5-2002

Abundance and Density of Florida Black Bears in Okefenokee National Wildlife Refuge and Osceola National Forest

Steven T. Dobey
University of Tennessee, Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Steven T. Dobey entitled "Abundance and Density of Florida Black Bears in Okefenokee National Wildlife Refuge and Osceola National Forest." 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.

Michael R. Pelton, Major Professor

We have read this thesis and recommend its acceptance:

Gary McCracken, Lisa Muller, Joseph Clark

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

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

To the Graduate Council:

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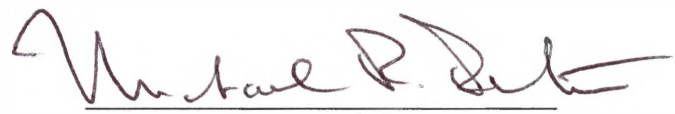

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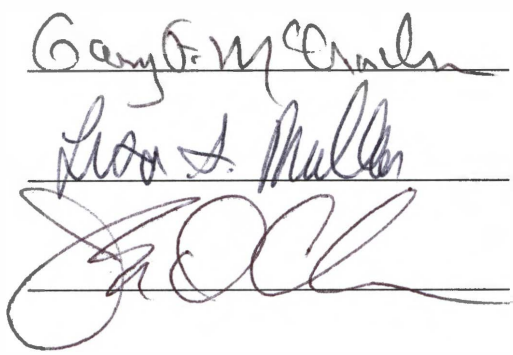

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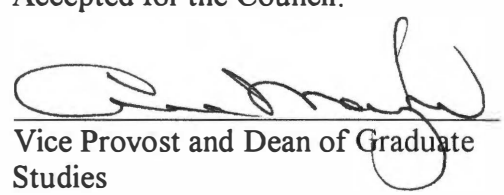

Vice Provost and Dean of Graduate Studies

ABUNDANCE AND DENSITY OF FLORIDA BLACK BEARS IN THE OKEFENOKEE NATIONAL WILDLIFE REFUGE AND OSCEOLA NATIONAL FOREST

A Thesis

Presented for the

Master of Science Degree

The University of Tennessee, Knoxville

Steven Thomas Dobey

May 2002

ACKNOWLEDGEMENTS

I am grateful to Dr. Michael Pelton, my major advisor, for giving me the opportunity to pursue a graduate degree under his direction. My field seasons in the Okefenokee Swamp provided me with some of the most difficult, enduring, and most enjoyable experiences of my life. I also extend my sincere thanks to Dr. Joseph Clark for stepping in as my second advisor following Dr. Pelton's semi-retirement. Your enthusiasm and willingness to help has provided with something that I could never have learned in a classroom.

I greatly appreciate all of the assistance and advice provided by the members of my graduate committee. They included Dr. Michael Pelton, Dr. Joseph Clark, Dr. Lisa Muller, and Dr. Gary McCracken. Their input and suggestions greatly improved the quality of my thesis. I also thank Dr. Frank van Manen for always taking time to answer my questions and providing invaluable computer assistance.

The staff at Okefenokee National Wildlife Refuge provided research personnel with all of the resources that we could have ever needed throughout the course of this 5-year study. This research would not have been possible without your generosity. I also would like to thank the Georgia Department of Natural Resources for all of the time and assistance that was so eagerly donated on their behalf.

I owe a special acknowledgement to the staff of Osceola National Forest, Jefferson Smurfit and Container Corporation, Gillman Paper Company, Champion International Corporation, Rayonier, and Superior Pine for allowing me to conduct research on their lands. I am grateful to the members of the Jamestown, Okefenokee

Sportsman, Big Swamp, Low Road, Bear Bay, and Banker's Trust hunting clubs for their cooperation.

I also thank the employees of Stephen Foster State Park for their hospitality and the invitation for Thanksgiving dinner when I couldn't go home. I extend a special thanks to Refuge employee's Stacey Williams and Stiner Jones for never being too busy to come by the house and see how things were going.

I express much appreciation to Dr. Tim King and Shannon Julian for providing invaluable assistance with hair preparations, DNA extractions, and analysis of genetic data. Although your patience and willingness to teach made my 2-week visits to the lab knowledgeable, your hospitality made them most enjoyable.

I greatly appreciate the help of my field technicians Jeremy Dixon and Amanda Jackson for their assistance with data collection. Both of you worked hard under extremely difficult conditions, and for that I am very grateful.

I am especially indebted to Rich Beausoleil for introducing me to bear research and graduate school at UT. I won't forget the lunch breaks spent in the Tiger Truck Stop and all the money we lost. I never suspected that trapping bears in Louisiana for $350 a month would lead to this. Thanks for all of your help along the way.

To all of my fellow graduate students I would like to say thank you for making my education at UT more rewarding than I could've ever imagined. These include Jennifer Murrow, Donny Martorello, Rich Beausoleil, Jay Clark, Thomas Eason, Daron Barnes, David Brandenburg, Mark Boersen, Brandon Wear, Meghan Carr, Andy Edwards, Jun Yoshizaki, Jason Kindall, Dave and Rebecca Telesco, Laura Thompson,

Daniel Moss, and Carrie Schumacher. Thank you all for your support, advice, and friendship.

I would like to especially thank Jennifer Murrow for her unwavering friendship and her ability to always say the right thing when I needed it the most. Through the good times and the not-so-good times, you always had a shoulder for me to lean on. Thank you for everything, I am proud of you.

Lastly, I must thank all of my family for their encouragement and support throughout my stay here at UT. Although I loved working in Okefenokee, you always made coming home worthwhile and I wouldn't trade that for anything. Thank you.

ABSTRACT

The Florida black bear (*Ursus americanus floridanus*) exists as 7 relatively disjunct populations in Alabama, Florida, Georgia, and possibly Mississippi. In 1974, the Florida Fish and Wildlife Conservation Commission listed the Florida black bear as threatened statewide because of habitat loss and illegal killing. Although the species has not been afforded federal protection, the U.S. Fish and Wildlife Service is currently involved in a lawsuit over this issue. Although a judge's decision is still pending in the case, the earlier ruling by the USFWS could be reversed and the Florida black bear would be granted federal protection as a "threatened" species.

I investigated population size and density of Florida black bears in the Okefenokee-Osceola ecosystem in southeast Georgia and northcentral Florida. I sampled bears at the Okefenokee National Wildlife Refuge (ONWR) and Osceola National Forest (ONF). This study provided a rare opportunity to compare estimates between a hunted (ONWR) and unhunted (ONF) assemblage of bears within the same population.

In addition to livetrapping, I also sampled each study area using a non-obtrusive sampling technique of collecting hair samples from free-ranging bears using baited barbed-wire enclosures. Individual identification was facilitated by microsatellite analysis of DNA extracted from collected hair samples.

From 1995–1998, I, along with other project personnel, live captured 123 individual bears 208 times on the Okefenokee area and 79 bears 132 times on the Osceola area. During the 15 weeks of hair sampling, 435 and 742 bear visits resulted in the collection of 374 and 637 hair samples on the Okefenokee and Osceola study areas,

respectively. A subsample of 79 hair samples was randomly selected for analysis from the Okefenokee data. Complete multi-locus genotypes were obtained for 78 of those samples, of which 39 individual bears were identified. Eighty-eight hair samples were chosen for analysis from the Osceola data; complete multi-locus genotypes from 37 bears were obtained from 84 samples. All samples were analyzed at the same 8 microsatellite loci.

The heterogeneity model M_h produced an estimate of 71 (95% CI = 59–91) bears for the Okefenokee study area, corresponding to a density of 0.14 bears/km^2. On the Osceola study area, the null model M_o estimated population size at 44 (95% CI = 40–57) bears, or 0.12 bears/km^2.

The hair-sampling technique is a promising new tool for mark-recapture experiments and bear research. Because large areas can be sampled at one time, spatial and temporal variation in capture probabilities can be overcome. Likewise, trap response bias is likely minimized because the "capture" involves no physical restraint or undo stress. Based on the above, large sample sizes can be collected in a relatively short period of time. Thereby facilitating the use of closed models for estimating population size.

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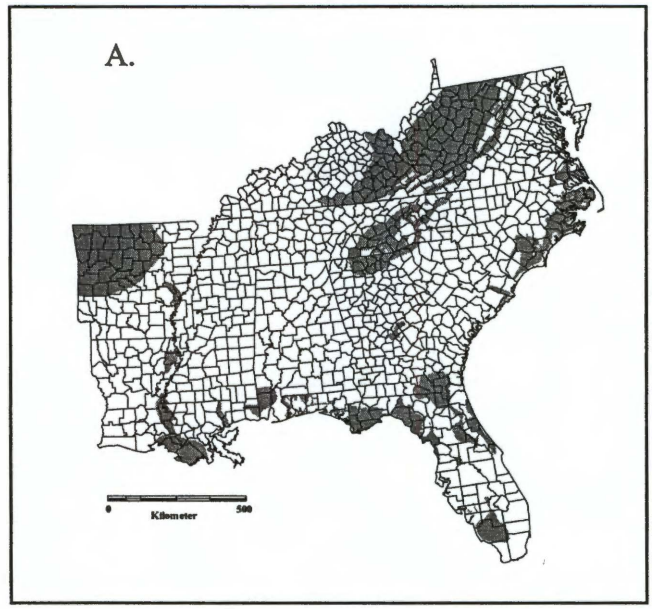
CHAPTER I

INTRODUCTION

General Problem Statement

The American black bear (*Ursus americanus*) once occupied most of the forested regions of North America. However, habitat loss and fragmentation by humans has significantly decreased that range (Pelton and van Manen 1994). In the southeastern United States, black bears currently exist in the Interior Highlands, the Appalachians, and the Southeastern Coastal Plain (Fig. 1). Within the Southeastern Coastal Plain, 3 subspecies of black bears exist: the eastern black bear (*U. a. americanus*), the Louisiana black bear (*U. a. luteolus*), and the Florida black bear (*U. a. floridanus*).

In addition to Florida, the Florida black bear occurred in the coastal plain of Georgia, Alabama, and Mississippi (Hall 1981). Since the late 1800s, however, land clearing for agriculture and urbanization significantly decreased available habitat in the southeastern U.S. More importantly, loss of those native forests has resulted in severe forest fragmentation and bear populations that are geographically isolated (Wooding and Hardisky 1992). Although black bears once occupied the entire Florida mainland and most coastal islands (Brady and Maehr 1985), their historic range has been reduced by nearly 83% (Florida Fish and Wildlife Conservation Commission [FFWCC] 1993). The current Florida black bear population exists as 7 relatively disjunct populations in Alabama, Florida, Georgia, and possibly Mississippi (Fig. 1). The largest of these bear populations are found in Apalachicola National Forest (NF), Ocala NF, Big Cypress National Preserve, and Okefenokee NWR-Osceola NF.



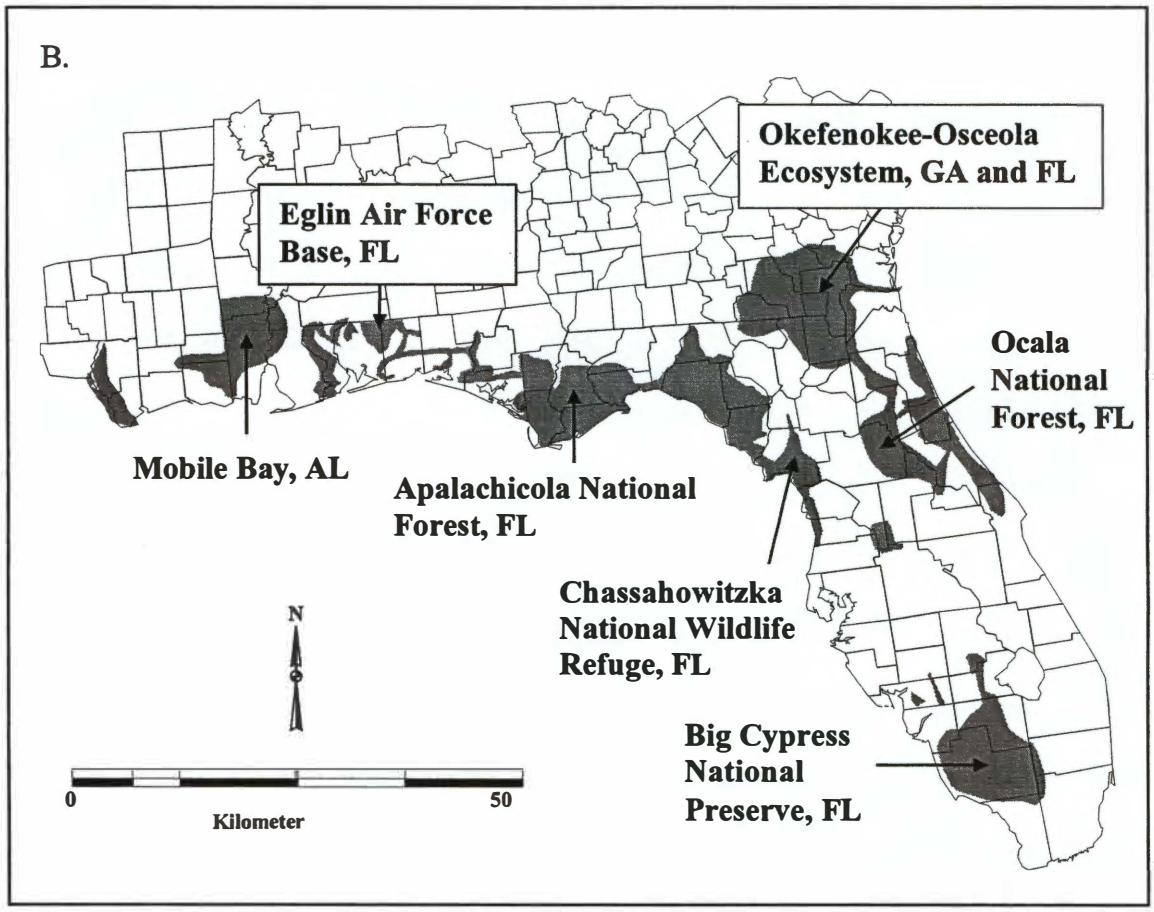


Fig. 1. Current distribution of the American black bear (*Ursus americanus*) in the southeastern United States (from Pelton and van Manen 1997) and (B) current distribution of the 7 relatively disjunct Florida black bear (*U. a. floridanus*) populations.

In 1974, the FFWCC listed the Florida black bear as threatened statewide because of habitat destruction and illegal killing. Black bear hunting seasons were closed except in Baker and Columbia counties, Apalachicola NF and Osceola NF, and Tyndall Air Force Base, where regulated harvests were allowed to continue. In 1990, the U.S. Fish and Wildlife Service (USFWS) was petitioned to list the Florida black bear as a federally threatened species under the Endangered Species Act of 1973. The petition cited illegal hunting, loss and fragmentation of habitat, hunting pressure, and road mortality as the primary justifications for federal protection. In 1992, the USFWS concluded that the status of the Florida black bear was "warranted but precluded" from official designation as a protected species by higher priority listing actions (Wooding 1992). Consequently, ONF was closed to bear hunting in 1992, and all black bear hunting seasons in Florida were terminated in 1994.

A subsequent reexamination by the USFWS to federally list this subspecies was mandated in 1998 and it was ruled that, based on current biological data, the Florida black bear did not warrant federal protection. The USFWS reported that the largest of the remaining Florida black bear populations (Apalachicola NF, Ocala NF, Big Cypress National Preserve, and Okefenokee NWR-Osceola NF) were viable and that habitat loss and fragmentation do not threaten their persistence because they are secure on public conservation lands (Bentzien 1998). It was concluded that, because those populations are distributed over most of the historical range of the species, the Florida black bear is not endangered or likely to become so in the foreseeable future (Bentzien 1998). The 1998 ruling by the USFWS, however, drew criticism from some conservation groups and a lawsuit has since been filed in an attempt to overturn the settlement. Although a judge's

decision is still pending on the case, the ruling could be reversed and the Florida black bear would be granted federal protection under the ESA. The subspecies, however, is still classified as a threatened species by the State of Florida.

Justification

Given the geographic isolation of populations of Florida black bears and the degree of public concern over their status, it is imperative that management decisions be based on the most recent and pertinent biological data. Most research on Florida black bears, however, was published in the 1980s (Maehr and Brady 1982, 1984). Even during the 1990s, research was concentrated only on the Apalachicola NF (Seibert 1993), Eglin AFB (Stratman 1998), and ONF (Mykytka and Pelton 1990, Wooding and Hardinsky 1992, Wooding and Hardinsky 1994, Scheick 1999) bear populations. Although those studies yielded valuable information on bear denning ecology, food habits, habitat use, mortality, movements, and the effects of prescribed fire on bears, none provided estimates of population size.

Considering the degree and rate of human development surrounding Florida black bear populations, obtaining current population estimates is paramount for developing sound management plans, especially where bears are hunted. However, public interest and management concerns vary greatly throughout the range of the Florida black bear. Whereas preservationists strive for legislation to protect the bear and its habitat, hunters believe the goal of management should be to restore the bear's status as a game species. Additionally, people suffering losses in revenue from agriculture or apiary damage typically view bears as a nuisance and desire more stringent depredation guidelines.

Regardless of management objectives, biologists cannot accurately predict the effectiveness of management actions without reliable information on population demographics and abundance.

In 1994 the USFWS contracted this study to aid in the development and implementation of management guidelines for black bears inhabiting the Okefenokee-Osceola ecosystem. Encompassing approximately 6,147 km^2 (1.5 million acres), this area is one of the largest contiguous habitats occupied by black bears in the Southeast. Although habitats within the ecosystem are biologically similar, management objectives are different within the range of bears in this population. Whereas bears are protected in Florida, there is a year-round chase season and a limited bear hunting season for counties surrounding portions of Okefenokee NWR (ONWR) in Georgia. Therefore, one of the primary objectives of this 5-year study was to document and compare population dynamics and habitat use of bears within the Okefenokee-Osceola ecosystem. We accomplished that goal by trapping and radio-collaring bears on 2 study areas; one consisting of land in and adjacent to ONWR and the other in ONF. The primary focus of my research in this study was to analyze capture data and provide estimates of abundance for each of the 2 study areas.

Objectives

The Okefenokee-Osceola ecosystem is regarded as one of the last strongholds of the Florida black bear within its range. Although this ecosystem serves as one of the remaining core populations for this species, human development continues to isolate those populations. The designation of the Florida black bear as a "threatened species" in

Florida, combined with the continued uncertainty of its federal status, identify the need for reliable estimates of population size for bears in the Okefenokee-Osceola ecosystem. Therefore, the objective of my study was to estimate population size and density of black bears in the Okefenokee and Osceola study areas.

CHAPTER II

STUDY AREAS

General

I conducted research on 2 study areas within the Okefenokee-Osceola ecosystem in southeast Georgia and north central Florida (Fig. 2). The center of this ecosystem is located at approximately 30° 40' north latitude and 82° 30' west longitude. The northern study area, which I will refer to as the Okefenokee study area, is located in the northwestern corner of the Okefenokee National Wildlife Refuge (ONWR). Approximately 40 km to the south, the second study area (Osceola study area) is situated within the northern section of Osceola National Forest (ONF) and includes the western edge of Pinhook Swamp. Comprising over 6,147 km^2, the Okefenokee-Osceola ecosystem contains one of the largest contiguous blocks of black bear habitat remaining in the Southeast.

Location

The Okefenokee Swamp occupies parts of Charlton, Clinch, and Ware counties, Georgia and Baker County, Florida. The ONWR was established in 1937 and encompasses approximately 1,580 km^2 of swamp and adjacent pinelands (Scheick 1999); the refuge includes over 90% of the swamp. The 511-km^2 Okefenokee study area included the swamp and islands of the Okefenokee NWR and the adjacent private lands to the northwest of the Refuge (Fig. 3). Interior portions of the swamp included in the

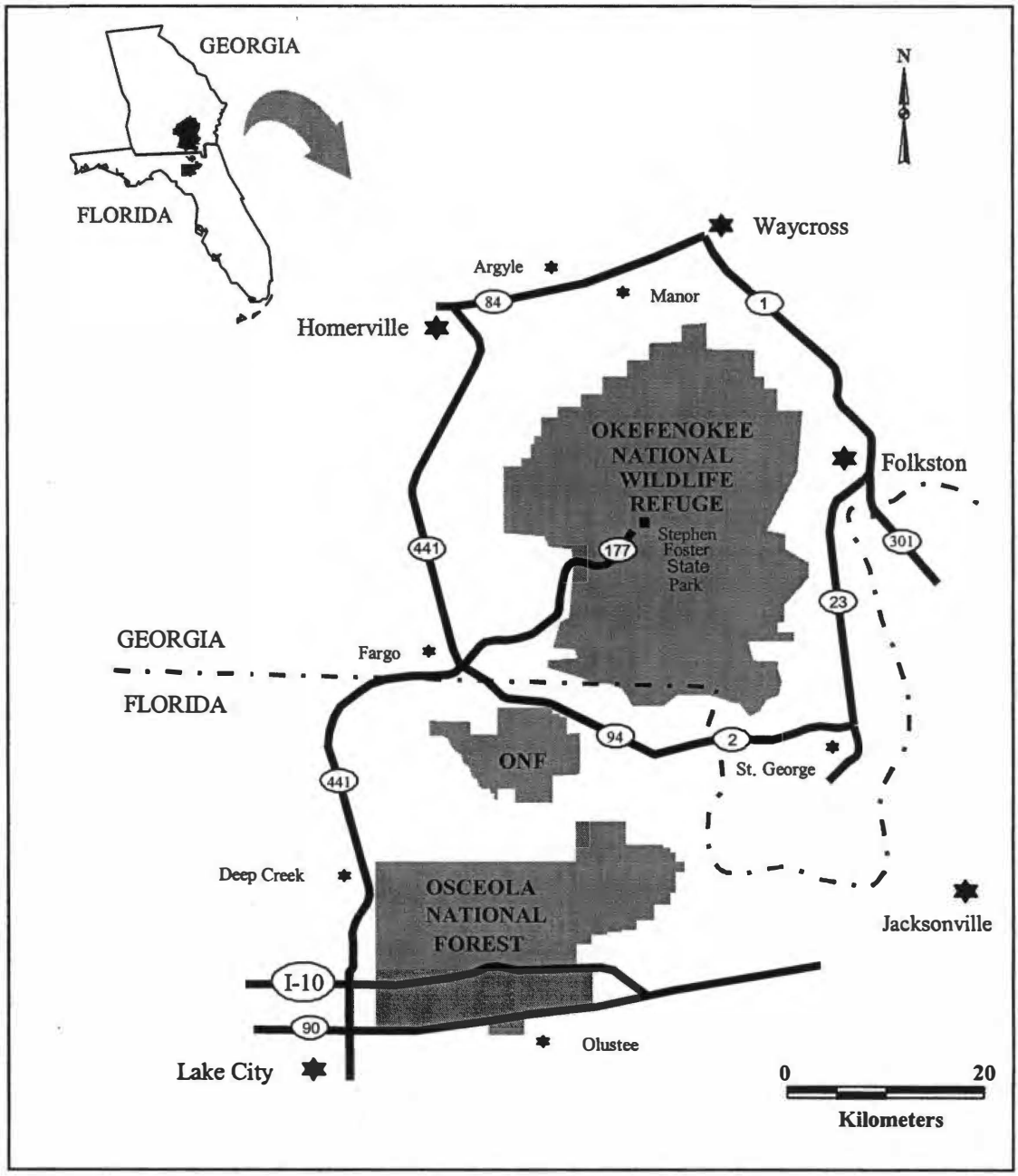


Figure 2. General area of the Okefenokee National Wildlife Refuge, Georgia, and the Osceola National Forest, Florida, 1995–1999.

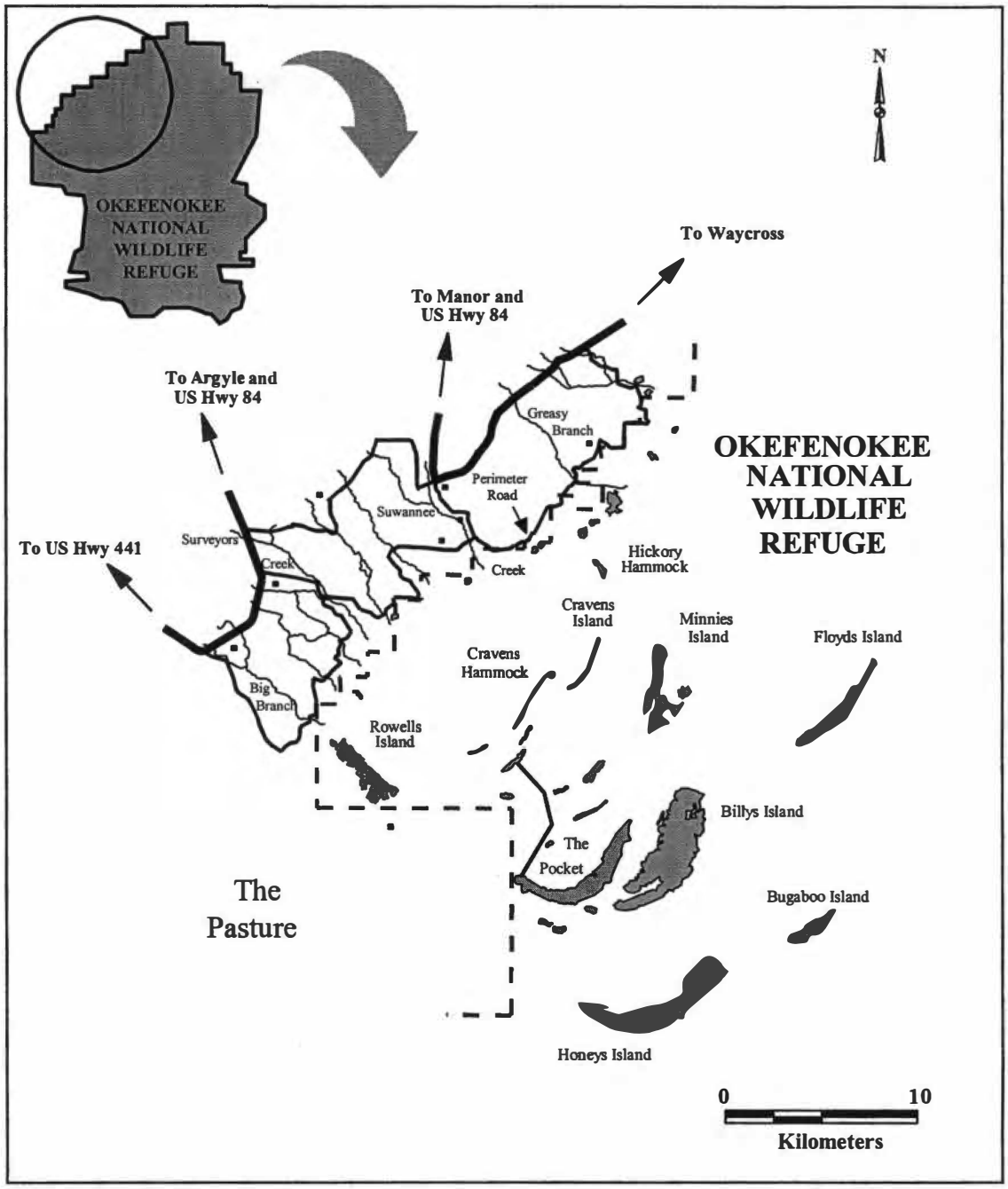


Figure 3. Black bear study area, Okefenokee National Wildlife Refuge, Georgia, 1995–1999.

study area were Craven's Hammock, Craven's Island, Hickory Hammock, and Pine Island. Private lands within the study area were predominately managed pine plantations owned by Jefferson Smurfit and Container Corporation and Rayonier. The nearest major roadways were US 84 to the north, US 1 and 23 to the east, US 2 to the south, and US 441 to the west. Portions of Charlton, Clinch, and Ware counties made up the Okefenokee study area. Nearby population centers were the cities of Waycross, to the north of the refuge, and Folkston, to the east.

Osceola NF, comprised of 2 tracts of land, encompassed approximately 798 km^2 in portions of Baker and Columbia counties in north central Florida. The 366-km^2 Osceola study area included the southwest portion of Pinhook Swamp, the northeast portion of Impassable Bay, and adjacent private lands (Fig. 4). Private lands within the study area were predominately managed pine plantations owned by Bankers Trust, Jefferson Smurfit and Container Corporation, and Rayonier. The nearest major roadways were 2, 127, US 90, US 441, which surround ONF. The closest areas of urban development were Lake City, to the southwest, and McClenny, to the southeast.

Topography and Geology

The Okefenokee Swamp was created by a landscape basin that was shaped by a sea level change approximately 200,000 years ago (Parrish and Rykiel 1979). As surface water accumulated the basin became increasingly inundated and hydrophytic plant communities were established (Loftin et al. 2000). Eventually, the Okefenokee Swamp became a peat-forming bog characterized by forested wetlands, marshes, and open water

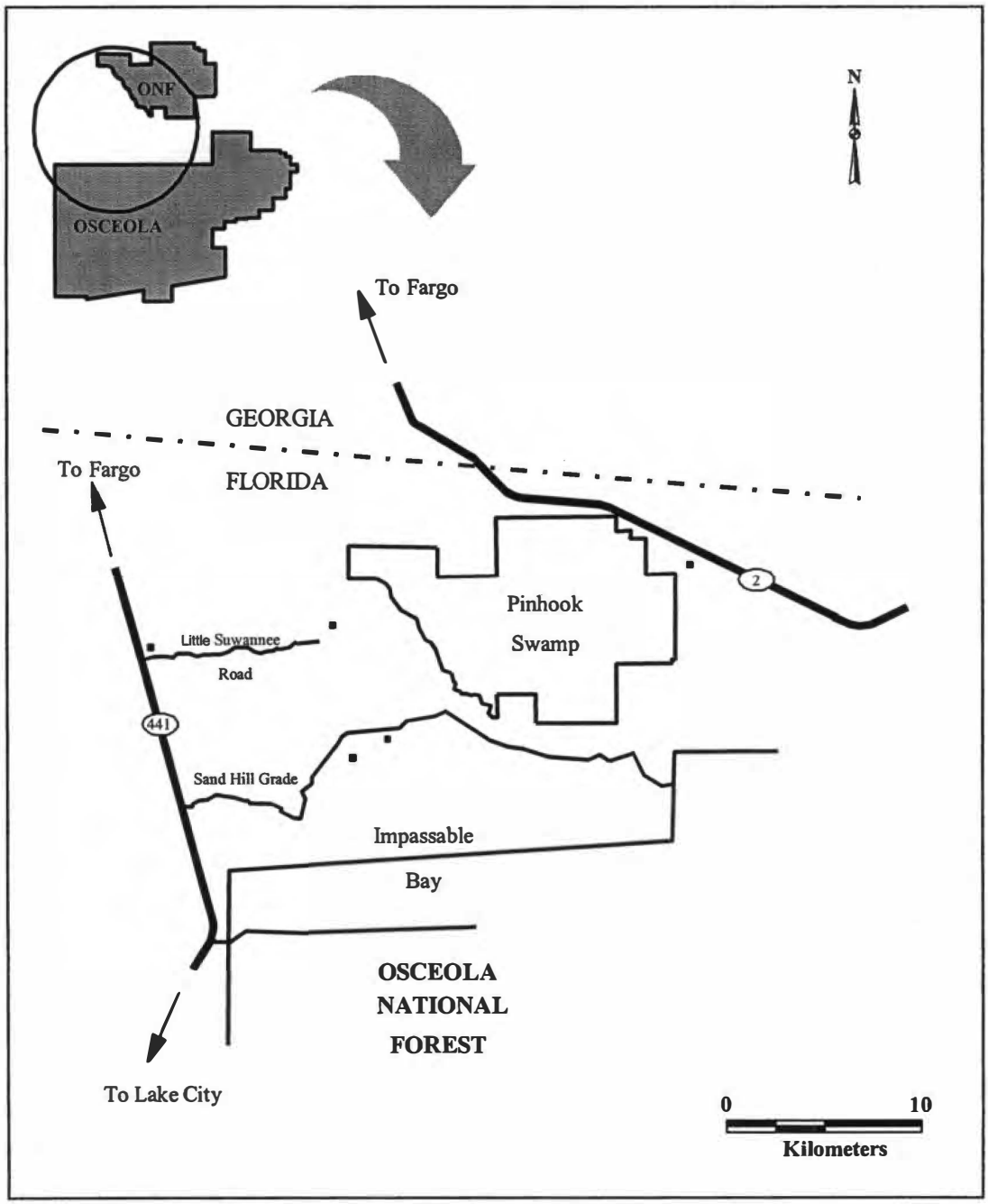


Fig. 4. Black bear study area, Osceola National Forest, Florida, 1996–1999.

maintained by periodic fires and drought (Meyers and Odum 1991). Currently, the topography of the Okefenokee Swamp is characterized by vast expanses of relatively flat land with elevations ranging from 34–40 m above sea level (Yin and Brook 1992). Occupying a portion of the Atlantic Coastal Plain, the Swamp is located approximately 160 km from the Atlantic Ocean. The name "Okefenokee" arises from the Native American term meaning "land of the quaking earth". The swamp acquired that name because of the floating peat layers that can be found within its boundaries. Those layers are so deep in some areas that trees are rooted entirely in the peat, creating free-floating islands that sway when walked on or disturbed. The Okefenokee Swamp is composed of a wide diversity of habitat types. Bay forests, blackgum (*Nyssa sylvatica*) forests, cypress forests, prairies, shrub swamps, and open water constitute the 1,360 km^2 of wetland habitats in the ONWR. Predominantly dry areas are comprised of large expanses of forested uplands and remote islands. Within ONWR, approximately 134 km^2 of upland habitat are managed for the protection and restoration of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) communities (U.S. Fish and Wildlife Service 2001).

The surface geology of the upland watershed of the Okefenokee Swamp is characterized by intensively leached sandy soils that have a marked increase in the amount of clay with increasing depth (Laerm and Freeman 1986). Soils in this region, formed from marine sediments deposited during the Pleistocene and Holocene epochs, are typically acidic and poor in nutrients.

Elevations within ONF range from 115–125 m above present sea level. Soils were primarily Mascotte-Oscilla-Surrency associations (U.S. Department of Agriculture

1984). Although a lack of topographic relief made this area similar to the Okefenokee Swamp, differences in habitat composition exist. Unlike the Okefenokee, ONF is composed of a large mosaic of smaller swamps, bayheads, and wet pine flatwoods interspersed in upland pine plantations. The largest contiguous swamp in ONF is the 243-km^2 Pinhook Swamp, often referred to as the southern extremity of the Okefenokee Swamp.

Hydrology

The Okefenokee Swamp is one of the largest freshwater wetlands in the United States. Water input to the swamp primarily occurs through precipitation. Rainfall and stream runoff from the northwestern portion of the swamp contribute to the Suwannee River drainage. Approximately 85% of the exiting flow occurs via the Suwannee River in the western portion of the swamp (Loftin et al. 2000). The remainder of the water flow out of the swamp is carried by the St. Mary's River drainage to the south (Rykiel 1977). Major tributaries in the study area are Alligator Creek, Barnum Branch, Bear Branch, Big Branch, Cane Creek, Goose Branch, Greasy Branch, Mill Branch, Surveyors Creek, Suwannee Creek, Turkey Branch, and Water Oak Creek. Many smaller creeks throughout the private lands surrounding the refuge also contribute to water input; these riparian corridors serve as important travel routes for bears moving into and out of the refuge. Practically all the water runoff occurs via the Suwannee and St. Mary's Rivers which exit the swamp to the southeast and south, respectively.

Like the Okefenokee, the primary source of water into ONF occurs through precipitation. However, because there are few channeled or natural streams in this

region, most flow occurs as sheet water. The most well developed channel is where Suwannee Creek drops from 120 m to 95 m above sea level, serving as Pinhook Swamp's primary drainage (Scheick 1999). Little Creek, the only other creek on the Osceola study area, flows west into the Suwannee River.

Climate

The climate of southeastern Georgia and north central Florida is subtropical. Summers were characterized as hot and wet and winters as cool and dry. In Georgia, mean summer high and low temperatures were 32.2°C and 17.8°C, whereas mean winter temperatures were 23.3°C and 8.9°C, respectively. Annual precipitation amounts during 1998 and 1999 were 86.6 cm with most rainfall occurring in July (23.6 cm) and least in May (0.51 cm) (National Climatic Data Center 1998, 1999).

Mean summer high and low temperatures in Florida were 31.7°C and 19.4°C, whereas mean winter temperatures were 23.3°C and 11.1°C, respectively. Annual precipitation during 1998 and 1999 was 114.2 cm with most rainfall occurring in September (28.5 cm) and least in November (0.46 cm) (National Climatic Data Center 1998, 1999).

Fauna

The ONWR and ONF support a diversity of wildlife species, including over 233 bird, 64 reptile, 49 mammal, 39 fish, and 37 amphibian species. Big game species include black bear (protected on the Osceola study area) and white-tailed deer (*Odocoileus virginianus*). Small game species include eastern cottontail (*Sylvilagus*

floridanus), marsh rabbit (*Sylvilagus palustris*), and gray squirrel (*Sciurus carolinensis*). Other common mammals include bobcat (*Felis rufus*), gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), opossum (*Didelphis virginianus*), raccoon (*Procyon lotor*), river otter (*Lutra canadensis*), and skunk (*Mephitis mephitis*). Common upland game birds are bobwhite quail (*Colinus virginianus*), mourning dove (*Zenaida macroura*), and wild turkey (*Meleagris gallopavo*). Resident species that are recognized as endangered by the USFWS include gopher tortoise (*Gopherus polyphemus*), Eastern indigo snake (*Drymarchon corais*), red cockheaded woodpecker (*Picoides borealis*), wood stork (*Mycteria americana*), and gray bat (*Myotis grisescens*).

Flora

The 2 study areas were dominated by an interspersion of pine flatwoods and hardwood swamps. Bald cypress (*Taxodium distichum*), black gum, and fetterbush (*Lyonia lucida*) dominated the larger swamps (Wooding and Hardinsky 1994). Pine flatwoods were dominated by slash pine (*Pinus elliotti*), saw palmetto (*Sereona repens*), and gallberries (*Ilex coriacea* and *I. glabra*) (Avers and Bracy 1973). Small cypress swamps and bays also were distributed throughout the pine flatwoods habitats in both study areas. Although the habitat types within the study areas were distributed differently, their proportions were similar (Scheick 1999) (Table 1).

History and Land Use

Historically, the primary use of land in the Okefenokee has been timber production. In 1889, the Suwannee Canal Company purchased 964 km^2 of the

Table 1. Proportions of habitat types within the Okefenokee and Osceola study areas, Georgia and Florida, 1999 (Scheick 1999).

Habitat Type	Proportion of GA Area	Proportion of FL Area
Bay/ Gum/ Cypress Forest	4.9%	3.2%
Loblolly Bay Forest	17.9%	18.7%
Slash Pine Forest	18.7%	27.6%
Cypress Forest	37.7%	28.5%
Mixed Hardwood Hammock	1.7%	1.5%
Mixed Hardwood Swamp Forest	13.2%	12.6%
Shrubland	1.1%	2.3%
Emergent Marsh/ Open Water	3.3%	0.4%
Bare Soil/ Urban	1.5%	5.2%

Okefenokee Swamp from the State of Georgia (McQueen and Mizell 1926). After a failed attempt at draining portions of the swamp to facilitate agricultural production, the company began harvesting cypress from the swamp. Before declaring bankruptcy in 1897, the Suwannee Canal Company harvested over 7 million board feet of cypress timber from the Okefenokee Swamp (Izlar 1984). Timber harvesting resumed in 1909 when the Hebard Cypress Company constructed several railroad trams that allowed access to the interior of the swamp. By the time logging in the swamp ceased in 1927, approximately 425 million board feet of timber had been harvested (Hopkins 1947). From 1890–1927, enough mature cypress were removed that approximately 40% of the forested area that was virgin old growth has now been replaced by younger second growth (Hamilton 1982). In 1936, the U.S. Fish and Wildlife Service purchased the Hebard Cypress Company's holdings and created the Okefenokee National Wildlife Refuge. Although logging within the refuge has ceased, the majority of land adjacent to and surrounding the swamp is now owned and intensively managed by large timber companies. Those private holdings are typically managed for slash pine production on a 20–25 year rotation. In the more remote areas of the interior refuge, virgin cypress forests are still present; the oldest trees have been aged at over 600 years (Duever and Riopelle 1983).

Excluding forestry uses, hunting is the most common use of private lands outside the ONWR. All private land holdings within the Okefenokee study area were leased to 3 hunt clubs. The bear hunting season consisted of 3, 2-day hunts occurring on the last Friday and Saturday of September and the first 2 Fridays and Saturdays in October. Beginning in 1998, the Georgia Department of Natural Resources permitted a 3-day hunt

in the Dixon Memorial Forest (adjacent to the northern edge of ONWR) during the first week of December. Hunting regulations stipulated that 1 bear may be harvested per licensed hunter per year by still-hunting (firearms and archery) or with the aid of dogs, and no baiting is permitted. Although hunting pressure is significant during the relatively short season, the majority of human presence on the Okefenokee study area was the result of a year-round dog chase season where baiting was allowed. On the Okefenokee study area, hunt club members chased bears with dogs approximately 3 days per week from April to mid-September. The only times that bears typically were not being chased was during the denning season, the 2-week period immediately prior to the hunt season, and the weekdays between the 3 consecutive hunt weekends. Access into the ONWR was restricted to designated entrances and canoe trails, and hunting of any kind is prohibited.

The Osceola area was originally occupied by the Timucuan Indians, as noted in 1535 by Hernando de Soto during his travels through the area that is now Lake City, Florida. During the early 1800's, Seminole Indians occupied much of the area until moving to an area further south (U.S. Department of Agriculture 1984).

Throughout the mid- to late-1800s much of the prosperity and growth in the Osceola area was associated with cotton production (U.S. Department of Agriculture 1984). As timber practices became more refined, however, the majority of land was converted for forestry practices. As is the case in Georgia, the majority of land within the Osceola study area, including ONF, is currently managed for slash pine production.

Access to the private lands in the Florida area was regulated by timber companies and is restricted to employees and members of leased hunt clubs. Unlike the ONWR,

however, ONF had free access via public roads. Although the bear season was closed in Florida, white-tailed deer and hogs were hunted on the Osceola study area.

CHAPTER III

MATERIALS AND METHODS

Study Design

Examining the dynamics of wild animal populations often requires estimates of population size (Pollock et al. 1990). Obtaining reliable population abundance data, however, has long been a challenge to wildlife biologists. Although mark-recapture analyses are the standard for estimating population size, models used for these analyses often require specific assumptions that are difficult to meet (Mowat and Strobeck 2000). The assumption of demographic closure, in which there are no additions or permanent deletions during the study, can be used to separate 2 types of population models (Menkens and Anderson 1988). The first being closed models, which assume population closure, and the second being open models, which allow for additions and deletions. Unfortunately, both open and closed models require additional assumptions that may be readily violated when applied to bears (Mace et al. 1994). The most important of these may be the assumption of equal catchability, which is that every individual in a population has an equal chance of being captured during a trapping session. Pollock et al. (1990) identified 2 forms of capture variation that violate the equal catchability assumption: (1) trap heterogeneity, whereby animals have different capture probabilities for reasons inherent to the individual (e.g. social status, age, sex); and (2) trap response, whereby an individual's capture probability is dependent upon its capture history (trap happy and trap shy response). Lastly, both closed and open models are based on the

assumption that marks are not lost and all marked individuals are recorded correctly (Otis et al. 1978, White et al. 1982, Pollock et al. 1990).

Of primary interest to this study are the effects of trap response and how biases associated with this response affect estimates of population size. Our original intent was to live trap black bears for 5 years in the Okefenokee-Osceola ecosystem and provide reliable estimates of population size for bears in the Okefenokee and Osceola study areas using mark-recapture models. Although researchers were successful in maintaining adequate capture and recapture samples in the 1995–1998 trapping seasons, analysis of capture data indicated that a trapping bias might be adversely affecting our capture success. In particular, we were concerned that our intense trapping efforts were resulting in a learned trap response (avoidance) among bears. Consequently, we decided to employ a relatively new recapture technique during the final year of the study in an attempt to alleviate such sampling bias.

Recent efforts to develop non-invasive genetic sampling techniques have resulted in promising new tools for bear research and management (Paetkau and Strobeck 1994, Paetkau et al. 1995, Mowat and Strobeck 2000). Of particular interest is the use of DNA fingerprinting techniques based on microsatellite loci to individually identify animals from hair, scat, or tissue (Woods and McLellan 1995). Consequently, microsatellite analysis can be used to "mark" animals, and provide recapture histories for all individuals sampled. Those genetic markers obtained from microsatellite loci can be identified from minute quantities of DNA, are highly variable, and easily interpreted in terms of allele frequencies (Wright and Bentzen 1995, Parker et al. 1998). When incorporated into mark-recapture models, recapture histories collected from non-obtrusive sampling

techniques may provide estimates of population size that help reduce biases such as those associated with live trapping. To investigate this, hair samples were collected from free-ranging black bears in the Okefenokee-Osceola ecosystem using baited barbed wire enclosures (Woods et al. 1996).

Considering the assumptions of open and closed population models, non-obtrusive sampling techniques and using DNA fingerprints as "marks" have several advantages over traditional methods of capturing and marking bears. Because bears do not have to be physically captured, restrained, or marked, there is no negative association with the sampling technique, thereby decreasing the likelihood for a learned trap response. Temporal and spatial biases in capture probabilities can also be minimized by because an entire study area can be sampled at one time using the hair-trapping technique. In addition, genetic markers cannot be lost, as is often the case with traditional marks. This is extremely important for mark-recapture studies since loss of marks always results in positively biased estimators (Pollock et al. 1990). Another advantage is that sample sizes will likely increase because trap response is minimized and trap densities can be higher. Lastly, there is no special expertise needed in capturing hair samples, so more effort can given to trapping rather than training.

Study Area Delineation

I delineated each of the respective study areas by circumscribing each of the 1999 hair trap sites with a circle, the area of which was equivalent to the average home range estimate for female bears. Home ranges were estimated using the 95% Minimum Convex Polygon estimator in ArcView® GIS (ESRI, Redlands, California). I limited the

telemetry data to bears with ≥30 locations collected from 1995–1999 and 1996–1999 on the Okefenokee and Osceola study areas, respectively. Furthermore, telemetry data were restricted to locations with collection dates that coincided with the months of the hair-trapping season (June to September, 1999). All home range data used in delineating study areas were collected during this study (J. D. Clark, U.S. Geological Survey, unpublished data).

Based on my criteria, average home range sizes for female black bears were 40.0 and 54.5 km^2 on the Okefenokee and Osceola study areas, respectively. I buffered each of the 1999 hair trap sites in the Okefenokee area with the average radius of 3,198 m. Each hair trap site in the Osceola area was buffered with the average radius of 4,330 m. Consequently, the Okefenokee study area was 511 km^2 and the Osceola study area was 366 km^2 in size (Fig. 5).

Trapping and Handling

Black bears were primarily trapped from early June through late September from 1995–1998 and 1996–1998 on the Okefenokee and Osceola study areas, respectively. Limited trapping sessions during late October and early November of 1995, 1996, and 1997 focused on more remote locations within the ONWR. All bears were captured using Aldrich spring-activated foot snares (Aldrich Animal Trap Company, Clallam Bay, Washington). Because inaccessible and impenetrable habitat precluded random trap placement, trapsites were established according to habitat type, known bear travel routes, and bear sign.

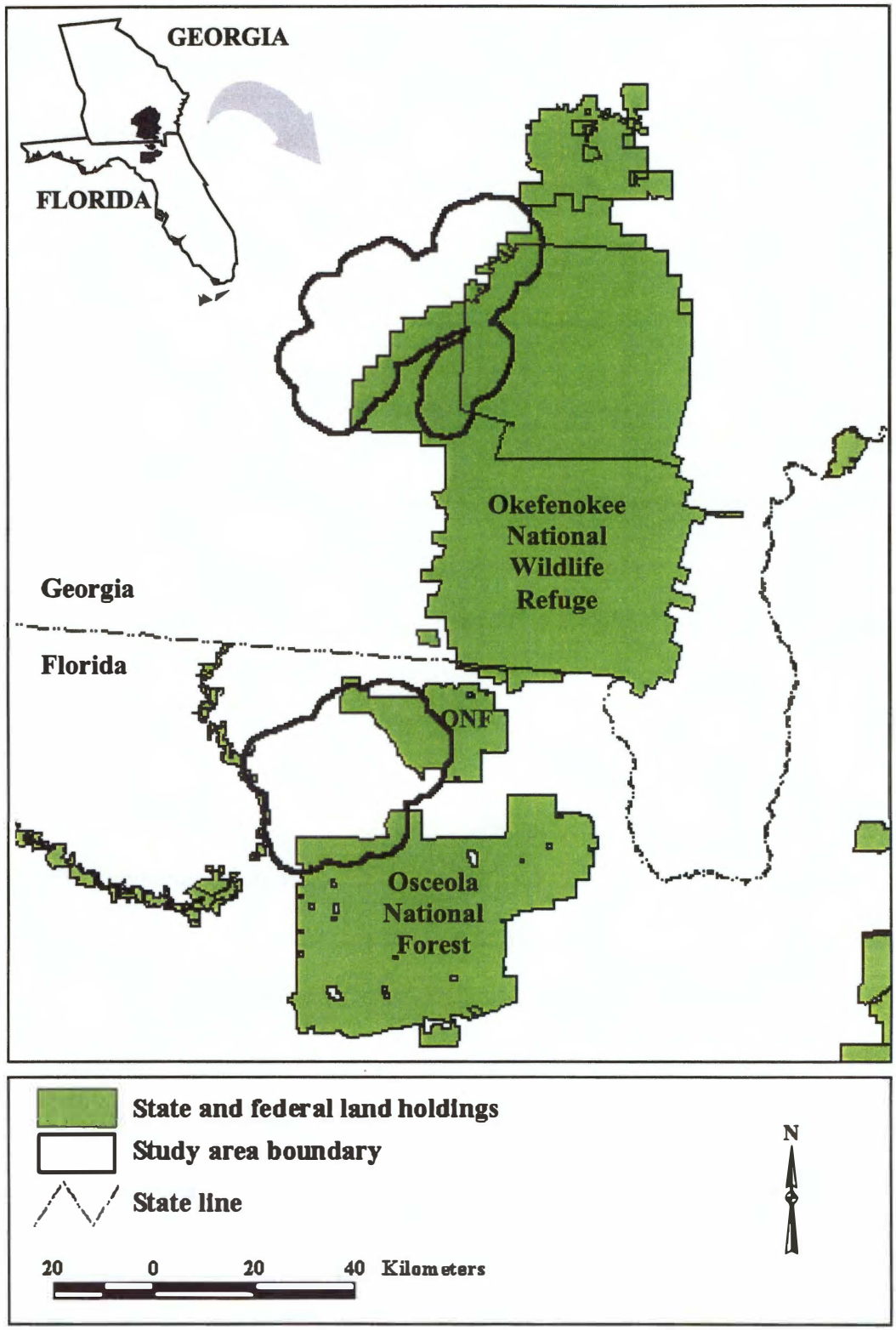


Fig. 5. Delineation of the Okefenokee and Osceola study areas using home range data, Georgia and Florida, 1999.

We primarily used 3 trapping techniques to capture bears on both study areas. Standard trail sets baited with dry corn placed in hanging plastic bottles were used as an initial attempt to catch bears at trapsites (Clark 1991, Brandenburg 1996). Bears were lured to those trapsites with artificial raspberry flavoring (Mother Murphy's, Greensboro, North Carolina). Blind sets (i.e., traps without bait) were used to capture bears that had learned to steal baits without being captured. Lastly, dirt-hole sets were used when blind sets failed to capture "trapwise" bears. A dirt-hole set consisted of a snare with the foot-loop placed atop a freshly dug hole and camouflaged with discarded trash. We used trees to secure snares, but we used mobile home anchors (123 cm long with a 10-cm auger) to secure snares when trees were unavailable.

We checked traps 1 to 2 times daily, depending on site conditions. In well-shaded areas, traps were usually checked by 1100. I checked trapsites without the cover of shade or in close proximity to human activity by 0800. Those traps were deactivated during the day to prevent bears from being captured in direct sunlight or full view of the public.

Captured bears were immobilized with a 2:1 mixture of ketamine hydrochloride (Ketaset, Burns Veterinary Supply Incorporated, Farmers Branch, Texas) and xylazine hydrochloride (Rompun, Haver-Lockhart Incorporated, Shawnee, Kansas). Immobilization drug was administered intramuscularly with a push pole at a dosage of 4.4 mg (1 ml/ 22.7 kg) of Ketaset and 2.2 mg (1 ml/ 45.5 kg) of Rompun per kg of estimated body mass. Bears with injuries received an injection of Liquamyacin (LA-200, Pfizer Animal Health, New York, New York) at a dosage of 8.8 mg/kg body mass. After immobilization, a wetting agent (Akwa Tears, Akorn Incorporated, Abita Springs,

Louisiana) was applied to the bears' eyes to prevent desiccation. A blindfold was then placed over the eyes to protect them from debris and to minimize visual stimuli.

A permanent identification number was tattooed on the inside upper lip of each bear using 0.8-cm numeric digits (Nasco, Fort Atkinson, Wisconsin) and animal tattoo ink (Ketchum Manufacturing, Ottawa, Canada). Numbered ear tags, corresponding to individual tattoo identification numbers, were placed in both ears of each bear. Male bears received a rectangular metal tag (Hasco Tag Company, Dayton, Kentucky) in the right ear and a plastic round colored tag in the left ear. Female bears received the same types of tags but they were placed in opposite ears. This method of tagging enabled hunters to identify male and female bears that were seen during the year-round dog chase season.

All female bears >1 year-old received a motion-sensitive radio-collar (Telonics Incorporated, Mesa, Arizona and Lotek Engineering Incorporated, Ontario, Canada). A select number of male bears on the Okefenokee study areas were radio-collared as part of another study (M. R. Pelton, University of Tennessee, unpublished data). I equipped each collar with a 12.5-cm by 0.4-cm leather spacer that served as a breakaway device (Hellgren et al. 1988). All spacers were soaked in vegetable oil for at least 1 month before being placed on a collar to prolong its durability. 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). Bears were weighed with a spring scale and standard morphological measurements were recorded. Body temperature, pulse, and respiration were monitored throughout each immobilization.

Information concerning the general description, reproductive status, tooth wear, and physical appearance were recorded for all bears. I collected tissue and hair samples from each bear to be used for microsatellite analysis. Lastly, yohimbine hydrochloride (Lloyd Laboratories, Shenandoah, Iowa), an antagonist for xylazine hydrochloride, was administered through the sublingual vein at a dosage of 0.2 mg/kg of body mass.

Hair Trapping

I collected hair samples from free-ranging bears on both study areas with bait surrounded by barbed wire. These baited "enclosures" consisted of a single strand of barbed wire (2-strand wire, 4 points, 7.5-cm spacing between barbs) attached to trees to form a polygon (Fig. 6). Wire was affixed to the outside of perimeter trees using 2.5-cm aluminum fence staples and tensioned by hand using fencing tools. Eighty-eight and 90 hair traps were maintained between 12 June and 27 September 1998 on the Okefenokee and Osceola study areas, respectively. This resulted in an average density of 1 hair trap per 5.8 km^2 on the Okefenokee study area, or approximately 7 and 24 hair traps per female and male home range, respectively. On the Osceola study area, hair trap density was 1 per 4.1 km^2, or approximately 13 traps per female home range. No male bears were radio-collared on the Osceola study area. Based on the average home range size for Okefenokee males, however, there were approximately 34 hair traps per male home range on the Osceola study area. Those hair trap densities were within those suggested by Otis et al. (1978) that population studies be designed so that animals have ≥4 traps in their estimated home range.

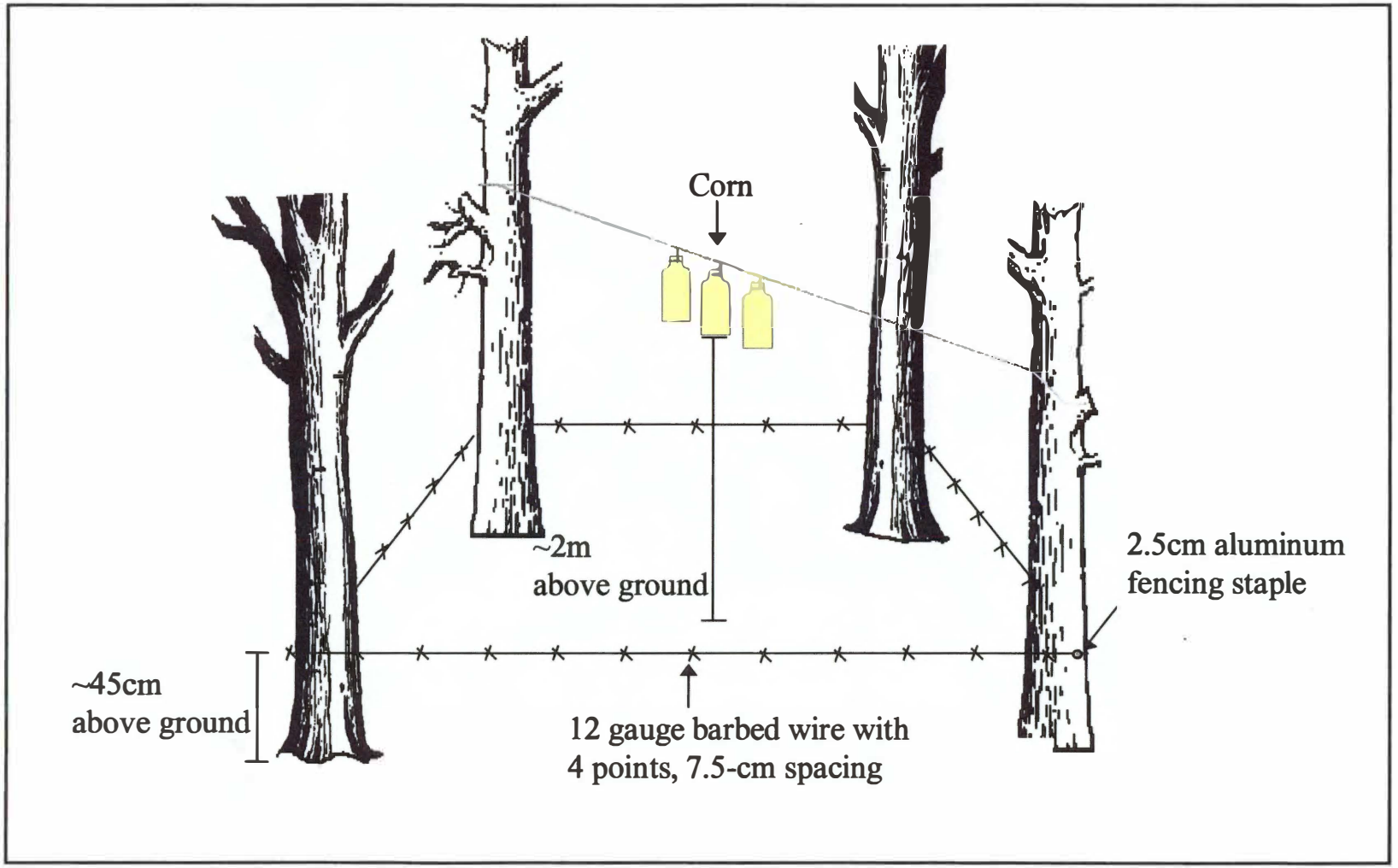


Fig. 6. Diagram of a baited barbed wire enclosure used to collect hair samples from black bears on the Okefenokee and Osceola study areas, Georgia and Florida, 1999.

Three 20-ounce plastic bottles filled with dried corn were hung approximately 2 m above the ground within the enclosures from a wire affixed to 2 perimeter trees. I positioned the bait so that no point on the perimeter fence was less than 3 m away to prevent bears from reaching baits without crossing the barbed wire. Furthermore, I was careful to ensure that the barbed wire was approximately 45 cm from the ground. If necessary, terrain irregularities were blocked with debris to ensure uniform wire height above ground. I used 3 bottles of corn to entice bears to enter an enclosure multiple times, thereby increasing the likelihood that a hair sample of sufficient size (≥5 hairs) would be collected. I refrained from using scent attractants so that bears would not be enticed into enclosures after bait had already been taken. That was done to decrease the chance of cross-contaminating samples with hair from multiple bears.

I checked hair traps at intervals of about 9 days; each of interval was considered a single sampling occasion. From June-September, I sampled the Okefenokee and Osceola study areas on 10 and 11 occasions, respectively. The Okefenokee study area received 1 less sampling occasion because it took longer to install hair traps on that area. Nine days was selected as the interval between hair collections to minimize the risk of DNA degradation, to decrease the chance of having individual samples contaminated by multiple bears, and due to logistical constraints of travelling between 2 study areas. I examined each barb for hair by placing my hand or a white card behind each barb and removing any hairs. Groups of hairs collected from individual barbs were considered separate samples and placed in individual manila coin envelopes. Each envelope was labeled with the date, trap identification number, number of hairs in the sample, and number of roots in the sample. I placed all collected hair samples in airtight storage

containing desiccants. Samples were then frozen until microsatellite analysis could be performed.

As was the case with trapping using foot snares, inaccessible and impenetrable habitats within both study areas precluded random placement of hair traps. Therefore, I established hair trap locations according to habitat type, known bear travel corridors, and bear sign. Every effort was made to ensure adequate coverage without major gaps in the trapping grid on each study area. All hair traps were mapped using a Global Positioning System (GPS) unit and Universal Transverse Mercator (UTM) coordinates were recorded.

Subsampling

Bear visits to hair traps typically resulted in multiple hair samples being left on barbs. Although all samples were individually collected, only samples with ≥5 hairs were good candidates for microsatellite analysis (T. King, U.S. Geological Survey, personal communication). Because of the large number of hair samples collected, however, a subsampling design was implemented to reduce the number of samples for analysis. To accomplish that, I randomly chose 8 hair samples from each of the 10 and 11 trapping periods on the Okefenokee and Osceola study areas, respectively. I selected 8 samples for microsatellite analysis based on simulation results of the modified Lincoln-Petersen estimator using live-capture data from 1998. Those simulations suggested that 8 samples per sampling period should provide enough recaptures to provide population estimates with coefficients of variation ≤0.25. The method of uniform random sampling

was chosen to ensure equal sampling effort from every trapping period (K. Pollock, N. C. State University, personal communication).

Microsatellite Analysis

Removal of hair roots and preparation for DNA extraction was performed at the University of Tennessee. 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. DNA extractions, replication by polymerase chain reaction (PCR), and microsatellite analysis were performed at the U.S. Geological Survey Aquatic Ecology Laboratory at the Leetown Science Center, Kearneysville, West Virginia (see Table C1 for details of genetic analyses).

Hair samples selected for analysis were identified based on 8 individual microsatellite loci. Those loci included G1A, G1D, G10B, and G10L (Paetkau and Strobeck 1994), and G10C, G10M, G10P, and G10X (Paetkau at al. 1995).

Probability of Identity

One of the primary assumptions of open and closed population models is that marks are not lost or overlooked (Pollock 1990). Furthermore, it imperative that individuals be correctly identified. Genetic marks, in the form of microsatellite genotypes, have the potential to replace conventional marks if the tags correctly identify individuals in trapping sessions (Woods et al. 1999). Although I assumed matching hair samples represented a recaptured animal, it was possible that different individuals could share identical genotypes at the 8 loci examined (Woods et al. 1999, Mills et al. 2000).

Factors influencing the likelihood of hair samples having an identical genotype include the number of loci examined (Woods et al. 1999) and the degree of genetic variability present in the population (Paetkau et al. 1998).

To assess the variability of the loci examined, I estimated the probability that 2 individuals drawn at random from a population would share an observed genotype. That statistic, referred to as the probability of identity (PI), is defined as the proportion of the population possessing genotypes that cannot be distinguished from one other individual (Mills et al. 2000). In studies of this type, PI essentially provides a measure of how useful a suite of loci will be for individual identification. The PI for individual loci can be calculated as follows:

$$\mathrm{PI}_{\text{single locus}} = \sum p_i^4 + \sum_i \sum_{j>i} \left(2 p_i p_j\right)^2,$$

where p_i and p_j are the frequencies of the ith and jth alleles (Paetkau and Strobeck 1994). Small PI values (indicating a small proportion of matching genotypes) typically occur in the presence of many alleles of approximately equal frequency, whereas large PI values can be expected in populations with low genetic variation (Mills et al. 2000). When calculating $\mathrm{PI}_{\text{single locus}}$, however, it is necessary to assume that allele genotypes are in Hardy-Weinberg equilibrium (Taberlet and Luikart 1999). In the Hardy-Weinberg law, the following conditions are presumed (Klug and Cummings 1991):

1) large population size,

2) random mating within the population,

3) there is no selective advantage for any genotype,

4) there is an absence of genetic mutations, and

5) gene flow is prohibited due to population isolation.

Assuming loci are independent (Mills et al. 2000), a PI across all loci can then be calculated as (Paetkau et al. 1995):

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

Assuming the conditions of Hardy-Weinberg proportions are met, the calculation of $PI_{overall}$ serves as a statistical basis for genetic match declarations among individuals.

It is uncommon, however, for natural populations to successfully meet all of the assumptions that are associated with Hardy-Weinberg equilibrium. Telemetry data from this study indicate that spatial organization and movement by bears are not restricted (J. D. Clark, U.S. Geological Survey, unpublished data). Therefore, isolation does not appear to be a detriment to gene flow for the Okefenokee-Osceola population. The number of bears inhabiting the ecosystem, however, is unknown. Furthermore, research indicates that mating may not be random within black bear populations (Rogers 1987). Therefore, addressing assumption violations in relation to PI values is important to identify potential biases that can affect the ability to correctly identify animals based on genotypes. The most probable form of bias will arise in populations that are highly substructured (Taberlet and Luikart 1999), species that exhibit a high incidence of philopatry (Avise et al. 1995), and in populations containing many siblings (Donnelly 1995). In all of these cases, it is likely that samples will come from individuals with shared ancestry, resulting in a PI that is biased low (Taberlet and Luikart 1999). In the Okefenokee-Osceola black bear population, survival rates and reproduction were high during this study (J. D. Clark, U.S. Geological Survey, unpublished data). Therefore, it is

possible that bears sampled at hair traps in 1999 possessed shared ancestry, which could hinder my ability to correctly identify individuals.

Consequently, I used an alternative computation for PI that estimates a probability of identity among randomly sampled siblings (PI*sibs*) (Taberlet and Luikart 1999). That statistic provides a more conservative means of identifying how many loci are needed to obtain a sufficiently low PI, thereby increasing the likelihood that all individuals are correctly identified. A PI for randomly sampled siblings can be estimated by:

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

Additionally, a PI*sibs* across all loci can then be calculated by:

$$\text{PI}sibs = \prod\left(\text{PI}sibs_{\text{single locus}}\right).$$

Like $\text{PI}_{\text{overall}}$, this equation assumes random sampling of individuals and independence among alleles within and between loci. However, by assuming that genotypes are arising from closely related individuals, PI*sibs* represents an upper limit on the range of PI values across all observed genotypes within a population (Taberlet and Luikart 1999).

Two additional tests, developed by Woods et al. (1999), calculate the probabilities that a parent or offspring of an individual ($P_{\text{par-offs}}$) or their sibling (P_{sib}) would have the same genotype. As a result of the close genetic relations between siblings, the sibling match test (P_{sib}) is the most conservative of all tests described and can be calculated by (Woods et al. 1999):

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

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

I used the sibling match test to identify 8-loci genotypes that are potentially shared between >1 individual. Genotypes were accepted as unique bears when $P_{sib} < 0.05$. Hair samples failing to meet that criterion were excluded from analysis (Woods et al. 1999, Mowat and Strobeck 2000).

Hardy Weinberg and Linkage Disequilibrium Tests

In order to make valid inferences from calculations of $PI_{single\ locus}$, the assumptions of the Hardy-Weinberg law must be upheld. For studies of this type that are concerned with individual identification from microsatellite loci, the assumptions of random mating and an absence of genetic mutations are particularly important. Violations of those assumptions are often the result of breeding between closely related animals. Differentiating individuals with shared ancestries is complicated by the fact that these animals may be sharing identical genotypes at several loci (Taberlet and Luikart 1999). Furthermore, there is potential for inbreeding to cause genetic mutations within the genome, which is a direct assumption violation of the Hardy-Weinberg law. To investigate the likelihood of inbreeding in the Okefenokee-Osceola population, I used the Hardy-Weinberg probability test in Program GENEPOP 3.1 (Raymond and Rousset 1995). That analysis tests the null hypothesis that there is a random union of gametes and homozygote genotypes occur at a frequency expected from the overall allele frequency distribution. I performed individual tests at each locus for every 8-loci genotype that was identified (Paetkau et al. 1998, Boersen 2000). Rejection of H_o would imply a likelihood of inbreeding or other form of non-random mating in the population.

I also used the linkage disequilibrium test in Program GENEPOP 3.1 (Raymond and Rousset 1995) that tests the null hypothesis that genotypes at one locus are independent from genotypes at another. Rejection of that hypothesis would indicate some non-random association between alleles of different loci (i.e. linkage disequilibrium) (Avise 1994). Because the 8 microsatellite loci used in my analysis have been found to be independent (Paetkau and Strobeck 1994, Paetkau et al. 1994), any significant linkage observed among loci pairs may indicate sampling bias, non-random mating within the population, or stochastic processes which affect population genetics (T. L. King, U.S. Geological Survey, personal communication).

Estimation of Population Size

General. Population models for estimating wildlife abundance can be classified as either closed or open. Closed models are constrained by the assumption of no births, immigration, deaths, or emigration during and between sampling periods (Otis et al 1978, Pollock et al. 1990). Therefore, closed models are best suited for experiments estimating population size where sampling effort is maintained for relatively short periods of time (Pollock et al. 1990). Conversely, open models typically span longer time periods, consist of ≥3 sampling occasions, and allow for fluctuations in population size between sampling periods. Consequently, open models can be used to estimate additional parameters such as survival and recruitment rates, as well as population size. The assumptions that marks are not lost or overlooked and all animals in a population have an equal probability of capture are required of both open and closed population models.

I chose to use a combination of closed and open models to estimate black bear population size on the Okefenokee and Osceola study areas (Fig. 7). Estimates for 1999 were obtained by dividing the hair-trapping season into halves and using the modified Lincoln-Petersen model (Pollock et al. 1990). Within-year estimates for 1999 were also calculated using several closed multiple mark-recapture models described by Otis et al (1978), White et al. (1982), and Chao (1987, 1988, 1999) (Table 2). Estimates from closed multiple mark-recapture models were obtained using Program CAPTURE (Rexstad and Burnham 1992). Additionally, several pooling configurations of the 1999 hair trap sessions were considered for all models (Boersen 2001) (Fig. 8 and 9). Collapsing complete capture history matrices allowed me to reduce the number of trapping occasions and increase sample sizes within sampling sessions. Unfortunately, the disadvantage of pooling sampling periods is that some recaptures will be lost due to multiple observations within a session. Therefore a trade-off exists; identify the pooling configuration that maximizes capture probabilities while minimizing the loss of data. I used the criteria described by Otis et al. (1978) to select the model that was most appropriate for my data.

I also used the open Jolly-Seber models (Jolly 1965, Seber 1965, Pollock et al. 1990) provided in Program JOLLY (Pollock et al. 1990) to estimate population size by including the 1999 hair-capture data as an additional year of captures for the live-trapping data. Although population closure was not a concern when using the open Jolly-Seber model, every effort was made to identify potential assumption violations and minimize potential biases. In this study sex ratios of captured bears did not differ from 1:1 on either study area (GA, FL: $P = 0.015, 0.033$). However, annual home range sizes of

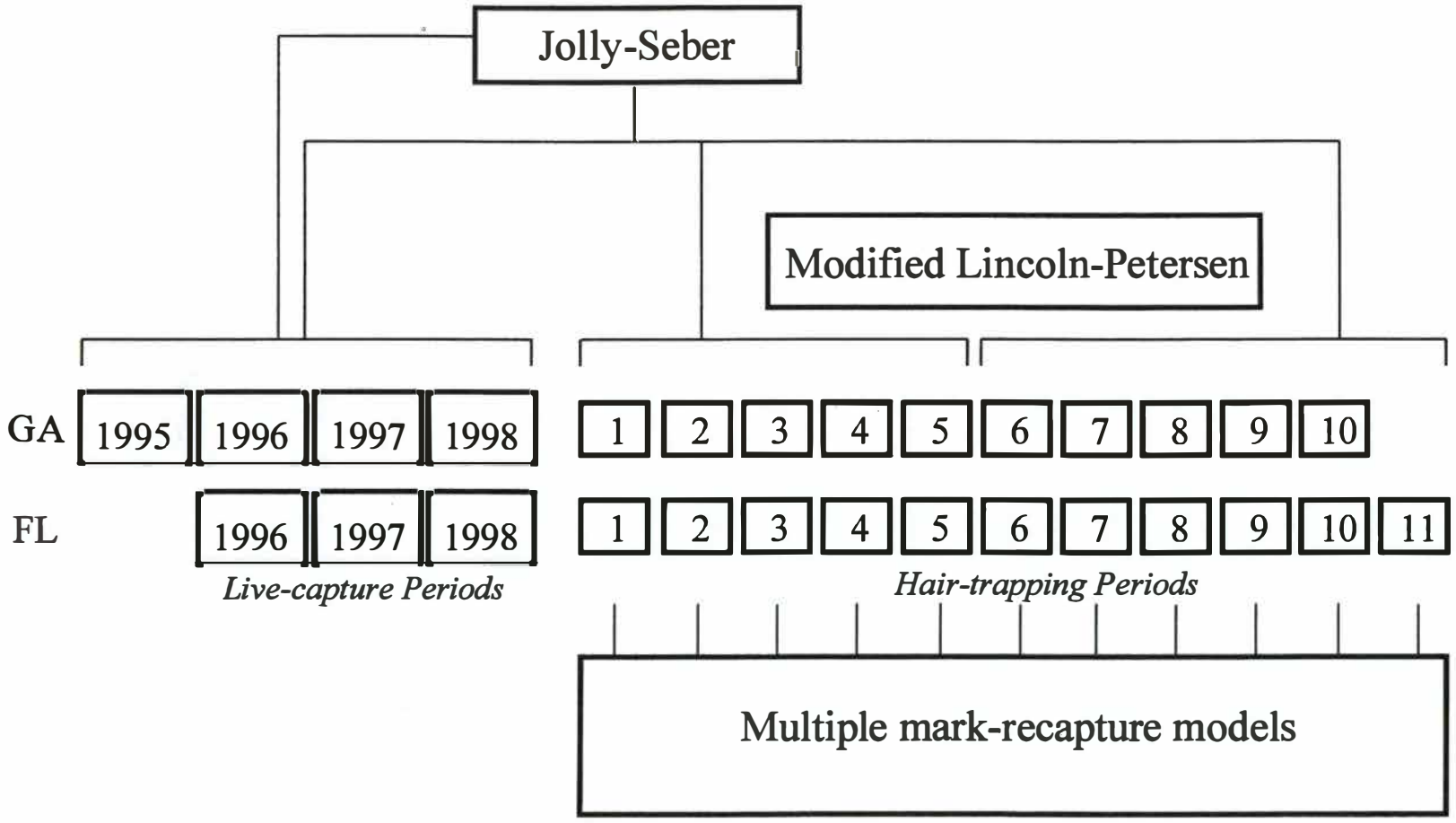


Fig. 7. Capture-recapture models used to estimate black bear population size on the Okefenokee and Osceola study areas, Georgia and Florida, 1995–1999.

Table 2. Closed multiple mark-recapture models used to estimate within-year population size from 1999 hair capture data (Otis et al. 1978 and Chao 1987, 1988, 1989).

Model	Description of Capture Probabilities
M_o	Constant
M_t, Chao M_t	Vary with time
M_b	Vary by behavioral response to capture
M_h, Chao M_h	Vary by individual animal
M_{th}, Chao M_{th}	Vary by time and individual animal
M_{bh}	Vary by behavioral response to capture and individual animal
M_{tbh}	Vary by time, behavioral response to capture, and individual animal

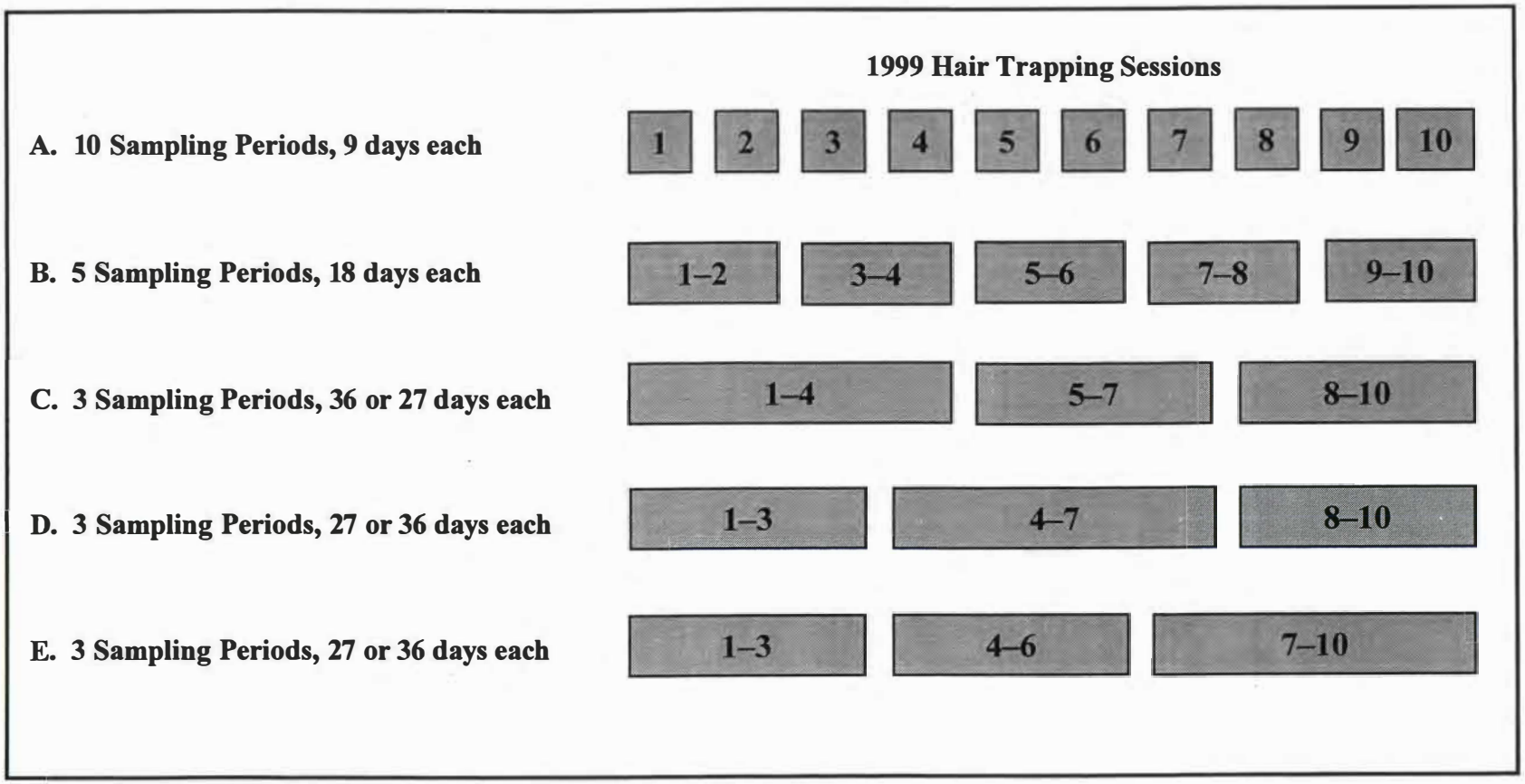


Fig. 8. Pooling configurations of the hair trapping sessions considered for multiple mark-recapture models to estimate population size on the Okefenokee study area, Georgia, 1999.

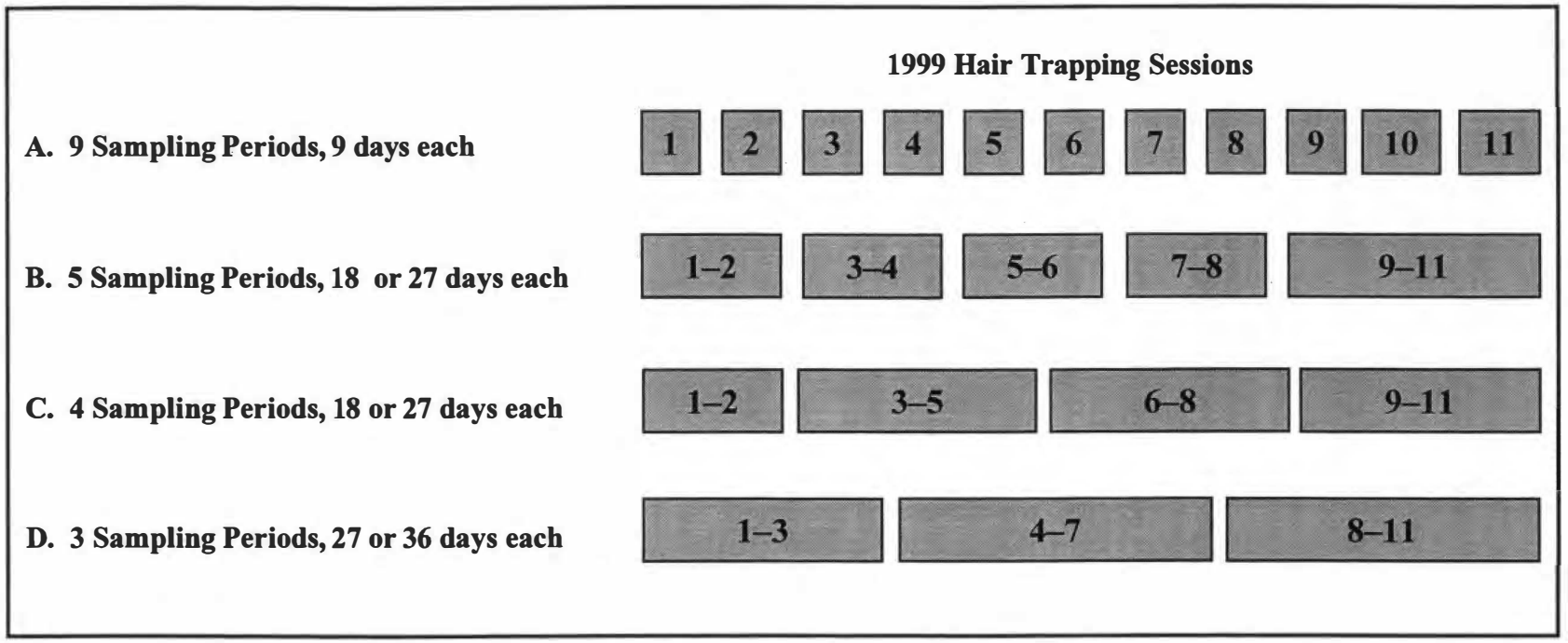


Fig. 9. Pooling configurations of the hair trapping sessions considered for multiple mark-recapture models to estimate population size on the Osceola study area, Florida, 1999.

male bears on the Okefenokee study area were approximately 50% larger than those of females (J. D. Clark, U.S. Geological Survey, unpublished data). Consequently, there is potential for capture probabilities to be biased as the likelihood of encountering traps differs by sex. One way to minimize the effects of heterogeneity in capture probabilities is to stratify capture data into groups exhibiting similar capture probabilities and estimate population size for each strata (Pollock et al. 1990). The advantage of not stratifying data, however, is that the increase in sample size as a result of pooling will often result in higher capture probabilities (Pollock et al. 1990). Furthermore, an increase in capture probabilities will make mark-recapture experiments more robust to model violations. I tested that hypothesis by running the Jolly-Seber models using data pooled by sex and age classes and stratified by sex.

Closed Models. The modified Lincoln-Petersen model yields an estimate of population size based on a mark-release period followed by a recapture period. Assumptions of the modified Lincoln-Petersen model are (Otis et al. 1978, Pollock et al. 1990):

1) the population is geographically and demographically closed,
2) all animals have the same capture probability in each sample,
3) marks are not lost or overlooked and are recorded correctly upon capture, and
4) marking does not affect the catchability of the animal.

This model estimates population size as (Chapman 1951):

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

where n_1 is the number of animals captured in the first sample, n_2 is the total number of animals captured in the second sample, m_2 is the number of marked animals captured in the second sample, and $\hat{N}_c$ is the estimated population size.

An approximate unbiased estimate of variance (Seber 1982) is calculated as

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

Using only the hair trap data from 1999, the capture periods for the modified Lincoln-Petersen model were from mid-June to early August (1st period), and early August to mid-September (2nd period).

I also used 9 of the closed models described by Otis et al. (1978) to provide estimates of population size using capture histories obtained from 1999 hair trapping data. Those models were developed for use with mark-recapture experiments involving >2 capture occasions. Therefore, the multiple pooling configurations of my hair trap data were appropriate for within-year population estimates for 1999.

The simplest, yet most restrictive, of the multiple mark-recapture models used in this analysis was the equal catchability model (M_o). Like the Lincoln-Petersen estimator, this model is based on the assumption of population closure, equal capture probabilities, no lost marks, and constant capture probabilities. Consequently, model M_o is one in which there is no heterogeneity associated with capture probabilities, no behavioral response to capture, and no temporal variation in the experimental situation (Otis et al. 1978). It is unlikely, however, that all of these assumptions can be met in most wild populations (White et al. 1982, Pollock et al. 1990).

Assumptions of model M_t, the time variation model, are the same as those of model M_o, with one exception. Although it is assumed that capture probabilities are constant within individual trapping sessions, these probabilities can change between sessions (Otis et al. 1978). The behavioral response model, M_b, allows for behavioral responses (i.e., trap happy or trap shy) to influence capture probabilities. The heterogeneity model, M_h, assumes that capture probabilities vary between individuals. Models M_{tb}, M_{bh}, and M_{tbh} were also used to provide estimates of population size. These 3 models allow for different forms of heterogeneity to simultaneously affect capture probabilities.

I also considered a suite of 3 additional multiple mark-recapture models described by Chao (1987, 1988, 1989) that were designed for use with relatively sparse capture frequency data. Two of those models (M_h and M_t) are modified forms of the heterogeneity and time models described by Otis et al. (1978). However, when mean capture probabilities are relatively small (e.g. animals caught 1–2 times during sampling), the Chao estimators are usually less biased than the heterogeneity and time variation models presented by Otis et al. (1978) (Chao 1988).

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

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

or,

$$\text{Chao } \tilde{N} = S + \left[\frac{f_1^2}{2f_2}\right]\left\{\left[1 - \frac{2f_2}{tf_1}\right] \Big/ \left[\frac{(1-3f_3)}{tf_2}\right]\right\} \text{ if } tf_1 > 2f_2, tf_2 > 3tf_3, \text{ and } 3f_1f_3 > 2f_2^2,$$

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). To calculate confidence intervals, variance estimators 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

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

Model assumptions associated with Chao M_h and Chao M_t are identical to those of their M_h and M_t counterparts. Estimators for models Chao M_t and Chao M_{th} are described by Chao (1988) and Chao et al. (1992). Those models consider time variation in capture probabilities and time variation in the presence of heterogeneity.

Estimates of population size and associated standard errors were calculated for all multiple mark-recapture models using Program CAPTURE (Rexstad and Burnham 1992). Because model M_{tbh} is useful only conceptually (Otis et al. 1978), an estimator for this model does not exist (White et al. 1982). I used chi-square goodness-of-fit tests

within Program CAPTURE to identify variation in capture probabilities as a result of time, behavior, and individual heterogeneity effects. Program CAPTURE incorporates the results of these chi-square tests into a discriminant function procedure which constructs a model classification function (Otis et al. 1978). This classification function was then used to aid in selecting the most appropriate model for the different pooling configurations of the 1999 hair data. Additionally, I tested for equal catchability by comparing observed capture frequencies to a zero-truncated Poisson distribution (Caughley 1977).

One of the most critical assumptions of multiple-mark recapture models is that of population closure. Failure to meet that assumption indicates additions (birth or immigration) and/or deletions (death or emigration) to the population during the sampling period. In this study I was only concerned with geographic closure since bears were sampled outside of the birthing season. I attempted to minimize violations of the geographic closure assumption by delineating study area boundaries using 3 and 4 years of telemetry data collected during this study. I created a buffer around each hair trap, the area of which was equivalent to the average home range estimate for female bears on each study area. Therefore, I hoped to increase the likelihood that my hair traps would be sampling more resident bears than temporary immigrants. I used the procedure in Program CAPTURE to test for population closure for all pooling configurations of my hair-trapping data. Simulation results from Otis et al. (1972) indicated that the closure test is often not valid when a behavioral response bias was present. However, the test does not appear to be affected by individual heterogeneity or random time variation (Otis et al. 1972).

Open Models. I used the open Jolly-Seber model (Pollock et al. 1990), provided with Program JOLLY, to calculate estimates of population size across years using capture and hair-trapping data. Assumptions of that model are (Pollock 1990):

1) the population is open to additions from births and immigration, and deletions from deaths and permanent emigration,
2) individuals have an equal probability of capture in the i^{th} sample,
3) every marked individual in the population at the time of i^{th} sample has the same probability of survival until the $i^{th} + 1$ sample,
4) marks are not lost or overlooked, and
5) all samples are instantaneous and each individual is released immediately after capture.

Program JOLLY provides 5 models for estimating population size: model A, A', B, D, and 2. Model A is the general model in Program JOLLY and allows capture and survival probabilities to vary. The deaths only model, model A', allows for losses (deaths and emigration) in a population but not additions. Model B, the constant survival model, assumes survival probabilities are constant throughout the experiment. Model D is the constant survival and capture model, which assumes that probabilities of capture and survival remain constant over the entire study. Model 2, the temporary trap response model, allows for a short-term effect of marking on the survival and capture probabilities. Population size is estimated by:

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

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 is the number of animals caught in the i^{th} sample, m_i is the number of marked animals caught in the i^{th} sample, z_i is the number of animals caught before the i^{th} sample that are not caught in the i^{th} sample, but are captured in a later sample, r_i is the number of animals released from the i^{th} sample that are subsequently recaptured, R_i is the number of animals released with marks from the i^{th} sample, $\hat{N}_i$ represents the total number of animals in the population just before the i^{th} sample, and $\hat{M}_i$ represents the total number of marked animals in the population just before the i^{th} sample.

The sampling periods for the Jolly-Seber estimates consisted of the 1995–1998 and 1996–1998 live-capture seasons combined with the 1999 hair-capture session on the Okefenokee and Osceola study areas, respectively. Capture histories were generated based on genotypes obtained from hair and tissue samples collected from live-captured bears and those identified at hair traps. Program JOLLY uses chi-square analyses to identify any variation in capture probabilities due to trap heterogeneity or trap response. These goodness-of-fit tests were used to aid in the selection of appropriate models.

Population Density

I calculated average density estimates for black bears on the Okefenokee and Osceola study areas by dividing the population estimates by the sizes of the 1999 study areas. Dividing the upper and lower limits of the population estimates by the sizes of the study areas produced 95% confidence intervals for each density estimate.

CHAPTER IV

RESULTS

Trapping

Between June 1995 and September 1998, 377 traps (Fig. 10) produced 6,357 trap nights resulting in 208 captures of 123 individual black bears (75M: 48F) on the Okefenokee study area (Table A.1). Overall, trap success was 3.3%, or approximately 31 trap nights per capture (Table 3). The age of marked bears on the Okefenokee study area ranged from 1 to 12 years (Table A.1). The sex ratio of captured bears (75M: 48F) differed from 1:1 ($\chi^2_{0.05} = 5.93$, 1 df, $P = 0.0149$).

On the Osceola study area, 296 traps (Fig. 11) were set for 5,120 trap nights from June 1996 to September 1998. Project personnel captured 79 individual black bears (49M: 30F) 132 times (Table B.1). Overall, trap success was 2.6%, or approximately 39 trap nights per capture (Table 3). The age of marked bears on the Osceola study area ranged from <1 to 13 years (Table B.1). Like the Okefenokee study area, the sex ratio of captured bears (49M: 30F) differed from 1:1 ($\chi^2_{0.05} = 4.57$, 1 df, $P = 0.0325$).

Hair Trapping

From 12 June to 17 September 1999, 88 and 94 barbed wire hair traps (Fig. 12) were maintained simultaneously on the Okefenokee and Osceola study areas, respectively. Eight hundred and eighty hair-trap sessions (88 traps x 10 trapping occasions) were recorded on the Okefenokee study area in 1999. Overall, 435 bear visits

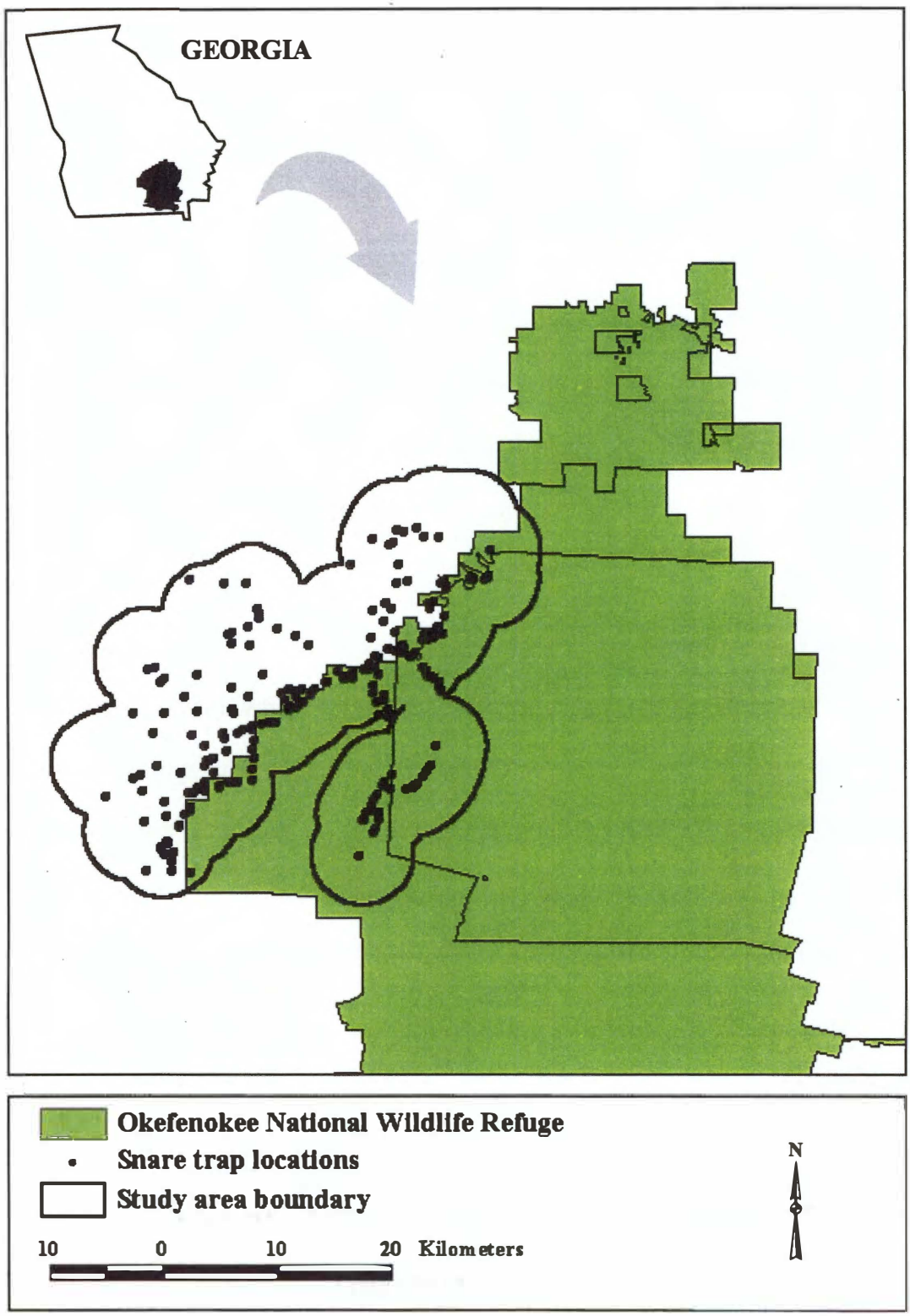


Fig. 10. Locations of snare trapsites on the Okefenokee study area, Georgia, 1995–1998.

Table 3. Trapping summaries for the Okefenokee (1995–1998) and Osceola (1996–1998) study areas, Georgia and Florida.

Georgia Study Area

Year	Number of Trap Sites	Number of Trap Nights	Number of Bear Visits	Number of Bear Escapes	Number of Bear Captures	% Rate of Capture[a]	# Trap Nights per Capture
1995	116	1,323	133	13	78	58.6	17.0
1996	93	1,581	57	2	32	56.1	49.4
1997	79	1,691	204	3	49	24.0	34.5
1998	89	1,762	410	7	49	12.0	36.0
Total	377	6,357	804	25	208	25.9	30.6

Florida Study Area

Year	Number of Trap Sites	Number of Trap Nights	Number of Bear Visits	Number of Bear Escapes	Number of Bear Captures	% Rate of Capture[a]	# Trap Nights per Capture
1996	82	1,454	48	3	40	83.3	36.4
1997	101	1,829	107	3	47	43.9	38.9
1998	113	1,837	418	8	45	10.8	40.8
Total	296	5,120	573	14	132	23.0	38.8

[a] = % rate of capture defined as number of bear captures divided by number of bear visits.

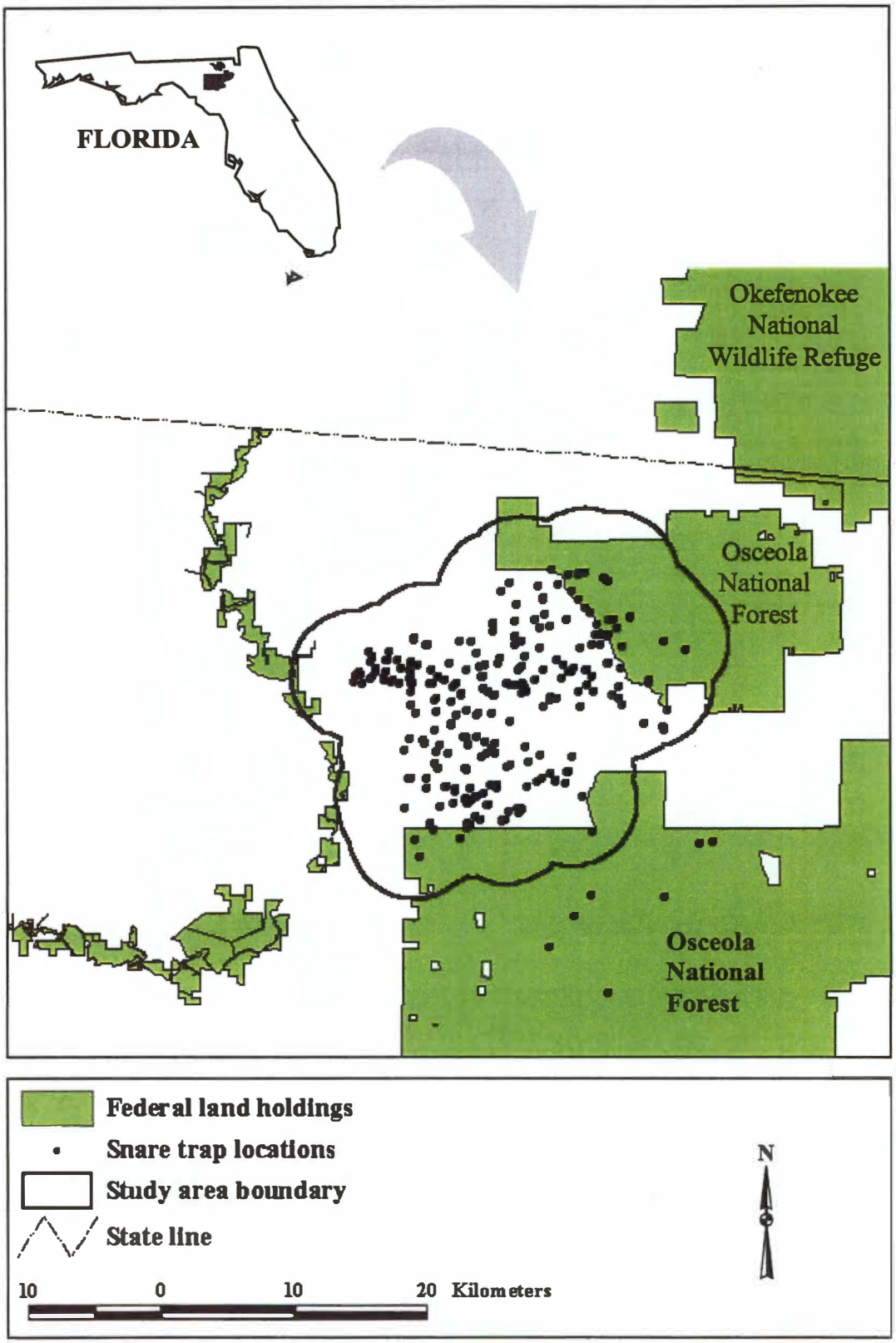


Fig. 11. Locations of snare trapsites on the Osceola study area, Florida, 1996–1998.

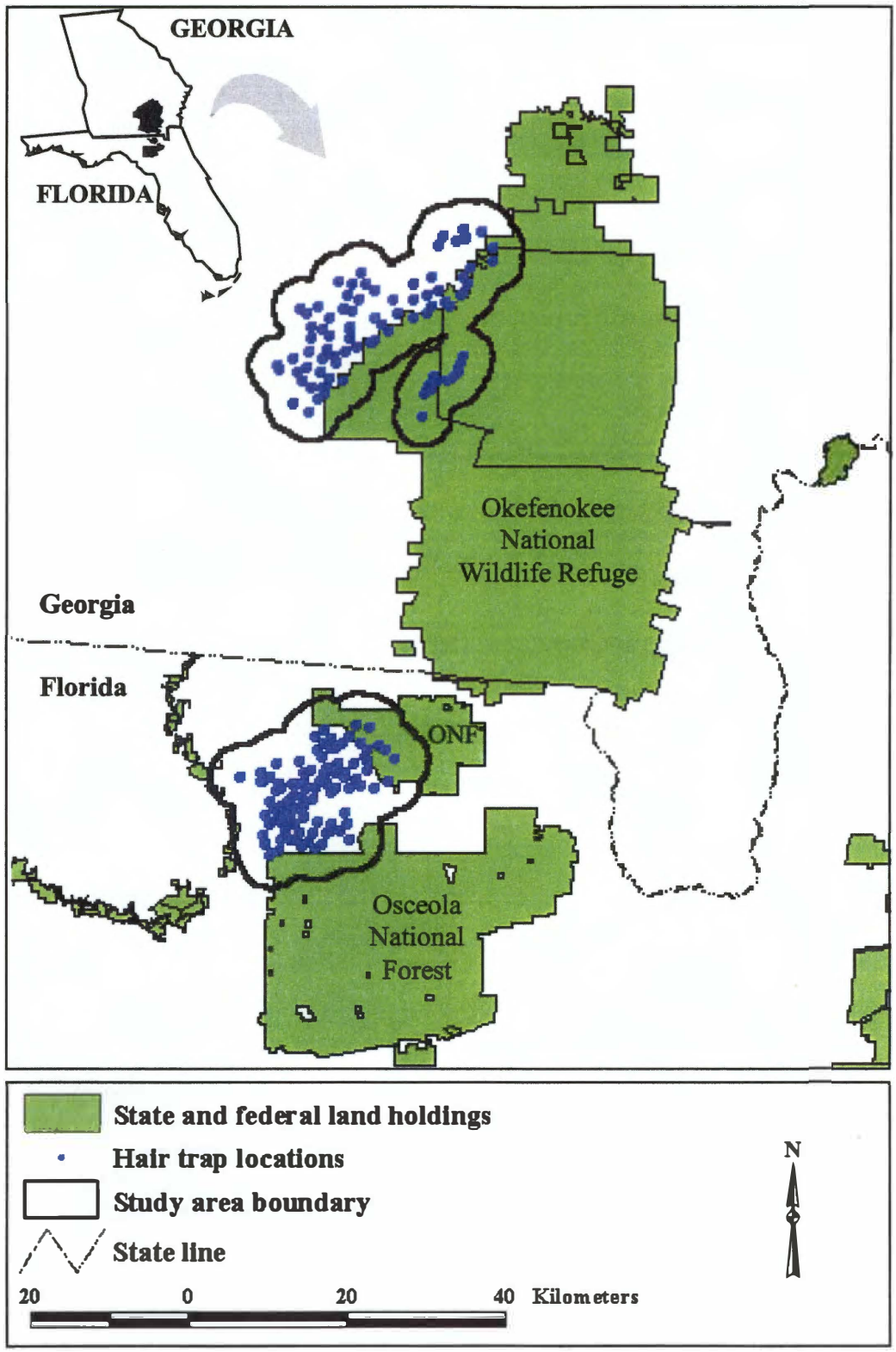


Fig 12. Locations of barbed-wire hair traps on the Okefenokee and Osceola study areas, Georgia and Florida, 1999.

were documented, of which 374 (86%) produced ≥1 hair sample per visit (Table 4). Of the 374 hair captures on the Okefenokee study area, 109 (29%) samples contained ≥5 roots, making them candidates for microsatellite analysis. Nineteen bears (9M:10F) live captured from 1995–1998 were detected at hair traps during the 1999 hair-trapping season. Hair trapping success was 42.5% on the Okefenokee study area in 1999, averaging 2.4 trap sessions per hair capture event.

On the Osceola study area, 1,034 hair trap sessions resulted in 742 bear visits in 1999, of which 637 (86%) produced ≥1 hair sample (Table 4). Two hundred and seventy two (43%) of the 637 hair samples collected contained ≥5 roots. Twenty three bears (12M:11F) livecaptured from 1996–1998 were detected at hair traps during the 1999 hair-trapping season. Hair trapping success on the Osceola study site was 61.6%, averaging 1.6 trap sessions per capture event.

Microsatellite Analysis

Complete multi-locus microsatellite genotypes were obtained from hair and tissue samples for 111 of 121 (92%) and 72 of 79 (91%) live-captured bears on the Okefenokee and Osceola study areas, respectively.

On the Okefenokee study area, 79 hair samples were selected for microsatellite analysis from the 1999 hair-trapping season. Complete multi-locus genotypes were obtained for 78 (99%) of those samples, of which 39 individual bears were identified. At each locus, 5–8 alleles were observed (Table 5) and average heterozygosity for the 8 loci was 66.3% (n = 39). Microsatellite analysis resulted in 8, 3, 3, and 5 bears being

Table 4. Summaries of black bear hair trapping on the Okefenokee and Osceola study areas, Georgia and Florida, 1999.

Georgia Study Area

Trapline	Number of Trap Sites	Number of Trap Sessions[a]	Number of Bear Visits	Number of Bear Captures	% Rate of Capture[b]	Trap Sessions per Capture
Big Swamp	23	230	111	93	83.8	2.5
Ok. Sportsman	27	270	148	123	83.1	2.2
Jamestown	24	240	75	69	92.0	3.8
Craven's Island	14	140	101	89	88.1	1.6
Total	88	880	435	374	86.0	2.4

Florida Study Area

Trapline	Number of Trap Sites	Number of Trap Sessions[a]	Number of Bear Visits	Number of Bear Captures	% Rate of Capture[b]	Trap Sessions per Capture
Banker's Trust	40	440	354	295	0.83	1.5
Bear Bay	34	374	233	205	0.88	1.8
Low Road	20	220	155	137	0.88	1.6
Total	94	1,034	742	637	0.86	1.6

[a] = Number of trap sessions refers to the number of hair traps times the number of periods the hair traps were activated.
[b] = % rate of capture equals the number of bear captures divided by the number of bear visits.

Table 5. Observed alleles and frequencies for 39 black bears identified from barbed-wire hair traps for the Okefenokee study area, Georgia, 1999.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10C	106[a]	0	0.000	G10X	140	6	0.077
	110	1	0.013		142	5	0.064
	112	3	0.038		144	26	0.333
	114	29	0.372		152	8	0.103
	116	42	0.538		154	26	0.333
	118	3	0.038		156	1	0.013
					160	6	0.077
G1A	183	20	0.256	G10P	148	15	0.192
	187	29	0.372		158[a]	0	0.000
	189	5	0.064		160	4	0.051
	191	9	0.115		162	47	0.603
	193	15	0.192		166	7	0.09
					168	5	0.064
G10B	153	17	0.218	G10L	133	2	0.026
	155	9	0.115		135	1	0.013
	157	10	0.128		137	29	0.372
	159	5	0.064		143	1	0.013
	161	30	0.385		149	12	0.154
	165	5	0.064		151	8	0.103
	167	2	0.026		153	22	0.282
					155	3	0.038
					165[a]	0	0.000
G10	207			G1D			
M		7	0.09		176	38	0.487
	211	4	0.051		178	5	0.064
	213	23	0.295		180[a]	0	0.000
	215	26	0.333		184	15	0.192
	217	5	0.064		186	10	0.128
	219	13	0.167		188	8	0.103
					190	2	0.026

[a] Indicates alleles that were observed in bears from the Osceola (Florida) study area

identified at hair traps in 1999 that were initially captured in 1995, 1996, 1997, and 1998, respectively. On the Osceola study area, 88 hair samples were selected for microsatellite analysis; complete genotypes were obtained for 84 (96%) samples. Thirty-seven individual bears were identified on the Osceola study area. At each locus, 4–8 alleles were observed (Table 6) and average heterozygosity was 67.9% (n = 37). Twelve, 5, and 6 bears that were initially captured in 1996, 1997, and 1998 were identified at hair traps in 1999, respectively.

Probability of Identity

Based on the frequency distribution of alleles at the 8 microsatellite loci, the $PI_{overall}$ for 39 individual bears sampled with hair traps on the Okefenokee study area was 6.57×10^{-8} (Table 7). That corresponded to a chance of 1 in 15,223,017 that 2 individuals drawn at random from the Okefenokee population would share an identical genotype across all loci. The overall PI*sibs* was estimated at 1.00×10^{-3} (n = 39) (Table 7), or 1 chance in 1,000 of encountering matching genotypes. Estimates of PI*sibs* for individual loci ranged from 0.388 to 0.533. The sibling match test for each 8-loci genotype was $P_{sib} < 0.003$. Consequently, all genotypes identified from 1999 hair traps were included in the capture history data based on my criterion for inclusion ($P_{sib} \leq 0.05$).

The $PI_{overall}$ for 37 individuals identified with hair traps on the Osceola study area was 2.92×10^{-7} (Table 8), or 1 chance in 3,421,763 of randomly sampling 2 bears possessing identical genotypes. PI*sibs* across the same 8 loci was estimated at 2.00×10^{-3} (n = 37) (Table 8), approximating a 1 in 500 chance of encountering matching genotypes in the Osceola bear population. PI*sibs* estimates for individual loci ranged from 0.349 to

Table 6. Observed alleles and frequencies for 37 black bears identified from barbed-wire hair traps for the Osceola study area, Florida, 1999.

Locus	Allele	*n*	Frequency	Locus	Allele	*n*	Frequency
G10C	106	1	0.014	G10X	140[a]	0	0.000
	110[a]	0	0.000		142[a]	0	0.000
	112	2	0.027		144	38	0.514
	114	37	0.500		152	4	0.054
	116	32	0.432		154	26	0.351
	118	2	0.027		156	4	0.054
					160	2	0.027
G1A	183	5	0.068	G10P	148	11	0.149
	187	31	0.419		158	1	0.014
	189	4	0.054		160	5	0.068
	191	20	0.270		162	57	0.770
	193	14	0.189		166[a]	0	0.000
					168[a]	0	0.000
G10B	153	4	0.054	G10L	133	11	0.149
	155	12	0.162		135[a]	0	0.000
	157	25	0.338		137	10	0.135
	159	1	0.014		143	2	0.027
	161	27	0.365		149	12	0.162
	165	3	0.041		151	6	0.081
	167	2	0.027		153	22	0.297
					155	5	0.068
					165	6	0.081
G10				G1D			
M	207	13	0.176		176	32	0.432
	211	4	0.054		178	5	0.068
	213	14	0.189		180	1	0.014
	215	28	0.378		184	8	0.108
	217	2	0.027		186	6	0.081
	219	13	0.176		188	22	0.297
					190[a]	0	0.000

[a] Indicates alleles that were observed in bears from the Okefenokee (Georgia) study area

Table 7. Probability of identity estimates based on 39 individual black bears identified from barbed-wire hair traps on the Okefenokee study area, Georgia, 1999.

Locus	Number of Alleles	Probability of Identity	Probability of Identity (siblings)
G10C	5	0.269	0.533
G1A	5	0.109	0.406
G10B	7	0.085	0.388
G10M	6	0.095	0.394
G10X	7	0.099	0.399
G10P	5	0.211	0.510
G10L	8	0.103	0.403
G1D	6	0.129	0.435
Overall	6.13[a]	6.57×10^{-8} [b]	1.00×10^{-3} [b]

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

Table 8. Probability of identity estimates based on 37 individual black bears identified from barbed-wire hair traps on the Osceola study area, Florida, 1999.

Locus	Number of Alleles	Probability of Identity	Probability of Identity (siblings)
G10C	5	0.287	0.541
G1A	5	0.133	0.429
G10B	7	0.124	0.421
G10M	6	0.096	0.396
G10X	5	0.225	0.503
G10P	4	0.417	0.664
G10L	8	0.051	0.349
G1D	6	0.135	0.433
Overall	5.75[a]	2.92×10^{-7} [b]	2.00×10^{-3} [b]

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

0.664. The sibling match test for each 8-loci genotype was $P_{sib} < 0.005$, allowing me to include all observed genotypes in the capture history data.

Hardy Weinberg and Linkage Disequilibrium

For the 39 individual bears identified at hair traps on the Okefenokee study area in 1999, the Hardy-Weinberg equilibrium test detected evidence of non-random mating for 2 loci (G10M, $P = 0.016$; G10P, $P = 0.0003$) at the 5% significance level. Only loci G10P provided evidence of non-random mating, however, after applying the Bonferroni experimentwise error rate (Rice 1989, Sokal and Rohlf 1995). On the Osceola study area, the Hardy-Weinberg test detected no evidence of non-random mating among the 8 microsatellite loci examined for the 37 individual bears that were identified in 1999.

Linkage disequilibrium tests were used to identify possible non-random associations between alleles of different microsatellite loci. On the Okefenokee study area, 4 loci pairs (G10C vs. G10B, $P = 0.00014$; G1A vs. G10B, $P = 0.00103$; G1A vs. G1D, $P = 0.000$; G10X vs. G1D, $P = 0.000$) had probability values smaller than the comparison-wise significance level of 0.0018. Pairwise tests comparing the 37 individual bears identified at hair traps on the Osceola study area in 1999 detected no associations between any loci pairs.

Population Size and Density

Closed Models. Capture histories were pooled for the first and second halves of the 1999 hair-trapping periods. The modified Lincoln-Petersen model produced a population estimate of 86 bears on the Okefenokee study area in 1999, for a density

estimate of 0.17 bears/km^2 (Table 9). Because there was an odd number of total trapping periods on the Osceola study area (n = 11), 2 estimates were calculated using the Lincoln-Petersen model. The first pooling configuration, 5 and 6 periods, resulted in an estimate of 53 bears. Conversely, dividing the 1999 hair-trapping season into 6 and 5 periods produced an estimate of 47 bears. Resultant bear densities on the Osceola study area during 1999 were 0.14 and 0.13 bears/km^2 using the 5/6 and 6/5 session pooling configurations, respectively (Table 10).

The equal catchability test described by Caughley (1977) indicated that observed capture frequencies from the Okefenokee study area differed from the expected zero-truncated Poisson distribution when all of the hair-captures from 1999 were considered ($\chi^2_{0.05}$ = 13.790, 1 df, P = 0.0002) (Table 11). Although the behavioral response test within Program CAPTURE produced nonsignificant results for the 10 session pooling arrangement, the probability value associated with this test was questionable ($\chi^2_{0.05}$ = 3.533, 1 df, P = 0.060). Additional tests, however, detected individual heterogeneity among capture probabilities for all pooling configurations (n = 5) of the 1999 hair data. Time variation was not detected as a significant influence on capture probabilities in any of the pooling arrangements. Based on the above, I gave further consideration only to models that allowed for variation in capture probabilities as a result of behavioral response or individual heterogeneity.

To aid in selecting the most appropriate pooling configuration for my analysis, I used the population closure test in Program CAPTURE. The tests for closure detected lack of closure when 10 (Z = -3.451, P = 0.00028) and 5 (Z = -2.485, P = 0.00649)

Table 9. Estimated black bear population size from hair captures using multiple mark-recapture models in the Okefenokee study area, Georgia, 1999.

Model	Population Size Estimate	Coefficient of Variation (%)	95% Confidence Interval	Density (bears/km^2)	95% Confidence Interval
Mod. Lincoln-Petersen	86	28	39–133	0.17	0.08–0.26
M_o	84	26	57–151	0.16	0.11–0.30
M_h[a]	71	11	59–91	0.14	0.12–0.18
M_t	84	26	55–148	0.16	0.11–0.29
M_b	117	118	47–849	0.23	0.09–1.66
M_{bh}	117	119	47–851	0.23	0.09–1.67
M_{tb}[b]	---	---	---	---	---
Chao M_h	175	48	84–452	0.34	0.16–0.88
Chao M_t	110	38	64–243	0.22	0.13–0.48
Chao M_{th}	292	88	88–1,357	0.57	0.17–2.66

[a] Indicates selected model

[b] Population size estimate and associated standard errors were impossibly large

Table 10. Estimated black bear population size from hair captures using multiple mark-recapture models in the Osceola study area, Florida, 1999.

Model	Population Size Estimate	Coefficient of Variation (%)	95% Confidence Interval	Density (bears/km^2)	95% Confidence Interval
Mod. Lincoln-Petersen (5–6)[a]	53	16	36–70	0.14	0.10–0.19
Mod. Lincoln-Petersen (6–5)[b]	47	12	36–58	0.13	0.10–0.16
M_o[c]	44	9	40–57	0.12	0.11–0.16
M_h	50	12	43–66	0.14	0.12–0.18
M_t	44	9	40–56	0.12	0.11–0.15
M_b	48	21	40–87	0.13	0.11–0.24
M_{bh}	48	21	40–87	0.13	0.11–0.24
M_{tb}	47	35	39–130	0.13	0.11–0.36
Chao M_h	48	15	41–71	0.13	0.11–0.19
Chao M_t	45	12	40–63	0.12	0.11–0.17
Chao M_{th}	47	16	40–73	0.13	0.11–0.20

[a] Two sampling sessions of 5 and 6 periods each
[b] Two sampling sessions of 6 and 5 periods each
[c] Indicates selected model

Table 11. Observed capture frequencies of bears identified at hair traps on the Okefenokee study area and the zero-truncated Poisson frequencies to be expected if catchability is constant (1999).

Number of times captured (i)	Number of individuals (f)		Expected frequencies E(f)		$\frac{[f - E(f)]^2}{E(f)}$
1	27		15.785		7.967
2	5		12.628		4.608
3	3		6.735		
4	1		2.694		
5	2		0.862		
6	0		0.230		
7	0		0.053		
8	0		0.011		
9	0		0.002		
10	0	7	0.000	10.586[a]	1.215
11	0		0.000		
12	0		0.000		
13	0		0.000		
14	0		0.000		
15	0		0.000		
16	0		0.000		
17	0		0.000		
18	1		0.000		
	39		39.000		$\chi^2 = 13.790$
					df = 1
					$P = 0.0002$

[a] Capture frequencies ≥3 were pooled so that expected frequencies would be ≥5 (Caughley 1977).

session pooling configurations were considered. Additionally, lack of closure was detected for 1 of the 3-session (3-3-4) pooling configurations (Z = -1.732, P = 0.0416). The population closure test failed to detect a lack of closure, however, for the 4–3–3 (Z = -1.414, P = 0.0787) or 3–4–3 (Z = -1.581, P = 0.0569) session pooling configurations. Unfortunately, collapsing sampling occasions results in the exclusion of hair samples from analysis due to individual bears being observed multiple times at hair traps within sessions. The resultant decrease in sample size, however, tends to result in higher overall capture probabilities, thereby improving model performance. Although 41% (n = 32) of the 79 samples were excluded from my analysis using the 4–3–3 arrangement, capture probabilities were higher than for any other pooling configuration. Furthermore, estimates provided from the 4–3–3 arrangement produced the lowest standard errors of all models analyzed. Therefore, I selected the 3-session pooling configuration that divided capture histories into sampling periods of 36, 27, and 27 days each (Fig. 8).

Multiple mark-recapture models produced population estimates that ranged from 71–292 bears on the Okefenokee study area in 1999 (Table 9). The jackknife heterogeneity model M_h produced a population estimate of 71 bears during the 1999 hair-trapping season, corresponding to a density of 0.14 bears/km^2. Model Chao M_h estimated population size at 175 bears, or 0.34 bears/km^2 on the Okefenokee study area. Considering the possibility of a behavioral response bias in capture probabilities, model M_b produced a population estimate of 117 bears during the 1999 hair-trapping season, or 0.23 bears/km^2. The goodness-of-fit test for the individual heterogeneity models did not

indicate a poor fit ($\chi^2_{0.05}$ = 0.054, 2 df, P = 0.973), whereas a poor fit was indicated for model M_b ($\chi^2_{0.05}$ = 7.356, 2 df, P = 0.0253).

On the Osceola study area, the equal catchability test (Caughley 1977) indicated that the observed capture frequencies from 1999 did not differ from the expected zero-truncated Poisson distribution when all hair-captures were considered ($\chi^2_{0.05}$ = 1.457, 2 df, P = 0.483) (Table 12). Furthermore, chi-square goodness-of-fit tests indicated that capture probabilities were not significantly influenced by trap heterogeneity, behavioral response, or time variation for any pooling configurations (n = 4). The population closure test in Program CAPTURE failed to detect a lack of closure for all pooling configurations (P = 0.06–0.60). The largest probability value was associated with the pooling configuration that collapsed capture histories into 5 sampling sessions (Z = 0.262, P = 0.60337). Furthermore, only 19 (23%) of the 84 hair samples were excluded from analysis due to multiple observations within a session. Therefore, I selected the 5-session pooling configuration that divided capture histories into 4 sampling periods of 18 days with the fifth session lasting 27 days (Fig. 9).

Population estimates ranged from 44–50 bears on the Osceola study area using the multiple mark-recapture models within Program CAPTURE (Table 10). The null model M_o produced a population estimate of 44 bears during the 1999 hair-trapping period, for a density estimate of 0.14 bears/km^2. The largest estimate was provided by model M_h, the heterogeneity model, which estimated population size on the Osceola study area at 50 bears, or 0.16 bears/km^2. The goodness-of-fit tests did not indicate a

Table 12. Observed capture frequencies of bears identified at hair traps on the Osceola study area and the zero-truncated Poisson frequencies to be expected if catchability is constant (1999).

Number of times captured (i)	Number of individuals (f)		Expected frequencies E(f)		$\frac{[f - E(f)]^2}{E(f)}$
1	14		11.999		0.334
2	13		11.675		0.150
3	5		7.573		0.874
4	3		3.684		
5	0		1.434		
6	1		0.465		
7	0	5	0.129	5.753[a]	0.098
8	0		0.031		
9	0		0.007		
10	0		0.001		
11	1		0.000		
	37		37.000		$\chi^2 = 1.457$
					df = 2
					$P = 0.483$

[a] Capture frequencies ≥4 were pooled so that expected frequencies would be ≥5 (Caughley 1977).

poor fit for the individual heterogeneity, behavior response, or time variation models.

Open Models. Estimates produced from Jolly-Seber models using stratified data indicated that capture probabilities were higher when capture data were pooled. In addition, differences in population size estimates were negligible between pooled and stratified models. If heterogeneity in capture probabilities was present, it appears that increasing sample sizes made the Jolly-Seber models more robust to that violation. Therefore, I chose to pool sex and age classes for the 1995–1998 livetrapping data.

The equal catchability test described by Caughley (1977) indicated that the observed capture frequencies differed from a zero-truncated Poisson distribution ($\chi^2_{0.05}$ = 17.337, 2 df, $P = 0.000129$) on the Okefenokee study area, but not ($\chi^2_{0.05}$ = 7.092, 3 df, $P = 0.06902$) on the Osceola study area (Tables 13 and 14). Models A, A', B, and D produced estimates of population size for both study areas. However, chi-square goodness-of-fit tests indicated that model A', the deaths only model, did not provide a good fit for the Okefenokee data ($P = 0.0004$). In addition, capture probabilities for model A' ($p = 0.28$) were low in comparison with models A, B, and D ($p = 0.48$–0.52). Therefore, only models A, B, and D were given further consideration. Model A produced a mean population estimate of 68 bears, corresponding to a density of 0.13 bears/km^2 on the Okefenokee study area (Table 15). Models B and D produced mean estimates of 73 and 77 bears, or 0.14 and 0.15 bears/km^2, respectively (Table 15).

On the Osceola study area, Jolly-Seber models produced mean population estimates that ranged from 90–114 bears (Table 15). Individual tests between models indicated that allowing survival and capture probabilities to vary did not provide a better

Table. 13. Observed capture frequencies of bears identified at snares and hair traps on the Okefenokee study area and the zero-truncated Poisson frequencies to be expected if catchability is constant (1995–1999).

Number of times captured (i)	Number of individuals (f)		Expected frequencies $E(f)$		$\frac{[f - E(f)]^2}{E(f)}$
1	82		61.991		6.458
2	28		46.184		7.159
3	16		22.938		
4	9		8.544		
5	7		2.546		
6	0		0.632		
7	0		0.135		
8	0		0.025		
9	0		0.004		
10	0	17	0.001	11.887[a]	2.119
11	0		0.000		
12	0		0.000		
13	0		0.000		
14	0		0.000		
15	0		0.000		
16	0		0.000		
17	0		0.000		
18	1		0.000		
	143		143.000		$\chi^2 = 17.915$
					df = 2
					$P = 0.000129$

[a] Capture frequencies ≥4 were pooled so that expected frequencies would be ≥5 (Caughley 1977).

Table 14. Observed capture frequencies of bears identified at hair traps on the Osceola study area and the zero-truncated Poisson frequencies to be expected if catchability is constant (1999).

Number of times captured (i)	Number of individuals (f)		Expected frequencies E(f)		$\frac{[f - E(f)]^2}{E(f)}$
1	35		28.638		1.413
2	32		28.996		0.311
3	11		19.572		3.754
4	7		9.908		0.854
5	2		4.013		
6	2		1.354		
7	2		0.392		
8	0	8	0.099	5.886[a]	0.759
9	1		0.022		
10	0		0.005		
11	0		0.001		
12	1		0.000		
	93		93.00		$\chi^2 = 7.092$
					df = 3
					$P = 0.06902$

[a] Capture frequencies ≥5 were pooled so that expected frequencies would be ≥5 (Caughley 1977).

Table 15. Estimated black bear population size from the Jolly-Seber models in Okefenokee (OKE) and Osceola (OSC) study areas using a combination of live-capture and hair-trapping data, Georgia and Florida, 1995–1999.

Study Area	Year	Model A[a,e]		Model A'[b]		Model B[c,f]		Model D[d]	
		N	(95% CI)	N	(95% CI)	N	(95% CI)	N	(95% CI)
OKE	1995	---	---	304	(209–398)	---	---	---	---
OKE	1996	58	(33–83)	153	(104–201)	79	(53–105)	63	(46–81)
OKE	1997	82	(44–119)	137	(93–181)	84	(57–110)	79	(57–101)
OKE	1998	64	(41–87)	110	(72–148)	64	(48–79)	86	(62–111)
OKE	1999	---	---	---	---	65	(40–89)	81	(55–107)
OKE	Mean	68	(50–85)	176	(144–207)	73	(41–104)	77	(41–113)
OSC	1996	---	---	117	(96–138)	---	---	---	---
OSC	1997	102	(54–149)	128	(92–164)	95	(64–125)	98	(66–131)
OSC	1998	77	(44–111)	95	(63–127)	92	(58–127)	89	(59–119)
OSC	1999	---	---	---	---	99	(51–147)	91	(55–127)
OSC	Mean	90	(61–119)	114	(96–131)	95	(38–153)	93	(43–143)

[a] Model A allows for survival and capture probabilities to vary
[b] Model A' is for cases where death is allowed but immigration is not
[c] Model B assumes survival is constant over the entire study
[d] Model D assumes both survival and capture probabilities are constant over the entire study
[e] Indicates selected Jolly-Seber model for the Okefenokee capture data (1995–1999)
[f] Indicates selected Jolly-Seber model for the Osceola capture data (1996–1999)

fit to my data. Consequently, only models B and D were given further consideration. Model B, which is based on the assumptions of constant survival and time-specific capture probabilities, produced a mean population estimate of 95 bears on the Osceola study area, resulting in a density estimate of 0.26 bears/km^2 (Table 15). Model D, the constant survival and capture probability model, provided a mean population estimate of 93 bears, or 0.25 bears/km^2 (Table 15). Mean capture probabilities for models D and B were 0.40 and 0.41, respectively.

CHAPTER V

DISCUSSION

Population Size

The accuracy of estimates provided by open and closed models is largely dependent on whether requisite assumptions are met during sampling efforts. Furthermore, failure to identify model violations tends to result in estimates that are biased. Sampling the Okefenokee and Osceola study areas in 1999 using the hair-trapping technique had several advantages that enabled me to minimize model violations and reduce potential biases in the estimates of population size. First, I was able to trap each of the entire study areas at the same time. Doing so decreased any temporal or spatial variation in capture probabilities because a large portion of the bear population was concurrently sampled. During the 1995–1998 livetrapping seasons, only a minimal number of snares (15–25) could be employed at a time due to logistical constraints (e. g., travel time, remote access, safety risks for captured bears). Furthermore, the non-obtrusive nature of the hair-trapping technique probably decreased the likelihood of a trap response bias. In fact, the proportion of bear visits that resulted in the collection of ≥1 useable hair sample (≥5 hairs) was 25% and 37% on the Okefenokee and Osceola study areas, respectively. During the 1998 live trapping season only 49 (12%) of 410 bear visits resulted in captures on the Okefenokee study area; likewise, capture success on the Osceola study area was 11% in 1998. Although the observed increase in capture success does not indicate the absence of a trap response bias, it does suggest that the effects of trap avoidance were lessened using the hair-trapping technique.

Population closure also is an important assumption of the closed models that I used to provide within-year estimates. Fortunately, the closure assumption can be met if the interval between samples is short (Otis et al. 1978). In this study intervals between hair collections were approximately 9 days; the entire sampling duration lasted only 4 months from June through September. Naturally, no reproduction occurred during that period. Furthermore, I documented only 5 bear mortalities during June through September sampling periods from 1995–1998 (J. D. Clark, U.S. Geological Survey, unpublished data). Therefore, the assumption of demographic closure probably was not violated during the 1999 hair-trapping period.

Whether the requirements of geographic closure were upheld for both study areas, however, is questionable. Although the closure test in Program CAPTURE rejected the null hypothesis of population closure in all of the pooling configurations of the Osceola hair-capture data, only two 3-session pooling arrangements met the closure assumption in the Okefenokee study area ($P_{4\text{–}3\text{–}3} = 0.08$ and $P_{3\text{–}4\text{–}3} = 0.06$). However, the performance of the closure test lacks power when capture probabilities are affected by behavioral variation (Otis et al. 1978). Considering the significant results of Caughley's (1977) test for equal catchability, the closure tests for the Okefenokee data were probably influenced by a behavioral response. If that variation was extreme, however, I would expect a significant result from Program CAPTURE's goodness-of-fit test, which did not occur. Although capture rates declined markedly on both study areas with each year of live trapping, the number of marked and unmarked bears caught each year were relatively stable. Therefore, I suspect that influence of any behavioral bias on the within-year estimates for the Okefenokee study area was negated by the intensive sampling design.

In addition to population closure, the mark-recapture models that I used to provide within-year estimates of population size require that marks are not lost and every marked individual is correctly identified. Based on the low average probability of identity estimates for bears in the Okefenokee-Osceola population, each observed genotype should represent a single individual. Consequently, it is highly unlikely that marked and unmarked bears were incorrectly identified as such in the capture history data.

Most mammal studies have detected variation in capture probabilities (Young et al. 1952, Carothers 1973, Seber 1982). The statistical challenge using closed mark-recapture models, therefore, is not to achieve equal catchability, but to select the appropriate model for the data (Mowat and Strobeck 2000). I used the model selection procedure in Program CAPTURE to assist in my selection of the model that best fitted my data. Simulation studies of populations of known size have indicated that this selection algorithm does not always select the most appropriate model (Menkins and Anderson 1988, Manning et al. 1995). Consequently, I used the selection procedure only as an aid in selecting the most appropriate model for my data by identifying significant sources of variation in capture probabilities.

On the Okefenokee study area, the population estimate of 86 bears produced by the modified Lincoln-Petersen model fell within the 95% confidence intervals of all the multiple mark-recapture models. The Lincoln-Petersen estimator may be biased, however, as suggested by the small number of recaptures in the second sample ($n = 5$). Although the equal catchability test (Caughley 1977) indicated a behavioral response bias in the hair-trapping data, I would not expect trap shy behavior using this sampling

technique. In addition, the uniformly random subsampling design that I employed appears to have minimized time variation in capture probabilities. Therefore, I suspect that individual capture heterogeneity was the cause of the low recapture rate associated with the Lincoln-Petersen model.

Program CAPTURE's chi-square goodness-of-fit tests identified significant patterns of variation in capture probabilities for many of the data pooling configurations I considered. The most obvious pattern was a consistent detection of individual heterogeneity in capture probabilities for all pooling arrangements of the Okefenokee data. Therefore, models that allow for individual capture heterogeneity were given primary consideration. The population estimate of 175 bears produced by model Chao M_h was the second highest of all multiple mark-recapture models considered. However, simulation results indicate that model Chao M_h tends to overestimate in the presence of weak heterogeneity (Mowat and Strobeck 2000). The jackknife heterogeneity model M_h produced a population estimate of 71 bears on the Okefenokee study area. Although model Chao M_{th} also considered heterogeneity, I disregarded it and all other time variation models (M_t, Chao M_t, and M_{tb}) because there was no indication of a temporal influence on capture probabilities for any pooling configurations of the Okefenokee hair trapping data.

Behavioral variation was only detected by the equal catchability test (Caughley 1977) when the full capture history matrix from 1999 was considered. Program CAPTURE did not detect a behavioral response, however, when sampling occasions were ≤ 10. Furthermore, the probability of rejecting the null hypothesis (i.e., no behavioral response exists) increased as the number of sampling occasions decreased. It

appears that the increase in sample size within each sampling occasion and the increase in capture probabilities as a result of data pooling minimized any potential behavioral effects. Consequently, the behavioral models M_b and M_{bh} were not suitable for the 3-session pooling configuration that was selected for the Okefenokee hair data. Considering all of the closed models, I conclude that the within-year estimate of 71 bears (95% CI = 59–91) produced by the jackknife heterogeneity model M_h is the most appropriate for the Okefenokee hair-trapping data.

The Jolly-Seber model A produced a mean population estimate of 68 bears (95% CI = 50–85) on the Okefenokee study area based on 4 years of live-capture data and 1 year of hair-trapping data. With the exception of the deaths only model A', all models exhibited similar annual trends and produced mean estimates that differed by only 9 bears. Estimates from model A' were seriously elevated and lacked precision relative to other models. The deaths only model also was probably biased due to bears moving out of ONWR and onto the study area. Although the assumptions of model B (constant survival) and model D (constant survival and capture probabilities) probably were not met during this study, high capture probabilities made these models robust to model violations. However, 52 bear mortalities were documented during the 4 years of live trapping on the Okefenokee study area; 88% (n = 46) of mortalities were due to hunting. Considering that 123 individuals were captured during that period, there appears to be a high rate of population turnover on the Okefenokee study area. Therefore, the general Jolly-Seber model A, which accounts for variation in survival probabilities, was the more appropriate open model.

Unlike the Okefenokee study area, capture probabilities for the Osceola hair-trapping data did not appear to be influenced by individual heterogeneity. Because time and behavioral variation also were not detected, it is not surprising that Program CAPTURE selected the null model M_o as most appropriate. Although the assumption of equal catchability is typically considered unrealistic in most mark-recapture experiments (Otis et al. 1978, White et al. 1982, Pollock et al. 1990), the 1999 sampling period on the Osceola study area appears to be an uncommon situation where this assumption was upheld. Fortunately, selecting the most appropriate closed model for the Osceola data became less critical because the highest and lowest estimates differed by only 9 bears (Table 10). Based on the absence of heterogeneity in capture probabilities, however, I selected the estimate of 44 bears provided by the null model M_o as most appropriate.

The Jolly-Seber models B and D produced mean population estimates of 95 (95% CI = 38–153) and 93 (95% CI = 43–143) bears on the Osceola study area, respectively. Because capture probabilities were different between the 2 sampling techniques, however, I selected against model D for the Osceola data. Therefore, I chose model B, which is based on the assumption of time-specific capture probabilities, as the most appropriate open model.

Although estimates provided by Jolly-Seber models B and D differed by only 2 bears, they were much higher than the within-year estimate of 44 provided by the closed model M_o. I suspect that the discrepancy between the open and closed estimators is the result of a combination of factors. Firstly, it appears that the Jolly-Seber models using only the 1996–1998 live-trapping data performed poorly. In addition to relatively low capture probabilities, estimates for all Jolly-Seber models were significantly higher ($\hat{N}$ =

112–143) relative to those of the multiple mark-recapture models ($\hat{N}$ = 44–50). Furthermore, all survival estimates produced from 3 years of live-capture data exceeded 1.20, an impossibility. Unfortunately, the poor performance of the Jolly-Seber models seems to be the result of an unexplainable lack of recaptures from the 1997 trapping season. Of the 26 bears that were initially marked in 1997, only 5 were recaptured in 1998; 15 bears from 1996 were caught in 1998. Likewise, only 5 bears that were initially marked in 1997 were identified at hair traps in 1999, whereas 12 bears from 1996 were observed in 1999. It appears that the observed positive bias is most likely due to an inability to recapture some marked individuals, which will always result in an overestimation of population size (Pollock et al. 1990). Although the performance of the Jolly-Seber models was improved by including a fourth year of capture data, estimates remained elevated.

In addition to model performance, I suspect that the discrepancy between the closed and open model estimates can also be explained largely based on several biological factors. From 1996–1998, only 1 bear mortality was documented on the Osceola study area; that bear was found dead in a trap. In addition, 23 (29%) of the 79 individual bears that were live-trapped from 1996–1998 were identified at hair traps in 1999. The relatively high proportion of bears remaining on the study area throughout the duration of the study suggests that, unlike the Okefenokee study area, population turnover is low for Osceola bears. The low turnover is not surprising considering there is no significant mortality factor (i.e. hunting) to remove bears from this portion of the Okefenokee-Osceola bear population. Consequently, I believe that the within-year estimates provided by multiple mark-recapture models, although lower than those

provided by the open Jolly-Seber models, are more appropriate for the Osceola study area.

Considering all data pooling configurations and model types used in this analysis, I conclude that the most reliable estimates of population size were obtained from closed models using the 1999 hair-trapping data. For the Okefenokee study area, I select the estimate of 71 bears (95% CI = 59–91) obtained from the individual heterogeneity model M_h as the most appropriate for my data. I selected model M_h over the Jolly-Seber model A because the closed model required fewer assumptions and arrived at approximately the same estimate using only 2 parameters. Because fewer parameters were involved, precision was likely increased as a result of individual model assumptions being met. I conclude that the estimate produced by the null model M_o of 44 bears (95% CI = 40–57) is the most appropriate for the Osceola study area. Although all Jolly-Seber estimates appeared to be biased high, the degree of that bias is unknown. Therefore, it is possible that the number of bears that were on the Osceola study in 1999 area may have been closer to the upper range of the 95% confidence interval for model M_o.

Population Density

The estimated densities of black bears on the Okefenokee and Osceola study areas were 0.14 and 0.12 bears/km^2, respectively. Those estimates fell within the range of densities reported for other black bear populations throughout the southeastern US (Table 16). Direct comparisons of population densities between areas, however, should be made with caution because of differences in spatial extent, sampling methodology, and habitat

Table 16. Population densities of black bears in the southeastern United States.

Locality	Bears / km^2	Reference
Okefenokee Swamp, Georgia	0.14	This study
Osceola National Forest, Florida	0.12	This study
White River NWR, Arkansas	0.29	Smith 1985
White Rock, Arkansas	0.08	Clark 1991
Dry Creek, Arkansas	0.09	Clark 1991
Deltic, Tensas River Basin, Louisiana	1.43	Beausoleil 1999
Tensas River NWR, Louisiana	0.35	Boersen 2001
Alligator River NWR, North Carolina	0.86	Allen 1999
Big Pocosin, North Carolina	0.53	Martorello 1998
Gum Swamp, North Carolina	1.35	Martorello 1998
Camp Lejeune, North Carolina	0.02	Brandenburg 1996
Great Dismal Swamp, North Carolina-Virginia	0.47–0.68	Hellgren and Vaughan 1989
Great Smoky Mountains NP, Tennessee	0.87	J. Chadwick, University of Tennessee, unpublished report

quality. Although density estimates were similar between my study areas, significant differences in habitat use and land use practices existed that influenced those estimates.

The Okefenokee study area was situated adjacent to and incorporated a portion of 1,580 km^2 of federally protected habitat (ONWR) where hunting was prohibited and public access was virtually nonexistent. Consequently, ONWR may serve as an important source of bears to fuel the high population turnover caused by hunting mortality in the counties surrounding the Refuge. Conversely, the protected status of black bears on the Osceola study area may be creating a situation in which dispersal is becoming an increasingly important factor in population regulation. From 1997–1998, 18 (43%) of the 42 new bears that were live-captured on the Osceola study area were subadult males. However, only 3 of those subadults were ever captured again; 1 bear from 1997 was recaptured in 1998 and the other 2 were identified at hair traps in 1999. Those low recapture rates suggest that subadult males may be dispersing from the Osceola area at a relatively fast pace. In fact, 2 bears that were initially caught on the Osceola study area in 1996 were harvested on the Okefenokee study area in 1996 and 1999 (J. D. Clark, U.S. Geological Survey, unpublished data). In each of those cases, bears were subadult males that had traveled at least 50 km from their last capture location in ONF.

Based on the above, the density estimates for the Okefenokee and Osceola study areas appear to be influenced by completely different biological factors. Population turnover appears to be low on the Osceola study area, therefore competition for resources may be resulting in adult bears forcing younger males from the area. Conversely, population size and density of bears on the Okefenokee study area appear to be primarily

balanced by hunting mortality and immigration. Because density estimates are almost the same for each of the study areas, however, the average between the Okefenokee and Osceola densities may provide a rough estimate of population size for bears in this area. Based on the average density of 0.135 bears/km^2, approximately 830 bears (95% CI = 707–1,045) may inhabit the 6,147-km^2 Okefenokee-Osceola ecosystem.

Genetic Considerations

In mark-recapture studies it is imperative that individuals be correctly classified. The PI*sibs* statistic estimated the probability of randomly drawing 2 bears with identical genotypes from the Okefenokee population at 1.00×10^{-3}, or 1 chance in 1,000. The PI*sibs* for Osceola bears indicated a 1 in 500 chance of encountering matching genotypes across all 8 loci. Therefore, there was a high probability that multilocus genotypes identified at hair traps on ≥2 occasions were correctly classified as recaptures of an individual bear. That conclusion was supported by the results of the sibling match tests. Those tests concluded that 100% (n =162) of the hair samples that were analyzed passed my threshold of $P_{sib}<0.05$ and represented 76 individual black bears, 42 of which were identified from the 1995–1998 live-trapping data.

Eight-locus genotypes were obtained for 39 and 37 black bears on the Okefenokee and Osceola study areas, respectively (Tables 5 and 6). Although Okefenokee and Osceola bears seem to have roughly the same average number of alleles (6.13 vs. 5.75), noticeable differences were observed for 3 individual microsatellite loci. Bears from the Okefenokee study area displayed 2 unique alleles at loci G10X and G10P on 11 and 12 separate occasions. Likewise, 6 bears from the Osceola area exhibited 1 allele at loci

G10L that was never observed among Okefenokee bears. Despite the relatively infrequent occurrence of those alleles, their presence indicates genetic variability within this bear population. In addition, the significant results of the Hardy-Weinberg equilibrium test for locus G10P among Okefenokee bears appears to be the result of a select few individual bears possessing alleles at this locus that are uncommon to most other bears within the Okefenokee study area. It is possible that the Okefenokee-Osceola ecosystem is large enough and sufficient genetic variation exists to have bears that are genetically distinct from one another (T. L. King, U.S. Geological Survey, personal communication). Considering that population turnover was high on the Okefenokee study area, it is likely that some bears identified at hair traps in 1999 were immigrants from other areas within ONWR. If sufficient genetic variation existed between those bears and bears on the Okefenokee study area, that could explained the observation of relatively uncommon alleles at certain loci.

Average heterozygosity was calculated as a measure of variation and found to be 66.3% and 67.9% for the Okefenokee and Osceola bear populations. Those estimates may be relatively high in comparison to other black bear populations in the southeastern United States. Throughout much of the Southeast, habitat loss and fragmentation have been so extensive that gene flow may be restricted, resulting in geographically and genetically isolated populations. For example, average heterozygosity of black bears inhabiting the largely isolated Tensas River National Wildlife Refuge in northeast Louisiana was documented at 47.7% across the same 8 loci used in this study (Boersen 2001). When genotypes were extended to 12 loci for 36 individuals from the Tensas NWR study, average heterozygosity increased to 57.6%. That estimate, however,

remains approximately 10% lower than those obtained for bears in the Okefenokee-Osceola population using only 8 loci. Clearly, the effects of geographic isolation as a result of habitat loss and fragmentation play an important role in population genetics. In this study, population size and degree of habitat isolation did not appear to be a detriment to gene flow or genetic variability. Consequently, microsatellite DNA analysis using 8 multilocus genotypes was sufficient for individual identification.

CHAPTER VI

MANAGEMENT IMPLICATIONS

General

Although the estimated densities of bears were similar between the Okefenokee and Osceola study areas, these 2 areas may represent opposite ends of the spectrum in relation to population turnover. Turnover appears to be quite high on the Okefenokee study area as a result of losses from hunting mortality and additions by recruitment and immigration. Although the number of bear mortalities (n = 72) that was documented from 1995–1999 was high relative to the number of individual bears identified (n = 143), the proportion of unmarked bears captured each year was always >50%. The constant influx of new bears suggests that either reproduction is very high for Okefenokee bears, or ONWR may be serving as an important source for areas outside of refuge boundaries. I suggest that the latter is the more probable explanation. Black bear reproduction on the Okefenokee study area was heavily dependent on the swamp's black gum crop in the fall. Twelve of 13 radio-collared females failed to reproduce in 1996 following a failure of a black gum crop in 1995. In contrast, researchers observed an unusually abundant crop of black gum the following year that resulted in significantly higher reproductive success; 26 of 31 radio-collared females were observed with cubs in 1997 (J. D. Clark, U.S. Geological Survey, unpublished data). When fieldwork was completed in 1999, the majority of female bears on the Okefenokee area were still in reproductive synchrony from 1997.

Based on the above, population regulation on the Okefenokee area appears to be primarily governed by hunting mortality, emigration by bears out of ONWR, and black gum productivity. Because biologists have little control over the 2 latter factors, most management decisions concerning bears surrounding the Okefenokee Swamp involve harvest regulations. The Black Bear Management Plan for Georgia (Georgia Department of Natural Resources [GDNR] 1999) calls for a maximum harvest rate of 20% with females comprising no more than 50% of the harvest. Since 1984, the annual bear harvest for the 5 counties contiguous with the Okefenokee Swamp has averaged 35 bears. By extrapolating my density estimate of 0.14 bears/km^2 across the 1,580 km^2 ONWR, 20% of this population would be approximately 44 bears. Although actual harvest numbers are lower than my estimate, I would caution against increasing bear hunting opportunities to compensate for a difference of 9 bears. Annual harvest numbers will fluctuate around the 20% level, but there will undoubtedly be an occasion of black gum failure and a significantly higher proportion of bears will be outside of the swamp and available for harvest. Because black bears have such low reproductive potential (Pelton 1982), an excessively large harvest of females could depress bears numbers for years to come.

The situation on the Osceola study area is a marked contrast from that mentioned above, primarily as a result of the protected status of bears in the State of Florida. In the absence of a hunting season, bear numbers on the Osceola area may be approaching some biological or social threshold that is resulting in high rates of dispersal for subadult males. Unfortunately, identifying density-dependent factors that promote subadult dispersal is a difficult task. Nevertheless, future management efforts should be oriented

towards identifying and protecting bear habitat outside of ONF. In particular, special emphasis should be placed on maintaining and improving habitat connections between ONF and ONWR. We documented bears traveling from Florida into ONWR on 2 occasions, so exchange between the 2 areas is possible and likely occurs more often than expected. Although the 2 study areas are separated by approximately 50 km, the distance between the center of the Osceola study area and the southern edge of the Refuge is only 18 km. Consequently, the scarcity of data supporting interchange from Florida to the Okefenokee Swamp may exist because dispersing males are establishing territories in the southern half of ONWR. If that is the case, then future research needs to involve radio-collaring male bears from the Osceola study area, especially subadults, to document dispersal rates, movement patterns, and survival. The resultant data could then be used identify habitat that is serving as linkage zones between the Osceola and Okefenokee areas.

My study provided the first estimates of population size and density for bears in the Okefenokee and Osceola ecosystem using a rigorous mark-recapture experiment. Although the Okefenokee-Osceola bear population is relatively large and does not appear to be threatened with extinction, the long-term persistence of other Florida black bear populations is questionable. Habitat loss and fragmentation and human encroachment are resulting in populations that are becoming increasingly isolated from other bear populations. Of the 7 recognized Florida black bear populations, the USFWS has concluded that only the Apalachicola NF, Ocala NF, Big Cypress National Preserve, and Okefenokee-Osceola ecosystem populations are viable (Bentzien 1998). In contrast, the Chassahowitzka bear population, located on the central Gulf Coast of Florida, may

contain <20 individuals (Bentzien 1998). For the smaller, more isolated populations to persist into the foreseeable future, it may be necessary to augment them with bears from one of the larger populations. If augmentation were to be considered as a management option, the donor population must be able to withstand the loss of some bears, presumably adult females. Furthermore, the receiving population will need to have enough suitable resources to supply the habitat requirements of additional bears. Consequently, the current status of all Florida black bear populations, large and small, needs to be determined in order to make the most beneficial management decisions in the future.

In addition to biological concerns surrounding the status of the Florida black bear, there also are legal matters that have yet to be resolved. The possibility remains that the 1998 ruling made by the USFWS that precluded the Florida black bear from receiving federal protection could be reversed. If that decision were overturned, the Florida black bear would be classified as a threatened species in accordance with the ESA of 1973. As a result, current management guidelines for bears in the ONWR would have to be reconsidered because it is possible that the black bear hunting season would be terminated. Unfortunately, if that action were taken it would have serious biological and social consequences for bears and hunters.

Genetic Sampling as a Mark-recapture Method

Individual identification using genetic markers has the potential to become a powerful tool for estimating population size. This is especially true when non-invasive sampling techniques can be incorporated into mark-recapture studies. Before

implementing a mark-recapture experiment of this type, however, many aspects of study design require special attention. Although inaccessible and impenetrable habitat precluded systematic trap placement in my study, I would suggest the use of a grid system in which every cell is trapped whenever possible. This would likely prevent individual heterogeneity from imposing a significant bias on capture probabilities. If bait were to be used to lure animals into hair traps I would also recommend using minimal portions. Based on visitation rates from this study, bears exhibited no "trap-shy" behavior whatsoever in response to hair traps. Consequently, using excessive amounts of bait has the potential to quickly initiate a trap-happy response. That type of behavior is difficult to alleviate and typically results in a negatively biased estimate of population size. Although temporal variation in capture probabilities is often difficult to predict, serious biases can result if undetected. For example, animals that exhibit seasonal movements among sessions would inherently have lower capture probabilities than those that remained in the area to be sampled. In that scenario, mean capture rates would differ among sampling occasions and the time assumption would be violated. Fortunately, biases resulting from temporal variation can often be easily prevented by having an *a priori* understanding of the study animal's biology.

Sampling effort is an another matter that should be decided upon before trapping begins. The primary issue that needs to be addressed is approximately how many hair samples will be required to produce reliable estimates. Of course with too few data the performance of most models will be poor because of low capture probabilities as a result of small sample sizes (Otis et al. 1978, White et al. 1982). That problem can be alleviated, however, by deploying more traps, checking traps more frequently, or

lengthening the duration of the trapping season. Unfortunately, each of those options can produce negative effects as well. Although increasing the density of traps within a study area may result in more captures, that response could be due to heterogeneity or trap response, rather than trapping effort. The same dilemma applies to increasing the frequency that traps are checked and extending the sampling time. In addition, lengthening trapping seasons may violate the closure assumption, which can seriously bias estimates of closed models. The challenge of determining sampling effort, therefore, lies in maximizing capture probabilities while minimizing model violations to reduce bias and increase precision (Pollock et al. 1990). This challenge can be met by performing analyses on simulated data before fieldwork even begins. I suggest using the simulation procedure provided within Program CAPTURE that allows users to compare the performance of estimators for populations of known size in the presence of heterogeneous capture probabilities.

Of all the assumptions associated with open and closed models, the most important is that marks are not lost and marked animals are identified correctly. This is logical considering that most estimators of population size are derived from the proportion of marked and unmarked animals in a population. Although loss of marks is not a concern when using genetic markers, the misidentification of genotypes is possible and the result is seriously biased estimators. Fortunately, probability of identity (PI) statistics provide estimates of the probability that 2 individuals from a population will share an identical genotype. Conceptually that probability should be low since many microsatellites are typically used; 8 loci were used in this study. However, PI's will often be high if heterozygosity within a population is low, and this will increase the chance that

animals are misidentified in capture history data. Average heterozygosity estimates in my study fell within a range of 60–80%, qualifying them as good genetic markers for individual identification (Taberlet and Luikart 1999). For smaller, more isolated populations, however, researchers may have to contend with heterozygosity levels below that range. As a consequence, additional microsatellites will have to be analyzed to differentiate individuals that have similar genotypes.

Based on the above, I suggest conducting a pilot study to assess the sampling technique and the utility of the microsatellites to be used before initiating a mark-recapture experiment using genetic markers. The first step in the pilot study is to collect the biological material of interest (i.e., hair, scat, feathers) using the technique intended for the experiment. There is limited use in paying for genetic analyses if sampling methods are unproductive. Assuming that adequate sample sizes are obtainable, I would then evaluate the performance of the DNA extraction and amplification process. The amount of DNA contained in hair roots, for example, is so minute that microsatellite analyses would often be impossible without amplification by polymerase chain reaction (PCR). Once it is known that collection and analysis of samples is possible, I would then estimate the PI in the population of study. That will indicate whether the microsatellites that are chosen for analysis will adequately perform the task of correctly identifying individual animals. Furthermore, identification of genetic markers with high heterozygosity will permit the use of fewer microsatellites to reach the desired PI, which will reduce the cost of analysis and the risk of misclassifications (Taberlet and Luikart 1999).

Genetic sampling has great potential as a new technique for mark-recapture experiments. For studies primarily concerned with estimating population size, this method of sampling is especially promising. Because trap response bias appears to be minimized using this technique, many samples can be collected in an efficient manner over a relatively short time period. Consequently, those capture history data are best suited for closed models.

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APPENDICES

Appendix A. Trapping results for the Georgia study area, 1995–1998

Table A.1. Black bear captures on the Georgia study area, 1995–1998.

Date	Bear ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
06-Jun-95	001	Initial	Male	79.5	7
08-Jun-95	002	Initial	Male	63.6	5
09-Jun-95	003	Initial	Male	72.7	4
10-Jun-95	004	Initial	Male	125.0	10
11-Jun-95	005	Initial	Male	90.9	5
13-Jun-95	003	Recapture	Male	63.6	4
15-Jun-95	001	Recapture	Male	90.9	7
26-Jun-95	007	Initial	Female	54.5	5
26-Jun-95	008	Initial	Male	159.1	5
28-Jun-95	010	Initial	Female	40.9	3
30-Jun-95	011	Initial	Male	54.5	3
01-Jul-95	020	Initial	Male	63.6	3
03-Jul-95	012	Initial	Female	34.1	2
04-Jul-95	021	Initial	Female	45.5	10
05-Jul-95	022	Initial	Male	136.4	7
05-Jul-95	020	Recapture	Male	68.2	3
09-Jul-95	023	Initial	Female	36.4	5
09-Jul-95	011	Recapture	Male	54.5	3
13-Jul-95	021	Recapture	Female	56.8	10
14-Jul-95	024	Initial	Male	34.1	1
18-Jul-95	013	Initial	Male	45.5	2
19-Jul-95	014	Initial	Female	63.6	5
21-Jul-95	025	Initial	Male	68.2	2
26-Jul-95	026	Initial	Male	113.6	5
27-Jul-95	029	Initial	Male	72.7	3
27-Jul-95	030	Initial	Male	70.5	2
29-Jul-95	031	Initial	Female	47.7	2
30-Jul-95	032	Initial	Male	131.8	6
30-Jul-95	033	Initial	Male	43.2	1

Table A.1. (continued)

Date	ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
02-Aug-95	034	Initial	Male	68.2	4
04-Aug-95	013	Recapture	Male	45.5	2
09-Aug-95	035	Initial	Male	34.1	1
09-Aug-95	036	Initial	Male	125.0	6
09-Aug-95	037	Initial	Female	52.3	7
10-Aug-95	039	Initial	Female	38.6	2
11-Aug-95	015	Initial	Male	90.9	3
12-Aug-95	040	Initial	Female	50.0	10
13-Aug-95	016	Initial	Male	79.5	3
14-Aug-95	017	Initial	Male	81.8	8
16-Aug-95	018	Initial	Male	81.8	4
17-Aug-95	019	Initial	Male	50.0	2
17-Aug-95	040	Recapture	Female	50.0	10
18-Aug-95	027	Initial	Male	61.4	5
20-Aug-95	038	Initial	Male	75.0	3
24-Aug-95	022	Recapture	Male	90.9	7
27-Aug-95	041	Initial	Male	70.5	3
28-Aug-95	042	Initial	Male	131.8	6
29-Aug-95	043	Initial	Male	56.8	2
30-Aug-95	044	Initial	Male	79.5	6
31-Aug-95	015	Recapture	Male	93.2	3
01-Sep-95	045	Initial	Female	56.8	3
01-Sep-95	046	Initial	Female	50.0	4
03-Sep-95	047	Initial	Female	59.1	2
05-Sep-95	048	Initial	Female	61.4	5
06-Sep-95	049	Initial	Male	113.6	9
07-Sep-95	050	Initial	Male	72.7	4
12-Sep-95	051	Initial	Female	52.3	6
12-Sep-95	043	Recapture	Male	63.6	2

Table A.1. (continued)

Date	ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
15-Sep-95	051	Recapture	Female	52.3	6
18-Sep-95	028	Initial	Male	56.8	2
19-Sep-95	052	Initial	Female	50.0	8
23-Oct-95	053	Initial	Female	45.5	3
24-Oct-95	054	Initial	Female	50.0	7
25-Oct-95	055	Initial	Male	38.6	2
26-Oct-95	056	Initial	Female	52.3	5
30-Oct-95	057	Initial	Male	56.8	3
30-Oct-95	058	Initial	Male	50.0	2
31-Oct-95	059	Initial	Female	50.0	3
31-Oct-95	060	Initial	Female	56.8	6
03-Nov-95	061	Initial	Male	47.7	3
04-Nov-95	055	Recapture	Male	37.7	2
06-Nov-95	062	Initial	Male	61.4	2
07-Nov-95	063	Initial	Female	47.7	5
25-Nov-95	064	Initial	Female	45.5	6
26-Nov-95	065	Initial	Female	50.0	2
04-Dec-95	067	Initial	Female	40.9	10
04-Dec-95	068	Initial	Female	52.3	8
06-Dec-95	070	Initial	Female	40.9	3
16-Jun-96	071	Initial	Female	61.4	6
19-Jun-96	072	Initial	Female	50.0	7
24-Jun-96	073	Initial	Female	45.5	5
24-Jun-96	004	Recapture	Male	129.5	11
24-Jun-96	074	Initial	Male	54.5	1
26-Jun-96	020	Recapture	Male	61.4	4
26-Jun-96	023	Recapture	Female	45.5	6
28-Jun-96	014	Recapture	Female	75.0	6
28-Jun-96	075	Initial	Female	50.0	3

Table A.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
30-Jun-96	076	Initial	Male	50.0	3
30-Jun-96	077	Initial	Female	40.9	5
30-Jun-96	010	Recapture	Female	47.7	4
02-Jul-96	020	Recapture	Male	61.4	4
04-Jul-96	073	Recapture	Female	45.5	6
18-Jul-96	031	Recapture	Female	54.5	3
20-Jul-96	038	Recapture	Male	106.8	4
21-Jul-96	078	Initial	Female	50.0	6
22-Jul-96	074	Recapture	Male	54.5	1
22-Jul-96	038	Recapture	Male	106.8	4
25-Jul-96	079	Initial	Female	40.9	N/A
27-Jul-96	080	Initial	Male	38.6	1
29-Jul-96	021	Recapture	Female	52.3	11
31-Jul-96	081	Initial	Male	120.5	9
15-Aug-96	003	Recapture	Male	118.2	5
18-Aug-96	016	Recapture	Male	84.1	4
22-Aug-96	022	Recapture	Male	113.6	8
24-Aug-96	013	Recapture	Male	68.2	3
25-Aug-96	082	Initial	Female	77.3	Yng. adult
01-Sep-96	083	Initial	Male	61.4	2
25-Sep-96	004	Recapture	Male	113.6	11
03-Oct-96	051	Recapture	Female	68.2	7
20-Oct-96	091	Initial	Female	47.7	3
22-Oct-96	092	Initial	Female	79.5	N/A
26-May-97	103	Initial	Male	65.9	2
01-Jun-97	084	Initial	Male	56.8	1
09-Jun-97	038	Recapture	Male	136.4	5
11-Jun-97	103	Recapture	Male	61.4	2
13-Jun-97	085	Initial	Male	65.9	1

Table A.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
13-Jun-97	086	Initial	Male	36.4	1
14-Jun-97	013	Recapture	Male	136.4	4
15-Jun-97	043	Recapture	Male	90.9	4
15-Jun-97	104	Initial	Male	72.7	2
16-Jun-97	087	Initial	Male	43.2	1
17-Jun-97	085	Recapture	Male	65.9	1
19-Jun-97	088	Initial	Male	63.6	2
20-Jun-97	089	Initial	Male	59.1	1
21-Jun-97	038	Recapture	Male	147.7	5
03-Jul-97	045	Recapture	Female	68.2	4.5
13-Jul-97	089	Recapture	Male	72.7	1
15-Jul-97	078	Recapture	Female	50.0	7
20-Jul-97	104	Recapture	Male	75.0	2
21-Jul-97	103	Recapture	Male	70.5	2
23-Jul-97	093	Initial	Male	52.3	2
23-Jul-97	074	Recapture	Male	102.3	2
23-Jul-97	088	Recapture	Male	50.0	2
23-Jul-97	094	Initial	Male	54.5	4
30-Jul-97	016	Recapture	Male	115.9	5
30-Jul-97	093	Recapture	Male	45.5	2
01-Aug-97	084	Recapture	Male	56.8	1
04-Sep-97	049	Recapture	Male	181.8	11
05-Sep-97	095	Initial	Male	77.3	1
06-Sep-97	020	Recapture	Male	102.3	5
08-Sep-97	073	Recapture	Female	56.8	6
10-Sep-97	096	Initial	Male	127.3	5
11-Sep-97	075	Recapture	Female	52.3	4
11-Sep-97	025	Recapture	Male	127.3	4
11-Sep-97	002	Recapture	Male	122.7	7

Table A.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
11-Sep-97	098	Initial	Male	63.6	2
12-Sep-97	105	Initial	Male	45.5	1
14-Sep-97	100	Initial	Female	36.4	Yearling
15-Sep-97	101	Initial	Male	145.5	5
22-Sep-97	102	Initial	Female	56.8	4
24-Sep-97	093	Recapture	Male	50.0	2
16-Sep-97	075	Recapture	Female	52.3	4
17-Sep-97	095	Recapture	Male	77.3	1
19-Sep-97	002	Recapture	Male	122.7	7
25-Sep-97	107	Initial	Female	56.8	5
04-Nov-97	108	Initial	Female	59.1	4
08-Nov-97	109	Initial	Female	45.5	2
08-Nov-97	037	Recapture	Female	59.1	9
10-Nov-97	074	Recapture	Male	113.6	2
11-Nov-97	110	Initial	Male	68.2	1
13-Jun-98	110	Recapture	Male	61.4	1.5
16-Jun-98	131	Initial	Female	50.0	Adult
17-Jun-98	110	Recapture	Male	61.4	1.5
17-Jun-98	133	Initial	Male	72.7	Mid-adult
19-Jun-98	039	Recapture	Female	45.5	5.5
21-Jun-98	134	Initial	Female	25.0	Yearling
22-Jun-98	043	Recapture	Male	106.8	4.5
24-Jun-98	093	Recapture	Male	63.6	3
27-Jun-98	135	Initial	Male	125.0	Yng. adult
27-Jun-98	136	Initial	Male	95.5	Subadult
02-Jul-98	040	Recapture	Female	63.6	12.5
04-Jul-98	045	Recapture	Female	40.9	5.5
08-Jul-98	137	Initial	Female	22.7	Yearling
08-Jul-98	138	Initial	Female	27.3	Yearling

Table A.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
12-Jul-98	051	Recapture	Female	56.8	8.5
13-Jul-98	999[a]	Initial	Female	52.3	Mid-adult
24-Jul-98	140	Initial	Female	36.4	Subadult
25-Jul-98	141	Initial	Male	34.1	Yearling
26-Jul-98	085	Recapture	Male	93.2	2
27-Jul-98	084	Recapture	Male	68.2	2
29-Jul-98	094	Recapture	Male	63.6	5
30-Jul-98	093	Recapture	Male	61.4	3
30-Jul-98	143	Initial	Female	52.3	Mid-adult
01-Aug-98	039	Recapture	Female	54.5	5
10-Aug-98	144	Initial	Male	22.7	Yearling
11-Aug-98	037	Recapture	Female	63.6	10
15-Aug-98	003	Recapture	Male	125.0	7
15-Aug-98	145	Initial	Male	50.0	Yearling
17-Aug-98	146	Initial	Male	45.5	Yearling
18-Aug-98	074	Recapture	Male	104.5	3
18-Aug-98	094	Recapture	Male	63.6	5
24-Aug-98	138	Recapture	Female	29.5	Yearling
25-Aug-98	086	Recapture	Male	54.5	2
30-Aug-98	147	Initial	Male	54.5	Subadult
30-Aug-98	105	Recapture	Male	61.4	2
01-Sep-98	148	Initial	Male	109.1	Yng. adult
05-Sep-98	072	Recapture	Female	61.4	9
08-Sep-98	049	Recapture	Male	136.4	12
08-Sep-98	090[a]	Initial	Male	88.6	Old adult
10-Sep-98	076	Recapture	Male	79.5	5
11-Sep-98	088	Recapture	Male	68.2	3
12-Sep-98	149	Initial	Male	75.0	Subadult
12-Sep-98	087	Recapture	Male	54.5	2

Table A.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
13-Sep-98	020	Recapture	Male	102.3	6
14-Sep-98	073	Recapture	Female	56.8	7
14-Sep-98	150	Initial	Male	54.5	Subadult
16-Sep-98	151	Initial	Male	54.5	Yearling
17-Sep-98	096	Recapture	Male	118.2	6
23-Sep-98	152	Initial	Male	38.6	Yearling

[a] Initial captures of nuisance bears that were relocated onto the study area in 1997.

Appendix B. Trapping results for the Florida study area, 1996–1998

Table B.1. Black bear captures on the Florida study area, 1996–1998.

Date	Bear ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
07-Jun-96	201	Initial	Male	147.7	4
08-Jun-96	202	Initial	Female	38.6	3
11-Jun-96	203	Initial	Male	75.0	3
14-Jun-96	205	Initial	Female	68.2	4
14-Jun-96	207	Initial	Male	79.5	2
15-Jun-96	204	Initial	Male	88.6	3
16-Jun-96	209	Initial	Male	145.5	3
17-Jun-96	206	Initial	Female	52.3	3
17-Jun-96	208	Initial	Female	45.5	2
20-Jun-96	210	Initial	Male	63.6	3
24-Jun-96	211	Initial	Female	59.1	5
24-Jun-96	213	Initial	Male	147.7	6
25-Jun-96	207	Recapture	Male	79.5	2
26-Jun-96	215	Initial	Female	59.1	7
29-Jun-96	212	Initial	Male	25.0	1
29-Jun-96	214	Initial	Male	90.9	3
30-Jun-96	216	Initial	Male	61.4	2
08-Jul-96	217	Initial	Female	25.0	1
11-Jul-96	219	Initial	Female	56.8	3
12-Jul-96	218	Initial	Male	54.5	3
13-Jul-96	220	Initial	Male	40.9	1
14-Jul-96	221	Initial	Male	43.2	1
15-Jul-96	222	Initial	Male	97.7	2
20-Jul-96	223	Initial	Male	47.7	3
21-Jul-96	224	Initial	Female	63.6	3
24-Jul-96	225	Initial	Male	63.6	1
24-Jul-96	226	Initial	Female	59.1	5
26-Jul-96	227	Initial	Female	31.8	1
26-Jul-96	209	Recapture	Male	145.5	3

Table B.1. (continued)

Date	Bear ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
26-Jul-96	228	Initial	Female	52.3	3
29-Jul-96	229	Initial	Male	147.7	6
30-Jul-96	230	Initial	Male	45.5	1
01-Aug-96	231	Initial	Male	150.0	6
10-Aug-96	232	Initial	Female	75.0	3
17-Aug-96	233	Initial	Male	43.2	2
18-Aug-96	225	Recapture	Male	63.6	1
27-Aug-96	234	Initial	Female	0.0	4
02-Sep-96	235	Initial	Female	77.3	6
16-Dec-96	236	Initial	Male	181.8	4
02-Jan-97	216	Recapture	Male	113.6	2.5
15-Jun-97	237	Initial	Male	43.2	1
16-Jun-97	248	Initial	Female	59.1	10
18-Jun-97	249	Initial	Male	38.6	2
22-Jun-97	238	Initial	Male	61.4	1
22-Jun-97	239	Initial	Male	68.2	1
23-Jun-97	227	Recapture	Female	52.3	2
24-Jun-97	218	Recapture	Male	79.5	4
27-Jun-97	211	Recapture	Female	84.1	6
28-Jun-97	207	Recapture	Male	109.1	3
01-Jul-97	215	Recapture	Female	54.5	8
02-Jul-97	240	Initial	Male	93.2	5
09-Jul-97	241	Initial	Male	65.9	1
10-Jul-97	242	Initial	Male	111.4	2
15-Jul-97	241	Recapture	Male	61.4	1
15-Jul-97	239	Recapture	Male	63.6	1
17-Jul-97	243	Initial	Female	43.2	2
17-Jul-97	214	Recapture	Male	106.8	4
17-Jul-97	266	Initial	Male	143.2	5

Table B.1. (continued)

Date	ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
04-Aug-97	244	Initial	Female	40.9	1
05-Aug-97	245	Initial	Male	147.7	7
06-Aug-97	246	Initial	Female	97.7	7
14-Aug-97	247	Initial	Male	129.5	11
17-Aug-97	216	Recapture	Male	104.5	3.5
19-Aug-97	220	Recapture	Male	65.9	2
21-Aug-97	225	Recapture	Male	95.5	2
22-Aug-97	250	Initial	Female	50.0	1
22-Aug-97	251	Initial	Male	145.5	3
27-Aug-97	252	Initial	Male	125.0	13
29-Aug-97	246	Recapture	Female	79.5	7
02-Sep-97	233	Recapture	Male	77.3	3
03-Sep-97	253	Initial	Female	45.5	3
03-Sep-97	250	Recapture	Female	47.7	1
04-Sep-97	254	Initial	Female	68.2	9
04-Sep-97	255	Initial	Male	100.0	3
05-Sep-97	260	Initial	Female	45.5	1
06-Sep-97	219	Recapture	Female	50.0	4
07-Sep-97	256	Initial	Male	118.2	6
08-Sep-97	261	Initial	Male	52.3	3
09-Sep-97	254	Recapture	Female	68.2	9
11-Sep-97	257	Initial	Female	68.2	1
11-Sep-97	236	Recapture	Male	163.6	5
12-Sep-97	224	Recapture	Female	54.5	4
14-Sep-97	253	Recapture	Female	45.5	3
15-Sep-97	240	Recapture	Male	125.0	6
16-Sep-97	263	Initial	Male	120.5	5
18-Sep-97	220	Recapture	Male	75.0	2
20-Sep-97	234	Recapture	Female	86.4	5

Table B.1. (continued)

Date	ID#	Capture Type	Sex	Weight (kg)	Age (yrs)
16-Jun-98	258	Initial	Male	34.1	Yearling
16-Jun-98	259	Initial	Female	25.0	Yearling
18-Jun-98	205	Recapture	Female	N/R	6
19-Jun-98	258	Recapture	Male	34.1	Yearling
20-Jun-98	202	Recapture	Female	45.5	5
21-Jun-98	206	Recapture	Female	59.1	5
21-Jun-98	267	Initial	Male	181.8	Yng. adult
22-Jun-98	264	Initial	Male	38.6	Subadult
24-Jun-98	268	Initial	Female	27.3	Yearling
25-Jun-98	269	Initial	Male	31.8	Yearling
29-Jun-98	205	Recapture	Female	N/R	6
02-Jul-98	207	Recapture	Male	131.8	4
02-Jul-98	270	Initial	Male	59.1	Subadult
02-Jul-98	269	Recapture	Male	31.8	Yearling
03-Jul-98	248	Recapture	Female	63.6	11
08-Jul-98	271	Initial	Female	43.2	Yng. adult
09-Jul-98	215	Recapture	Female	65.9	9
10-Jul-98	209	Recapture	Male	159.1	5
11-Jul-98	272	Initial	Female	54.5	Yng. adult
14-Jul-98	211	Recapture	Female	59.1	7
15-Jul-98	208	Recapture	Female	56.8	4
16-Jul-98	273	Initial	Male	29.5	Yearling
22-Jul-98	258	Recapture	Male	34.1	Yearling
22-Jul-98	274	Initial	Female	31.8	Yearling
23-Jul-98	275	Initial	Female	27.3	Yearling
24-Jul-98	231	Recapture	Male	147.7	8
01-Aug-98	232	Recapture	Female	77.3	5
02-Aug-98	206	Recapture	Female	59.1	5
04-Aug-98	274	Recapture	Female	31.8	Yearling

Table B.1. (continued)

Date	ID#	Type	Sex	Weight (kg)	Age (yrs)
05-Aug-98	276	Initial	Male	106.8	Subadult
06-Aug-98	277	Initial	Male	25.0	Yearling
07-Aug-98	216	Recapture	Male	102.3	4.5
08-Aug-98	226	Recapture	Female	72.7	7
11-Aug-98	278	Initial	Male	102.3	Subadult
14-Aug-98	220	Recapture	Male	90.9	3
16-Aug-98	263	Recapture	Male	136.4	6
16-Aug-98	245	Recapture	Male	159.1	8
17-Aug-98	244	Recapture	Female	36.4	2
19-Aug-98	279	Initial	Male	104.5	Mid-adult
19-Aug-98	233	Recapture	Male	84.1	4
28-Aug-98	279	Recapture	Male	104.5	Mid-adult
29-Aug-98	203	Recapture	Male	136.4	5
16-Sep-98	216	Recapture	Male	90.9	4.5
17-Sep-98	253	Recapture	Female	59.1	4
21-Sep-98	283	Initial	Male	27.3	Yearling

Appendix C. 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.

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.

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

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VITA

Steven Thomas Dobey was born on September 11, 1972 in Tupelo, Mississippi. He graduated from Charles. E. Jordan High School in Durham, North Carolina in 1990. He attended East Carolina University in Greenville, North Carolina where he received a Bachelor of Science degree in Biology in December 1995. In August 1996, Steven was accepted into North Carolina State University as a non-degree student in the Department of Fisheries and Wildlife Sciences. Steven was hired as a research technician by the University of Tennessee in May of 1997 and spent 7 months trapping black bears in Louisiana. One year later, Steven began graduate school in the Department of Forestry, Wildlife and Fisheries at the University of Tennessee, Knoxville studying Florida black bears. He received his Master's of Science degree in Wildlife and Fisheries Science in May 2001.