. R. 1982. Black bear. Pages 504–514 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.

_____. 1990. Black bears in the Southeast: to list or not to list. Eastern Workshop for Black Bear Research and Management 10:155–161.

_____, and F. T. van Manen. 1997. Status of black bears in the southeastern United States. Pages 31–44 *in* A. L. Gaski and D. F. Williamson, editors. Proceedings of the Second International Symposium on the Trade of Bear Parts. Traffic USA/World Wildlife Fund, Washington D.C., USA.

Pemberton, J. M., J. Slate, D. R. Bancroft, and J. A. Barrett. 1995. Non-amplifying alleles at microsatellite loci: a caution for parentage and population studies. Molecular Ecology 4:249–252.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Ralls, K., P. H. Harvey, and A. M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pages 35–56 *in* M. E. Soulé, editor. Conservation Biology - The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Raymond M., and R. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Rexstad, E., and K. P. Burnham. 1992. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Ft. Collins, Colorado, USA.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Rich, C. N., and R. D. Thomas. 1981. A checklist of the vascular plants of Madison Parish, Louisiana. Proceedings of the Louisiana Academy of Sciences 44:93–100.

Rogers L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97.

SAS Institute Inc. 1985. SAS/STAT Guide for Personal Computers, Version 6 Edition. SAS Insitiute Inc., Cary, North Carolina, USA.

Schug, M. D., T. F. C. Mackay, and C. F. Aquadro. 1997. Low mutation rates of microsatellite loci in *Drosophilia melanogaster*. Nature Genetics 15:99–102.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

_____. 1970. The effects of trap-response on tag-recapture estimates. Biometrics 26:13–22.

_____. 1982. The estimation of animal abundance and related parameters. Second edition. MacMillan, New York, New York, USA.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman, New York, New York, USA.

Spencer, J. 1981. Soybean boom, hardwood bust. American Forests 87:22–25, 49–52.

Taberlet, P., J. J. Camarra, S. Griffin, E. Uhrès, O. Hanotte, L. P. Waits, C. Dubois-Paganon, T. Burke, and J. Bouvet. 1997. Non-invasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6:869–876.

_____, and G. Luikart. 1999. Non-invasive genetic sampling and individual identification. Biological Journal of the Linnean Society 68:41–55.

Taylor, E. 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, Louisiana, USA.

U. S. Census Bureau. 1992. Population estimates program, Population Division. United States Department of Commerce. Washington, D.C., USA.

U. S. Department of Agriculture. 1997. Census of agriculture, Madison Parish, Louisiana. National Agricultural Statistics Service. Washington, D.C., USA.

U. S. Fish and Wildlife Service. 1995. Louisiana black bear recovery plan. Jackson, Mississippi, USA.

Waples, R. S. 1991. Genetic methods for estimating the effective size of cetacean populations. Pages 279–297 *in* H. R. Hoelzel, editor. Report of the International Whaling Commission; Special Issue 13. The Red House, Cambridge, UK.

Weaver, K. M. 1999. The ecology and management of black bears in the Tensas River Basin of Louisiana. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

_____, and M. R. Pelton. 1994. Denning ecology of black bears in the Tensas River Basin of Louisiana. International Conference on Bear Research and Management 9:427–433.

_____, D. K. Tabberer, L. U. Moore, Jr., G. A. Chandler, J. C. Posey, and M. R. Pelton. 1990. Bottomland hardwood forest management for black bears in Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:342–350.

Weems, T. A., C. E. Martin, G. P. Colvin, S. D. Matthews, B. B. Nutt, R. F. Letlow, R. L. Leuth, and J. E. Seaholm. 1968. Soil survey of Tensas Parish, Louisiana. United States Department of Agriculture, Soil Conservation Service, and Louisiana Agriculture Experiment Station, Baton Rouge, Louisiana, USA.

Weems, T. A., E. F. Reynolds, R. L. Venson, E. T. Allen, and T. J. Smith. 1982. Soil survey of Madison Parish, Louisiana. United States Department of Agriculture, Soil Conservation Service, and Louisiana Agriculture Experiment Station, Baton Rouge, Louisiana, USA.

Wessells, N. K., and J. L. Hopson. 1988. Biology. Random House. New York, New York, USA.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, New Mexico, USA.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97–100.

Woods, J. G., B. L. McLellan, D. Paetkau, C. Strobeck, M. Proctor. 1996. DNA fingerprinting applied to mark-recapture bear studies. International Bear News 5:9–10.

_____, D. Paetkau, D. Lewis, B. L. McLellan, M. Proctor, C. Strobeck. 1999. Genetic tagging free-ranging black and brown bears in mark-recapture experiments. Wildlife Society Bulletin 27:616–627.

Wright, J. M. 1993. DNA Fingerprinting of fishes. Pages 57–91 *in* P. W. Hochachka and T. P. Mommsen, editors. Biochemistry and Molecular Biology of Fishes, Volume 2: Molecular Biology Frontiers. Elsevier Science, Amsterdam, New York, USA.

APPENDICES

Appendix A. Trapping Results for the Tensas River Tract Study Area, 1998–99

Table A.1. Black bear trapping results for the Tensas River Tract study area, Tensas River Basin, Louisiana, 1998–99.

Bear ID#	Date	Location[a]	Sex[b]	Mass (kg)	Age (Years)
402	29-May-1998	East Fool River	M	120.2	2
404	31-May-1998	East Fool River	M	104.3	3
406	3-Jun-1998	East Fool River	F	38.6	3
408	11-Jun-1998	East Fool River	F	59.0	11
410	11-Jun-1998	East Fool River	M	133.8	4
412	14-Jun-1998	East Fool River	F	54.4	2
414 (476[c])	18-Jun-1998	East Fool River	M	72.6	2
	23-Jun-1998	East Fool River			
	4-Jun-1999	East Fool River		90.7	
416	18-Jun-1998	East Fool River	F	49.9	7
418	21-Jun-1998	East Fool River	F	52.2	7
420	30-Jun-1998	Jud Brake	F	56.7	3
	10-Jul-1998	Jud Brake			
422	1-Jul-1998	Jud Brake	M	59.0	3
	2-Sep-1998	Jud Brake			
426	1-Jul-1998	Jud Brake	F	36.3	3
428	2-Jul-1998	Jud Brake	M	93.9	4[d]
	2-Sep-1998	Jud Brake			

Table A.1. (continued)

Bear ID#	Date	Location[a]	Sex[b]	Mass (kg)	Age (Years)
430	5-Jul-1998 11-Jul-1998	Jud Brake Jud Brake	M	86.2	2
432	11-Jul-1998	Jud Brake	F	38.6	2
434	12-Jul-1998 24-Jul-1998	Jud Brake Jud Brake	F	47.6	2
436	15-Jul-1998	Jud Brake	F	79.4	8
438	22-Jul-1998	Jud Brake	M	83.9	2
440	22-Jul-1998	Jud Brake	M	131.5	6[d]
442	2-Aug-1998	Jud Brake	F	54.4	4
444	8-Aug-1998	Jud Brake	M	129.3	4
446	29-Aug-1998	Jud Brake	F	63.5	4
448	2-Sep-1998	Jud Brake	F	88.5	9
450	3-Sep-1998	West Fool River	F	68.0	6
452	5-Sep-1998	West Fool River	M	99.8	4
454	5-Sep-1998	Jud Brake	M	117.9	5
456	8-Sep-1998	West Fool River	M	138.3	7
458	15-Sep-1998	Big Lake	M	40.8	1

Table A.1. (continued)

Bear ID#	Date	Location[a]	Sex[b]	Mass (kg)	Age (Years)
460	18-Sep-1998	West Fool River	F	52.2	3
462	19-Sep-1998	West Fool River	M	131.5	6
464	30-Sep-1998	West Fool River	M	59.0	2
466	14-Oct-1998	West Fool River	F	34.0	1
477	4-Jun-1999	East Fool River	F	59.0	3
478	6-Jun-1999	East Fool River	M	158.8	8
479	7-Jun-1999	East Fool River	F	45.4	6
480	14-Jun-1999	East Fool River	F	34.0	2
481	17-Jun-1999	East Fool River	F	63.5	4
482	20-Jun-1999	East Fool River	F	28.6	2
483	27-Jun-1999	Jud Brake	F	31.8	2
484	13-Jul-1999	Jud Brake	M	54.4	1
485	16-Jul-1999	Jud Brake	F	59.0	15
486	15-Sep-1999 20-Sep-1999	Jud Brake Jud Brake	F	27.2	1

[a] See Fig. 9 for unit locations
[b] M = Male, F = Female
[c] New tag number in 1999
[d] Age reported by the U.S. Fish and Wildlife Service from previous capture records

Appendix B. Laboratory Protocol for Microsatellite Analysis

MICROSATELLITE ANALYSIS

DNA Isolation

DNA was extracted from hair follicles using the InstaGene Matrix (Bio-Rad Laboratories, Hercules, California). Specifically, follicles were incubated in the InstaGene Matrix in the presence of Proteinase K at 65°C overnight. This mixture was boiled (100°C) for 8–10 minutes, followed by centrifugation at 10,000–12,000 rpm. The resulting supernatant was used in PCR reactions.

First Stage

Microsatellite DNA amplification was performed in 2 stages. *First Stage* analysis consisted of the amplification of 8 microsatellite DNA loci using the PCR primers described in Paetkau and Strobeck (1994) and Paetkau *et al.* (1995). These loci are: G1A, G1D, G10B, G10C, G10L, G10M, G10P, and G10X. Samples determined to be have identical genotypes were subjected to the *Second Stage* analysis of 4 microsatellite loci to improve the ability to discriminate between 2 closely related individuals.

First Stage PCR

Each PCR reaction consisted of 1.5 µl of genomic DNA extract, 0.875 X PCR buffer (59 mM Tris-HCl, pH 8.3; 15 mM $(NH_4)_2SO_4$; 9 mM β-mercaptoethanol; 6 mM EDTA), 2.25 mM $MgCl_2$, 0.2 mM dNTPs, 0.15–0.43 µM of each primer (forward primer fluorescently labeled with TET, FAM, or HEX; Applied Biosystems (ABI), Foster City,

California), 1.2 units of Taq polymerase (ABI), and deionized water added to achieve the final volume of 15 µl. The amplification cycle consisted of an initial denaturing at 94°C for 2 min followed by 35 cycles of 94°C denaturing for 30 sec, 56°C annealing for 30 sec, and 72°C extension for 1 min. Cycling culminated with a 5-min extension at 72°C. Thermal cycling was performed in an MJ DNA Engine PTC 200 (MJ Research, Watertown, Massachusetts) configured with a heated lid.

Second Stage

The *Second Stage* analysis involved the amplification of all identical samples at 4 additional microsatellite DNA loci developed by Taberlet et al. (1997; MU10, MU23, MU50) and Paetkau et al. 1998 (G10J).

Second Stage PCR

Each PCR reaction consisted of 1.0 µl of genomic DNA extract, 1X PCR buffer (10mM Tris-HCl, pH 8.3, 50 mMKCl), 2.25 mM $MgCl_2$, 0.2 mM dNTPs, 0.5 µM of each primer (forward primer fluorescently labeled with TET, FAM, or HEX; ABI), 1.2 units of Taq polymerase (ABI), and deionized water added to achieve the final volume of 10 µl. The amplification cycle consisted of an initial denaturing at 94°C for 2 min followed by 35 cycles of 94°C denaturing for 45 sec, 52°C annealing for 45 sec, and 72°C extension for 1 min. Cycling culminated with a 5-min extension at 72°C. Thermal cycling was performed in an MJ DNA Engine PTC 200 (MJ Research, Watertown, MA) configured with a heated lid.

Fragment Analysis

Generally, 1 µl of PCR product was diluted 1:1 with deionized water and thoroughly mixed. One µl of this dilution was added to 12 µl of deionized formamide and 0.5 µl of the internal size standard GENESCAN-500 (ABI). Alternatively, PCR products of separate multiplexed reactions (2–3 loci each) and multiple separate reactions (2–4) were combined and analyzed without dilution. Loci were identified in these multiplexed samples by virtue of their characteristic molecular mass and attached fluorescent label. The size standard contained DNA fragments fluorescently labeled with the dye phosphoramidite TAMRA (red). This PCR product/size standard/formamide mixture was heat denaturated at 95°C for 3 min and placed immediately on ice for at least 5 min. The mixture was subjected to capillary electrophoresis on an ABI PRISM 310 Genetic Analyzer (i.e., automated sequencer). Fluorescently labeled DNA fragments were analyzed, and genotype data generated using GeneScan software (ABI). GENOTYPER v. 2.0 (ABI) DNA fragment analysis software was used to score, bin, and output allelic (and genotypic) designations for each bear sample.

Statistical Analyses

The multilocus genotype generated for each individual from the series of PCR amplifications was analysed to determine the uniqueness of each hair sample. Estimates of individual pair-wise genetic distances, using the proportion of shared alleles algorithm, was calculated using a 32-bit version of Microsat 1.5d (Eric Minch, Stanford University, California).

Observed genotype frequencies were tested for consistency with Hardy-Weinberg and linkage equilibrium expectations using randomization tests implemented by GENEPOP 3.1 (Raymond and Rousset 1995). The Hardy-Weinberg test used the Markov chain randomization test of Guo and Thompson (1992) to estimate exact 2-tailed *P*-values for each locus. Bonferroni adjustments (Rice 1989) were used to determine statistical significance for these tests. Linkage disequilibrium tests used the randomization method of Raymond and Rousset (1995) for all pairs of loci. The amount of genetic variation in each sample was summarized by gene diversity (average expected heterozygosity) and the average frequency of unique alleles.

Literature Cited

Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy-Weinberg proportions for multiple alleles. Biometrics 48:361-372.

Raymond, M., and R. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

VITA

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