INTEGRATED DEMOGRAPHIC MODELING AND ESTIMATION OF THE CENTRAL GEORGIA, USA, BLACK BEAR POPULATION

by

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(Under the Direction of Michael J. Conroy)

ABSTRACT

The central Georgia population (CGP) of black bears is considered to inhabit mostly forested land in and around 186 km^2, and potentially an area of 1,200 km^2, associated with the Ocmulgee River drainage system, and likely a core area of contiguous forest in the Oaky Woods and Ocmulgee Wildlife Management Areas (WMAs). We document the density, survival and reproduction, as well as genetic structure, of the CGP under the sampling protocol, over the duration of the study from 2003 to 2008. We describe a joint model of population abundance with three data structures (DNA hair snares, camera traps, and radiotelemetry) that incorporates genetic error from replicate genetic samples and a calibration sample of known individuals. The hierarchical joint Bayesian model incorporates Markov-Chain Monte Carlo (MCMC) methods with Gibbs, Metropolis-Hastings, and reversible jump Metropolis-Hastings sampling algorithms of posterior distributions. Median posterior abundance estimates within the WMA land over five seasons from 2004 to 2006 were: 2004 summer 213 (95% BCI: 144-354), 2004 fall 106 (95% BCI: 72-179), 2005 summer 184 (95% BCI: 137-266), 2005 fall 131 (95% BCI: 91-207), 2006 summer 192 (95% BCI: 143-280). Adult annual survival estimates were 0.861 (95% CI: 0.746-0.976) for females and 0.845 (95% CI: 0.754-0.937) for males. Reproduction rates were

simulated from bootstrap simulations using mean birth interval and average number of cubs per female litter. Reproduction rates from the CGP only and the CGP combined with eastern black bear populations were 0.845 (95% CI; 0.843-0.847) and 1.139 (95% CI: 1.137-1.141), respectively. Population viability analyses using demographic parameters from the CGP and eastern black bear populations suggest that population growth is decreasing. The joint Bayesian hierarchical model also suggests that population growth is decreasing, since the Bayesian credible intervals of λ, the finite rate of population increase, included values above and below one. The λ from abundance models overlapped confidence intervals with λ from the population viability analyses, which suggest that conclusions based on increased harvest and population status are consistent with different data sources. Additional effort for the CGP should be focused on estimates of cub and sub-adult survival and reproduction.

INDEX WORDS: population modeling, *Ursus americanus*, *Ursus,* genetic error, population viability analysis, hierarchical modeling, MCMC, survival, reproduction, joint data structures

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Less than 10% of the original range of the American black bear (*Ursus americanus*) in the eastern United States is believed to support bear populations (Pelton 1982, Maehr 1984), with most bears surviving on scattered publicly-owned lands (Pelton 1985). Pelton (1990) describes at least 30 distinct populations in thirteen southeastern states. There are three populations of black bears consisting of two subspecies, with an unknown amount of connectivity, in Georgia. The northern population (*U. a. americanus*) is associated with the Appalachian Mountains of the northeast and north central area of Georgia. The central population (*U. a. americanus*) (CGP) is associated with the Ocmulgee River drainage system, south of Macon, while the southeastern population of black bears (*U. a. floridanus*) is associated with the Okefenokee Swamp (Figure 1.1). The central Georgia population (CGP) of black bears is considered to inhabit mostly forested land in and around 186 km^2 (and potentially upwards of 1,200 km^2) associated with the Ocmulgee River drainage system, and likely a core area of contiguous forest in the Oaky Woods and Ocmulgee Wildlife Management Areas (WMAs).

There are few studies that examine the demographics of a bear population before the potential of development and infrastructure. We document the density, survival and reproduction, as well as genetic structure, of a bear population under our sampling protocol. In the course of the study, the majority of the land (~145 km^2) of the wildlife management areas

was sold to private individuals, timber companies, and real estate agencies. The state owns a small portion of the land within the CGP, therefore much of the area has an unpredictable landuse future.

Population viability models can be constructed from the combination of abundance and demographic parameters (i.e., survival and reproduction). A sampling protocol for abundance, survival, and reproduction estimation relies on knowledge of several biological characteristics (e.g., habitat use, dispersal and movement patterns). Influences on capture probability and the genetic structure of a population are also integral to an optimal sampling design. Here I review the population biology, population genetics, conservation issues, and sampling and estimation techniques for black bear populations in the southeastern United States. I also review Bayesian hierarchical models, capture mark-recapture (CMR) models, and genetic markers.

Literature review

Bear abundance

Knowledge of abundance or density of black bear populations is important for the management of populations. Abundance, survival, reproduction, and movement estimates, are typical components of population viability models. Estimated densities for Eastern black bear populations, specifically southeastern populations, vary by location, habitat, and statistical procedures utilized (Table 1.1). Each density estimate also has associated errors with the estimate, as well as known biases in the study, discussed below.

Sampling methods for bear abundance

Field methods for estimating bear density or abundance include: physical captures (Smith 1985, McLean and Pelton 1994, Hellgren and Vaughn 1989b), camera detections (Grogan and Lindzey 1999, Martorello 1998, Beausoleil 1999, Mace et al. 1994), tetracycline markers and resighting with harvested bears (Garshelis and Visser 1997), DNA hair snares (Woods et al. 1999, Mowat and Strobeck 2000, Kendall et al. 2008, Kendall et al. 2009), aerial radiotelemetry and mark-resights (Miller et al. 1997), mark-recapture with dogs (Akenson et al. 2001), density based on bear-sign (Garshelis et al. 1999), and occupancy studies (Boulanger et al. 2008b). Some field methods are associated with more rigorous statistical estimation models than others. Methods also vary in the degree of handling of the animal from invasive to noninvasive.

Capture-mark-recapture models (CMR), for both open (Jolly-Seber) and closed populations, are used with physical captures, DNA hair snares, and mark-recapture with dogs. These methods require substantial sample sizes and physical effort to cover the population area where bears occur. Therefore, these methods are rare in large-scale and long-term bear studies. Less expensive and more practical methods include camera detections and mark-resighting from telemetry and tetracycline markers, where physical recaptures of animals are not necessary. Lastly, methods focused on bear presence or occupancy (MacKenzie et al. 2006), such as bear-sign (e.g., scats, bear tracks, scratching posts, or presence of bear hair), not necessarily abundance, are least expensive, but provide less information about abundance.

Detection probability considerations for bears

Capture variability can be classified into three main types: 1) heterogeneity, where each individual animal has a different probability of capture, or measurable individual attributes (e.g, group or individual covariates) that predict capture probability 2) behavior, where animals captured have different probabilities of capture than animals not captured, either trap-happy or trap-shy, and 3) time, where capture probability can vary over trapping sessions (White et al. 1982). The probability that a given black bear will be detected is influenced by several behavioral traits. Male black bears have a greater chance of encountering bait stations or being sited due to increased travel distances and large home ranges; and as a result, a greater chance of being captured than female black bears (Hellgren and Vaughan 1989b). Depending on the capture method used, detection also may depend on age, with juveniles and cubs being less likely to be captured than adults. Family groups, consisting of parent-offspring and siblings traveling together, are also a large source of nonindependent movement in bear populations (Kendall et al. 2009). However, simulation studies indicate that this movement will cause minimal bias in population estimates (Miller et al. 1997, Boulanger et al. 2004). Individual heterogeneity is considered a problem with animals sampled with mark-recapture techniques and other encounter techniques.

Black bears have large home ranges and are highly mobile, with males more mobile than females. Therefore, temporary emigration, or when an animal is temporarily unavailable for capture due to movement off of the sample area, is a concern in the sampling procedure. Individuals that temporarily emigrate are not available for detection and unique identification during a given period (Kendall and Nichols 1995, Kendall et al. 1995). The Robust Design (Pollock 1982) is a possible solution to temporary emigration. This design assumes primary

periods are open to births, deaths and movement, and secondary periods, or short intervals within a primary period, are assumed closed (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997).

The most common trap configuration for bears is a grid system. For example, the systematic grid design described in Mowat and Strobeck (2000) is based on female grizzly bear home range size in similar ecosystems of British Columbia. In a grid system, traps are evenly or randomly spaced on boxed grids over a study area. Density is calculated in a grid system by estimating the population size and dividing that value by the area of the trapping grid. Geographic closure under this design is difficult to meet because animals at the edge of the trapping grid may have only part of their home range in the study, thus the effective trapping area is actually larger than what is used in the density equation (White and Shenk 2001). Edge animals may move in and out of the sampling area during a sampling period, and may bias estimates of density and abundance. Alternate approaches include estimating density from explicit trapping arrays (Anderson et al. 1983) or trapping arrays of arbitrary geometry (Gardner et al. 2009, Efford 2004, Royle and Young 2008).

Noninvasive sampling techniques

Animals that occur at low densities or have elusive behavior are difficult to sample for population inference, and this often leads to low sample sizes with physical captures. Noninvasive sampling techniques, or techniques that do not require physical capture of animals, allow many populations of animal species to be monitored with greater detail. Noninvasive methods for sampling bear density include DNA hair snares and the use of remote cameras. Camera trapping is a technique that uses capture-resight data, much like radio telemetry.

Animals only need to be handled once at initial capture to mark, while resighting of those individuals are obtained through photography. At this point, focus will be on the biases associated with camera resighting, and genetic hair snare traps, since these two methods were utilized in the CGP study.

There are problems that may occur with camera detections. Marked bears may be less attracted to baits or flashes that occur in low-light situations. Those bears would be less likely to be photographed, and thus detected, than unmarked bears because of capture experience. This may lead to bears avoiding baits or reducing their movement patterns so not to encounter baits and not be captured or resighted (Grogan and Lindzey 1999). This is commonly referred to as a behavioral response. Under this scenario, selection of the closed capture model, M_b, can reduce bias in population estimates. Another problem with camera trapping is that unmarked bears may revisit a camera site within the same sampling period, which does not allow for individual identification. Capture-resight methods rely on the ability to distinguish individuals. Occupancy models (MacKenzie et al. 2006) would be better suited for these scenarios. Camera data is also less expensive than physical capture-recapture data.

Advances within the fields of molecular and genetic biology have increased the ability to use genetic analyses in wildlife studies. Genetic samples (e.g., shed hairs, feathers, feces, shed skin), collected noninvasively in the field, are often small and contain degraded DNA. The ability to create multiple copies of DNA from these samples with PCR (polymerase chain reaction) has advanced noninvasive genetic sampling techniques (Waits 1999). There are three types of genetic markers that can be used in DNA analysis: mitochondrial DNA (mtDNA) markers, Y chromosome markers, and nuclear DNA markers. Mitochondrial DNA, located in the mitochondria of mammalian cells, is maternally inherited and is used to study female

evolutionary history, gene flow, and genetic diversity. Nuclear DNA, located in the nucleus of mammalian cells, is inherited by both parents and can be used to study maternal and paternal evolutionary history, gene flow, genetic diversity and relatedness. The Y chromosome (i.e., sex chromosome) is inherited from father to son and can be used to study paternal evolutionary history, gene flow, and genetic diversity (Waits 1999). In most capture-recapture studies, nuclear DNA from microsatellite loci are used to determine individuals for bear identification (Waits 1999). Microsatellite loci are short tandem repeats of 1-5 bases. Noninvasive genetic samples are currently utilized with bear species globally for problems of demographics (Taberlet et al. 1997, Mowat and Strobeck 2000, Boulanger et al. 2002, Bellemain et al. 2005, Triant et al. 2004, Kendall et al. 2008), habitat relationships (Apps et al. 2004), and dispersal and/or effectiveness of corridors (Dixon et al. 2006, Schwartz et al. 2006, Dixon et al. 2007, Proctor et al. 2004).

Possible benefits of noninvasive genetic sampling are: 1) field methods that may be less expensive, and less harmful to the animal than physical captures, and 2) the mark, or genetic identity, is visible, read clearly, and permanent (Foran et al. 1997, Woods et al. 1999). These assumptions are adopted in many noninvasive studies, although they warrant further investigation. There remains doubt in the clarity of genetic identity (Taberlet et al. 1999, Bonin et al. 2004) and cost-effectiveness of noninvasive techniques. The presence of genetic error (allelic dropout or false alleles) is a key factor with accuracy measures for genetic noninvasive techniques. Allelic dropout is caused by PCR inhibitors, and sampling stochasticity in the laboratory from amplification and pipetting of small amounts of low quality DNA (Goossens et al. 1998, Taberlet et al 1999, Woods et al. 1999). False alleles can be a result of amplification artifacts from PCR (Goossens et al. 1998, Taberlet et al 1999, Woods et al. 1999).

Genetic errors can occur at various steps in a genetic study (e.g., sampling, DNA extraction, molecular analysis, scoring, data analysis) and be caused by human or technical error, or biological processes (Bonin et al. 2004). Technical error can include amplification artifacts (Rodriguez et al. 2001), biochemical anomalies (Smith et al. 1995), electrophoresis (Fernando et al. 2001), temperature variation in the laboratory (Davison and Chiba 2003), method of electrophoresis (Delmotte et al. 2001), and quality and type of DNA used (Goosens et al. 1998).

With improvements in laboratory and field sampling techniques, population monitoring with noninvasive samples has increased substantially since the methods were first available. However, there are limited analytical and statistical methods that incorporate multiple noninvasive sampling field methods (such as hair snags and bear rub trees: Boulanger et al. 2008a), particularly with the incorporation of genetic error into abundance estimates (but see Wright et al. 2009). If genetic error is ignored, population sizes estimates can be sensitive to genetic error and biased (Creel et al. 2003, Waits and Leberg 2000). Current methods of incorporating genetic error in noninvasive sampling mark-recapture models use maximum-likelihood methods (Lukacs and Burnham 2005, Kalinowski et al. 2006), Bayesian methods (Wright et al. 2009*,* Petit and Valière 2006), and *ad hoc* approaches (Paetkau 2003, McKelvey and Schwartz 2004). Many approaches also require multiple PCR attempts to assess error (i.e., multiple-tubes approach Taberlet et al. 1996), which increases the cost per sample.

Hierarchical modeling and Bayesian estimation

Hierarchical state-space models, provide a way of linking observations from data, such as capture-mark-recapture (CMR) or occupancy samples, to the underlying ecological or state processes (Royle and Dorazio 2008). Often, it is not possible to observe ecological processes

directly, and samples from a population or groups of populations are used to make inference on the processes. Hierarchical models can incorporate all components of variance (statistical from sampling and inherent biological), incorporate different scales of observation, and provide a way of combining multiple sources of data with common parameters. One of the main goals of this study is to estimate abundance of black bears in central Georgia using a combination of several sources of data. The common parameter of inference between the data sources is abundance, which cannot be directly observed. Species abundance is influenced by many biological processes, including habitat relationships, within population processes (*e.g.*, density-dependence), and species interactions (*e.g.*, Lotka-Volterra models of predator-prey relationships, species competition, mutualisms, and co-evolution).

Hierarchical models are often complex and difficult to make inferences on population parameters with classical methods of statistics, like maximum likelihood methods (MLE). Bayesian approaches do not rely on asymptotic properties of estimators, which are often difficult to achieve with biological sampling methods, or repeated samples. In the Bayesian paradigm, model parameters are treated as random variables with associated probability distributions. The Bayesian approach incorporates prior information along with observations of data, to achieve posterior inference on a parameter or parameters of interest. The fundamental basis of a Bayesian approach is with a rule of probability, proposed by the Reverend Thomas Bayes (1763), commonly referred to as Bayes' Rule. To make probability statements on the parameter θ, given the data y, the joint probability distribution for θ and y, is a combination of the prior distribution $p(\theta)$ and the sampling distribution, or likelihood function, $p(y|\theta)$, or:

$$p(\theta,y)= p(\theta)p(y|\theta)$$

Further, by conditioning on the known data, since this is observed, the posterior density of the parameter given data is as follows:

$$p(\theta \mid y) = \frac{p(\theta, y)}{p(y)} = \frac{p(\theta)p(y \mid \theta)}{p(y)}$$

The unnormalized posterior density omits the fixed data *y,* which is as a constant with respect to the parameter. Therefore an equivalent form of Bayes' Rule, is:

$$p(\theta \mid y) \propto p(\theta)p(y \mid \theta)$$

Black bear biology

The black bear, an omnivore and generalist, is a highly adaptable large mammal that inhabits many diverse forested areas in North America (Pelton 1985). Black bears live in varied habitats, such as the arid desert forests in the Southwest, the Northern Boreal forests, Florida subtropical forests, and temperate rain forests in the Appalachian Mountains (Powell et al. 1997). The basic needs of bears can be classified into categories of food, cover, and protection and, specifically, thick understory with plentiful hard and soft mast and limited road access with large home range areas (Pelton 1985). However, with increased urban sprawl, logging, and human population growth, forest habitat for the black bear is decreasing, but this does not always lead to decreased population growth for black bears. Some black bear populations are large and can sustain harvest, while other black bear populations are small and fragmented and hence, cannot sustain harvesting. Black bears usually exist in low densities, and often in dense vegetation due to their cryptic behavior. Bears also move large distances and inhabit wide-ranging areas, further increasing the difficulty in estimating demographic parameters.

Bear habitat use and home range size

Home range can be defined as the geographic area where an animal forages, mates, and reproduces (Burt 1943). Home range size can differ temporally, as well as by sex and age. Home range size of black bears also varies with population location in North America. Habitat models for the central Georgia population (CGP) indicate bear presence with annual home ranges in areas with low road density and possible effects from habitat diversity (Cook 2007). In the CGP, the mean 95% fixed kernel annual home range for adult female bears was 14.7 km^2 (95% CI: 9.8-19.6 km^2) and 195.3 km^2 (95% CI: 49.51-352.02 km^2) for adult male bears between May 2003 and August 2004 (Cook 2007). Male home range sizes for all seasons were larger than females for the CGP. These home range sizes are consistent with other populations in the southeastern US (Table 1.2). Smith and Pelton (1990) found summer ranges of adult black bear males to be significantly larger than spring home ranges, and solitary adult females had larger ranges in summer than spring or fall-winter. They also observed that female black bears with newborn cubs had smaller spring ranges than solitary adults or females with yearlings. The degree of overlap between individual animal home ranges will affect the density of a population. Smith and Pelton (1990) discovered adult male home ranges overlapped the most in the summer, rather than spring, fall, or winter seasons. On a larger scale, female black bears are known to defend and not overlap territories when food resources are less abundant and are more tolerant of other females when resources are abundant, as is the case in most Southeastern populations (Rogers 1987a).

Black bear habitat suitability models in Mississippi predict that soft mast basal area, hard mast canopy cover, and hard mast basal acre of mature trees are the best indicators of presence (Bowman 1999). Other important habitat indicators of presence in the Southeast include canopy

closure, horizontal cover, and den availability (Landers et al. 1979, Hamilton and Marchinton 1980, Smith 1986, Hellgren and Vaughan 1989a, Oli et al. 1997, Dobey et al. 2002).

Bear dispersal and movement

The dispersal and movement patterns of a species will contribute to either additions or deletions of individuals from a population. Dispersal and other types of movement maintain genetic diversity and supplement populations that may be experiencing low population numbers. Therefore it is important to understand why and how bears make movements and are distributed in space. Black bear movement is often dependent on food availability and distribution (Amstrup and Beecham 1976). Garshelis et al. (1981) determined that diurnal rates of travel of black bears in the Southern Appalachians were higher than nocturnal rates during spring and summer, but fall travel rates were slightly higher among females than males in their study. Males also traveled further per hour than females diurnally and nocturnally. Male black bears move more often and further, on average, than females. Black bears can disperse far distances from their natal home ranges (Rogers 1987b, Lee and Vaughan 2003).

Bear survival

Survival, the probability that an animal survives from time t to time $t+1$, in black bears can vary by space, time, sex, and age. The highest reported free-ranging female black bear longevity values are between 27 and 30+ years, and bears are self-sufficient at 1.5 years of age (range 0.5-2.5 years) (Bunnell and Tait 1985). Subadult bears are more prone to dispersal from a population, and may encounter lower survival rates than adults. Reported mortality rates vary between 15 to 35% annually (Bunnell and Tait 1985). Several studies have attributed causes of

adult mortality to legal harvest, illegal kills, vehicle collisions, nuisance mortalities, cannibalism, natural causes, and research handling. Cub survival at one year of age has been documented as 59%, and 39% by 2.5 years (Elowe and Dodge 1989). Causes of mortality attributed to bear cubs include: abandonment in dens, natural accidents, disease, mother died, vehicle collisions, hunting, research handling of cubs (Elowe and Dodge 1989), and unique to the Southeast, drowning in tree dens and complications from flooding habitats (Smith 1985).

Bear reproduction

Reproduction rate, or the number of young produced per female adult, determines the number of new individuals entering the population via *in situ* recruitment. Individuals also may be recruited into the population via immigration of juvenile or adult individuals, and it is important to distinguish these two types of recruitment in demographic analysis. Reproduction rate in bears is a difficult parameter to estimate due to their elusive behavior. Age of first reproduction, litter size, and breeding interval appear to be driven by nutritional condition within the genus *Ursus* in a density-independent way (Bunnell and Tait 1985). It is also hypothesized that body weight and age influence reproductive parameters (Rogers 1987a, Alt 1989, Elowe and Dodge 1989, Stringham 1990). Studies have shown that litter order is an important variable in determining litter size, with first litters being smaller (McDonald and Fuller 2001). The mating system is considered promiscuous and females have induced ovulation and delayed implantation (Bunnell and Tait 1985). These characteristics enhance the probability of successful matings and maximize reproductive success.

Bear conservation issues in the southeastern United States

Larger mammalian carnivores are known to be sensitive to habitat loss and fragmentation (Crooks 2002). With increased fragmentation in the southeastern US, habitat conservation and reduction of barriers to movement are of special concern. Fragmentation can lead to smaller populations with genetic consequences. Loss of genetic variability in small populations due to inbreeding and genetic drift increases the population probability of extinction (Gilpin and Soule 1986). Fragmentation essentially limits the amount of gene flow between populations.

Roads are often barriers to movement and genetic exchange for bears or other large mammals with wide home ranges (Thompson et al. 2005, Dixon et al. 2006). In the Southeast, secondary and primary roads are considered major fragmenting sources for black bear habitat (Hellgren and Maehr 1992, Brandenburg 1996, Brody and Pelton 1989, Beringer et al. 1990). Primary roads increase the chances of vehicular mortality and fragment contiguous forest types, displacing bears from quality habitat, while secondary roads provide increased access to habitats and lead to exposure to anthropogenic forms of mortality, such as poaching (McLellan 1990). Vander Heyden (1997) determined that female bears were negatively associated with roads and avoided crossing them. However, Brandenburg (1996) found that secondary roads did not appear to inhibit bear movement in coastal North Carolina, and some bears even used secondary roads as nocturnal travel corridors. Bears from the CGP were documented to cross high-traffic highways mainly during activity center shifts that occur during the fall (Cook 2007).

Georgia black bears

Georgia bear distribution

Research projects from the 1970s report densities in northern Georgia ranging from 1 bear per 1013 hectares to 1 bear per 202 hectares, and an increasing population estimate between 900 and 1100 animals (Carlock et al. 1999). Black bears in the northern Georgia population are associated with large areas of forested land and minimal human disturbance, found in 12 counties (Dawson, Fannin, Gilmer, Habersham, Lumpkin, Murray, Pickens, Rabun, Stephens, Towns, Union, and White) of about 657,132 hectares total (Carlock et al. 1999). Bear densities tend to be highest in areas with limited road access. Carlock et al. (1999) also reports densities of approximately 1 bear per 405-809 hectares on the Dixon Memorial State Forest, the Okefenokee Refuge, and privately-owned tracts on the swamp perimeter in Southeast Georgia. This is approximately equal to a range of 610-763 bears. It is speculated that the population declines as increasing distance from the swamp perimeter, based on scent post indices from Abler (1985). Black bears in Southeast Georgia are also associated with forested land and minimal human disturbance, found in Brantley, Charlton, Clinch, Echols, and Ware counties of about 614,133 hectares total (Carlock et al. 1999). Dobey et al. (2005) conducted an additional project in the Okefenokee Swamp using a combination of physical captures and DNA from hair snares. Their estimate was 0.12 bears per km^2 over an area of 593 km^2. Grahl (1985) reported a population estimate of 64 (*sd*=18) bears using the Lincoln Index method for the CGP, which corresponded to a density of 0.323 bears per km^2.

Comparisons from black bear studies across the southeastern United States, including the Georgia populations, may be limited due to a variety of methodologies from sampling and population estimate model assumptions. Specifically, the area and spatial extent inhabited by the

estimated population varies considerably. Interpretation and methods for calculating the area inhabited by the populations varies, and large differences in sample sizes from studies also make comparisons difficult.

Genetic structure of central Georgia population

Bears tend to have low levels of genetic variation because of low population densities and low effective population sizes (Paetkau and Strobeck 1994). These conditions may increase the difficulty of identifying individuals in capture-recapture studies. The southeastern black bear populations tend to be more fragmented than other populations in the United States. Miller (1995) conducted a multilocus DNA fingerprinting study of eight individual populations of *U. a. americanus* (sampled populations from Virginia, Tennessee, South Carolina, Arkansas, Minnesota) and additional populations of *U. a. floridanus* and *U.a.luteolus*. Miller (1995) reported the Ocmulgee River, central GA population (*n*=9 bears from physical captures), had the highest median genetic similarity of 0.82 within the eight sampled populations (Table 1.3). The median band-sharing similarity value between the CGP and Sumter National Forest in South Carolina was 0.45, with Okefenokee National Wildlife Refuge in Georgia was 0.485, and with Apalachicola National Forest in Florida was 0.29 (Table 1.4). This indicates the CGP is more related to itself than other nearby black bear populations. The Georgia population from the Okefenokee National Wildlife Refuge had the lowest within-population genetic similarity, which means it had the greatest genetic diversity within *U. a. floridanus* (Miller 1995).

The genetic status of the CGP is also of conservation interest. Miller (1995) suggested the CGP warranted further genetic investigation, since it lies on the interface between *U.a. americanus* and *U.a. floridanus*. Miller (1995) also suggests that the CGP 'may warrant

protection as a distinct population due to low population size and a high degree of within-population similarity'. Similar protections have been documented for populations of the Florida black bear subspecies, and Louisiana black bear subspecies (Warrilow et al. 2001).

Objectives

The main research objective for the study was to estimate bear abundance in an efficient and accurate manner. An additional objective was to estimate demographic parameters, specifically survival and reproduction, and use these estimates in demographic models to forecast the impact of harvest and project population viability for CGP black bears in Chapter 3 (Figure 1.2). To obtain efficient estimates of abundance within our first objective, we developed hierarchical Bayesian statistical models incorporating three data structures (DNA hair snares, camera traps, and radiotelemetry). The use of DNA hair snares introduces an additional source of error from genetic laboratory error, thus a model incorporating the three data structures and genetic error was developed in Chapter 2.

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Table 1.1. Density estimates for American black bear populations in the Southeastern US. Habitat types include: FW (forested wetland), TRF (temperate rainforest), BHW (bottomland hardwood), UHW (upland hardwood), P (pine), M (mixed), S (swamp), W (open water), F (flatwoods). Data types include: PC (physical captures), C (camera), and DNA (hair snares). Estimation methods include: LP (Lincoln-Petersen), JS (Jolly-Seber), BB (Bailey's binomial), MM (Minta-Mangel), BE (Bowden's estimator), and C (Closed models with program CAPTURE).

Location (Source)	State	Habitat	Study area size (km^2)	Data type	Sampling method (s)	Estimation method (s)	*N*	Density estimate bears/km^2
White River NWR (Smith 1985)	AK	BHW	212	PC		LP, BB	51	0.29 (0.17-0.42)
White Rock (Clark 1991)	AK	UHW, P, BHW	413.7			LP, JS	43	0.08
Dry Creek (Clark 1991)	AK	P, M	517.7			LP, JS	65	0.09
Osceola National Forest (Dobey et al. 2005)	FL	FW, S, F,	309	PC, DNA	1 trap/3.3 km^2	C, JS	78 PC, 37 DNA	0.14

Table 1.1 (continued)

Location (Source)	State(s)	Habitat	Study area size (km^2)	Data type	Sampling method (s)	Estimation method (s)	*N*	Density estimate bears/km^2
Ocmulgee River (Grahl 1985)	GA	P, FW	205	PC		LP	22	0.323
Tensas River Tract (Boersen 2001)	LA	FW, BHW	329	PC, DNA	sampling grid (1 trap/2.70 km^2)	LP, C, JS	42 PC, 58 DNA	0.35
Deltic, Tesas River Basin (Beausoleil 1999)	LA	FW		PC, C	>0.8 km apart with cameras	JS, BB, MM BE	24 PC, 193 C	1.43
Bladen County, Southeastern NC (Hamilton 1978)	NC							0.115

Table 1.1 (continued)

Location (Source)	State(s)	Habitat	Study area size (km^2)	Data type	Sampling method (s)	Estimation method (s)	*N*	Density estimate bears/km^2
Bladen County, Southeastern NC (Hamilton 1978)	NC							0.115
Dare County, Northeastern NC (Hardy 1974)	NC							0.063
Pisgah National Forest (McLean and Pelton 1994)	NC	TRF	114	PC		JS	60	0.211
Alligator River NWR (Allen 1999)	NC							0.86
Gum Swamp (Martorello 1998)	NC	P, HW, M, S	119	PC, C	systematic placement	JS, LP, BB, MM	136 PC, 35 C	1.35
Big Pocosin (Martorello 1998)	NC	P, HW, M, S	149	PC, C	systematic placement	JS LP, BB, MM	77 PC, 29 C	0.53

Table 1.1 (continued)

Location (Source)	State(s)	Habitat	Study area size (km^2)	Data type	Sampling method (s)	Estimation method (s)	N	Density estimate bears/km^2
Camp Lejeune MCB (Brandenburg 1996)	NC	P, HW, beach, wetland, pocosin	250	PC		LP	16	(0.005-0.033)
Great Smoky Mountains National Park (McLean and Pelton 1994)	TN	TRF	506	PC		JS	605	0.292
Cherokee National Forest (McLean and Pelton 1994)	TN	TRF	760	PC		JS	81	0.35
Great Dismal Swamp (Hellgren and Vaughn 1989b)	VA, NC	FW	555	PC		LP, Schnabel, JS, C	101	(0.47-0.68)

Table 1.2. Home range estimates for American black bear populations in the Southeastern United States. Home range estimation methods include: MCP (mimimum convex polygon), MA (maximum area method), HM (harmonic mean), K (95% fixed kernel), AK (adaptive kernel)

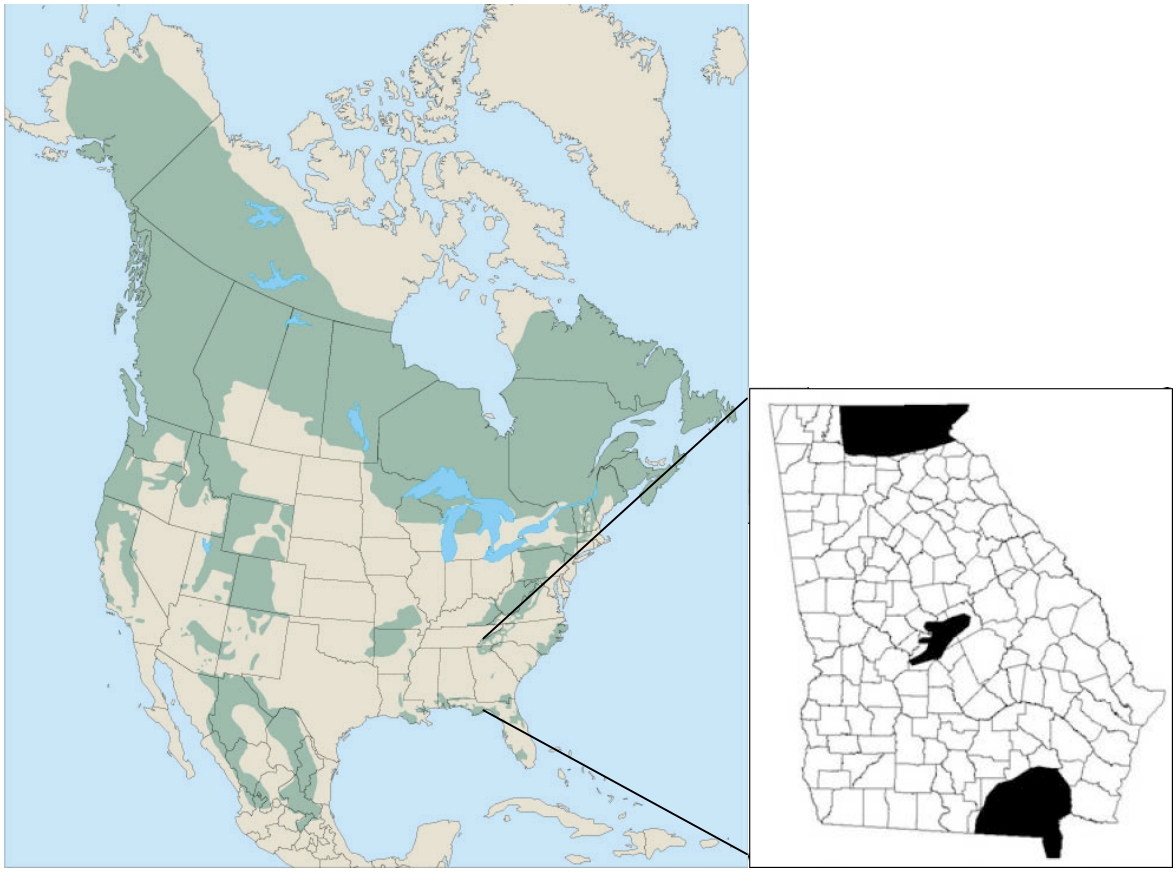
Study (citation)	Estimation method	N_f	N_m	Mean annual home range (M) (km^2)	Mean annual home range (F) (km^2)
White River NWR, AR (Smith 1985)	MCP, MA	9	9	128 (39-266)	11 (7-22)
Deltic, Tesas River Basin (Beausoleil 1999)	MCP,AK,HM	12	5	7,7.1,4.8	4.2, 12.6, 8.1
SC Pickens County (Butfiloski 1996)	MCP	15	7	44.1 (29.7)	16.1 (4.2),16.6 (2.2)
Northern Coastal Plain (Harter 2001)	MCP	10	8		
Central GA (Cook 2007)	K	9	15	195.3 (49.51-352.02)	14.7 (9.8-19.6)
Smoky Mountain National Park (Garshelis & Pelton 1981)	MCP	8	21	21 (13-28)	8 (2-23)
Pisgah Bear Sanctuary, NC (Powell et al. 1997)	K	38	43	44.1 (27.6)	16.9 (11.7)
North GA mountains (Carlock et al. 1983)	MCP	38	20	75	12
White River NWR, AR (Smith & Pelton 1989)	MCP	6	6	116 (39-266)	12 (7-22)
Okefenokee NWR (GA) (Dobey et al. 2005)	K	69	7	336.7 (95.6)	55.9 (6.96)
Osceola NF (FL) (Dobey et al. 2005)	K	53			30.3 (4.0)

Table 1.3. Median band-sharing values for genetic similarities within American black bear populations in the southeastern United States from Miller (1995).

Population	Bear subspecies	*n*	Median band-sharing
Ocmulgee River, GA	*U. a. americanus*	9	0.82
Shenandoah National Park, VA	*U. a. americanus*	16	0.74
Great Smoky Mountains National Park, TN	*U. a. americanus*	7	0.7
Myrtle Beach, SC	*U. a. americanus*	6	0.69
Sumter National Forest, SC	*U. a. americanus*	6	0.67
Ouachita National Forest, AR	*U. a. americanus*	8	0.635
Ozark National Forest, AR	*U. a. americanus*	8	0.63
Cook County, MN	*U. a. americanus*	31	0.57
Mobile River, AL and MS	*U. a. floridanus*	13	0.86
Big Cypress National Park, FL	*U. a. floridanus*	13	0.74
Apalachicola National Forest, FL	*U. a. floridanus*	39	0.73
Ocala National Forest, FL	*U. a. floridanus*	21	0.7
Okefenokee National Wildlife Refuge, GA	*U. a. floridanus*	20	0.69
White River National Wildlife Refuge, AR	*U. a. luteolus*	17	0.81
Tensas River National Wildlife Refuge, LA	*U. a. luteolus*	16	0.78
Lower Atchafalaya River Basin, LA	*U. a. luteolus*	12	0.78
Upper Atchafalaya River Basin, LA	*U. a. luteolus*	11	0.67

Table 1.4. Median band-sharing values for genetic similarities between American black bear populations in the southeastern United States from Miller (1995).

Population 1	Population 2	Bear subspecies	*n*	Median
Shenandoah National Park, VA	Great Smoky Mountains National Park, TN	U. a. americanus	14	0.540
Sumter National Forest, SC	Ocmulgee River, GA	U. a. americanus	12	0.450
Cook County, MN	Ozark National Forest, AR	U. a. americanus	18	0.300
Ozark National Forest, AR	Ouachita National Forest, AR	U. a. americanus	16	0.430
Cook County, MN	Ouachita National Forest, AR	U. a. americanus	18	0.230
Apalachicola National Forest, FL	Ocala National Forest, FL	U. a. floridanus	15	0.600
Apalachicola National Forest, FL	Mobile River, AL and MS	U. a. floridanus	14	0.430
Ocala National Forest, FL	Big Cypress National Park, FL	U. a. floridanus	14	0.640
Ocala National Forest, FL	Okefenokee National Wildlife Refuge, GA	U. a. floridanus	14	0.490
Apalachicola National Forest, FL	Big Cypress National Park, FL	U. a. floridanus	13	0.605
White River National Wildlife Refuge, AR	Tensas River National Wildlife Refuge, LA	U. a. luteolus	13	0.700
Tensas River National Wildlife Refuge, LA	Upper Atchafalaya River Basin, LA	U. a. luteolus	13	0.560
Upper Atchafalaya River Basin, LA	Lower Atchafalaya River Basin, LA	U. a. luteolus	18	0.500



(Pelton 1994) (Carlock et al. 1999)

Figure 1.1. Present distribution of the black bear, based on survey responses from provinces and states (left, from Pelton 1994) and research projects in Mexico (D. Doan, Texas A & I University, personal communication) and reported occupied habitat of black bears in Georgia (right, from Carlock et al. 1999).

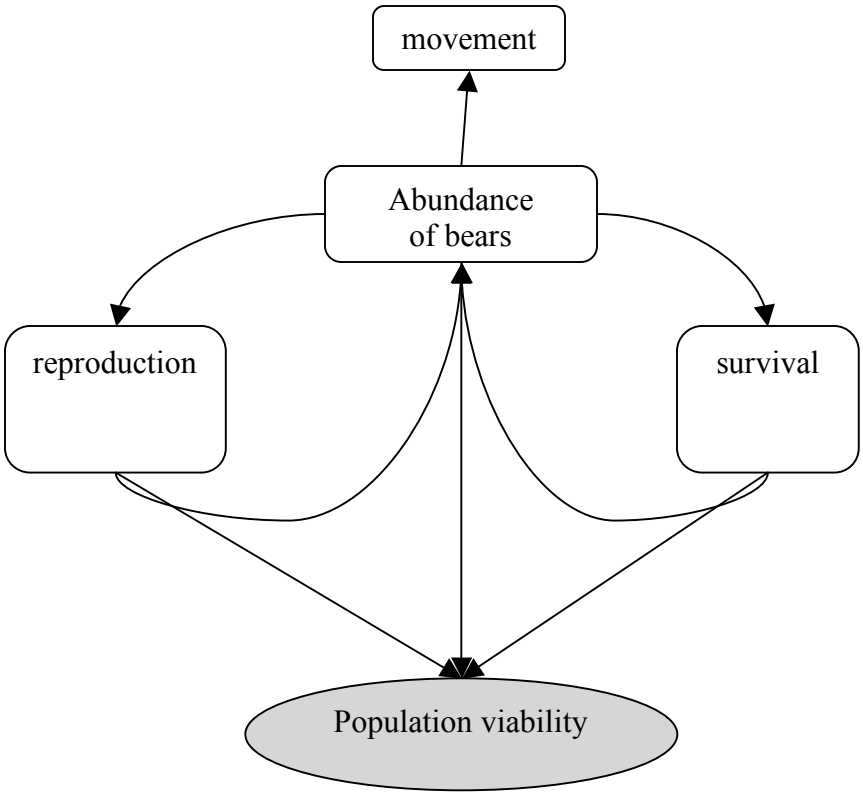


Figure 1.2. Main research objectives with the central Georgia population (CGP) of American black bears. This study focuses on estimating abundance, reproduction, and survival and combining these to make inference on population viability. This diagram also depicts a population flow chart.

CHAPTER 2

DENSITY ESTIMATION USING JOINT DATA STRUCTURES FROM CAMERAS, DNA HAIR TRAPS, AND TELEMETRY[1]

[1] Sanderlin, J. S., M. J. Conroy, et al. To be submitted to Ecology.

Introduction

Estimating demographic parameters of cryptic species, like the black bear, is difficult because of their elusive nature and low densities. Non-invasive sampling methods may be valuable for wildlife studies with consideration of incomplete detection. Often, it is not possible to observe ecological processes directly, and samples from a population or groups of populations are used to make inference on the processes. Hierarchical state-space models provide a way of linking observations from data, such as capture-mark-recapture (CMR) or occupancy samples, to the underlying ecological or state processes (Royle and Dorazio 2008). Hierarchical models can incorporate all components of variance (sampling and biological), incorporate different scales of observation, and provide a way of combining multiple sources of data with common parameters. One of the main goals of this study is to estimate abundance of American black bears (*Ursus americanus*) in central Georgia, USA, using several sources of data. The common parameter of inference between the data sources is abundance in the central Georgia population (CGP) of black bears, which cannot be directly observed. Species abundance is influenced by many biological processes, including habitat relationships, within population processes (*e.g*., density-dependence), and species interactions (*e.g*., Lotka-Volterra models of predator-prey relationships, species competition, mutualisms, and co-evolution).

Field methods for estimating bear density or abundance include: physical captures (Smith 1985, McLean and Pelton 1994, Hellgren and Vaughn 1989), camera detections (Grogan and Lindzey 1999, Martorello 1998, Beausoleil 1999, Mace et al. 1994), tetracycline markers and resighting with harvested bears (Garshelis and Visser 1997), DNA hair snares (Woods et al. 1999, Mowat and Strobeck 2000, Kendall et al. 2008, Kendall et al. 2009), aerial radiotelemetry and mark-resights (Miller et al. 1997), mark-recapture with dogs (Akenson et al. 2001), density

based on bear-sign (Garshelis et al. 1999), and occupancy studies (Boulanger et al. 2008b). Field methods vary in the degree of handling of the animal from invasive to noninvasive and some methods have more rigorous statistical estimation models than others.

Noninvasive methods for sampling bear density include DNA hair snares and the use of remote cameras. Camera trapping is a technique that uses passive encounter data, much like radio telemetry. Animals only need to be handled once at initial capture to mark, while reencounters of those individuals are obtained through photography. With this method, several unmarked bears may revisit a camera site within the same sampling period, which does not allow for individual identification. Because abundance estimation generally requires the ability to individually distinguish individuals, occupancy models (MacKenzie et al. 2006) may be more appropriate when individual encounter histories cannot be distinguished.

Advances within the fields of molecular and genetic biology have increased the ability to use genetic analyses in wildlife studies (Waits 1999). However, the genetic identity obtained with noninvasive genetic techniques may not be as clear (Taberlet et al. 1999, Bonin et al. 2004) and cost-effective as expected. The presence of genetic error (allelic dropout or false alleles) reduces the accuracy of genetic noninvasive techniques. Genetic errors can occur at various steps in a genetic study, e.g., sampling, DNA extraction, molecular analysis, scoring, data analysis, and caused by human or technical error, or biological processes (Bonin et al. 2004). Sampling stochasticity with small amounts of low quality DNA in the laboratory leads to allelic dropout (Goossens *et al*. 1998, Taberlet et al 1999, Woods *et al*. 1999). False alleles can occur with amplification artifacts from PCR (Goossens *et al*. 1998, Taberlet et al 1999, Woods *et al*. 1999).

With improvements in laboratory and field sampling techniques, the use of noninvasive genetic sampling for population monitoring has increased substantially since the methods were

first available. However, there are limited analytical and statistical methods that incorporate multiple noninvasive sampling field methods (such as hair snags and bear rub trees: Boulanger et al. 2008a). Additionally, few statistical methods incorporate genetic error into abundance estimates (but see Wright et al. 2009). If genetic error is ignored, population sizes estimates can be sensitive to genetic error and biased (Creel et al. 2003, Waits and Leberg 2000). Current methods of incorporating genetic error in noninvasive sampling mark-recapture models use maximum-likelihood methods (Lukacs and Burnham 2005, Kalinowski et al. 2006), Bayesian methods (Wright et al. 2009, Petit and Valière 2006), and *ad hoc* approaches (Paetkau 2003, McKelvey and Schwartz 2004). Some approaches also require multiple PCR attempts to assess error (i.e., multiple-tubes approach Taberlet et al. 1996), which increases the cost per sample.

In general, black bears are associated with large areas of forested land in Georgia with densities highest in areas with limited road access (Carlock et al. 1999). There are three populations of black bears in Georgia; one in the northern Georgia mountains, the CGP along the Ocmulgee River, and one in southeastern Georgia. In a preliminary study of the CGP, Grahl (1985) reported a population estimate of 64 (*sd*=18) bears using the Lincoln Index, which corresponds to a density of 0.323 bears per km^2. Thus, a current abundance estimate does not exist for the CGP.

We formulate hierarchical Bayesian statistical models incorporating multiple data structures (e.g., DNA hair snares, camera detections, telemetry), which also account for genetic laboratory error. Estimates from the abundance model will assist with evaluating population viability and harvest impact of the black bear CGP. Therefore, our objective was to estimate bear abundance in an efficient and accurate manner.

Methods

Study Area

The approximate CGP range, estimated by bear sightings and captures, encompasses an area southeast of Macon, Georgia along the Ocmulgee River (~1,200 km^2) falling between the Piedmont and the Upper Coastal Plain physiographic regions. The study area encompassed Ocmulgee and Oaky Woods Wildlife Management Areas (WMAs) in Bleckley, Bibb, Houston, Pulaski, and Twigg Counties, located in central Georgia. The average total annual precipitation is 119.1 cm (estimated from 1966-2003), and the average minimum and maximum temperature is 11.4 °C and 24.8 °C for this region (Georgia Automated Environmental Network 2006). The WMAs consist of a variety of habitat types (pine stands, bottomland hardwood, mixed forest, upland hardwood, black-belt prairie, clearcuts, thinned pine stands, and cypress-gum swamps). Hair snares were placed within the boundaries of Ocmulgee and Oaky Woods WMAs between 2003 and 2006 (Figure 2.1, Figure 2.2, Figure 2.3, Figure 2.4, Figure 2.5, Figure 2.6, Figure 2.7).

Descriptive statistics, such as vegetation associations, slope, and elevation, can be used as habitat covariates with future spatial models of bear density. Therefore, we present a descriptive summary of the sampled web areas. Descriptive statistics were summarized for each web by creating boundaries with a radius distance from the center point of each web to the maximum distance of a hair snare in the outermost ring of each web using BUFFER and MERGE procedures in ArcView® .

Vegetation associations were based on a digital map layer (30- x 30-m resolution; Georgia Gap Project) in ArcView®: vegetation associations were open water, transportation, utility swaths, clearcut/sparse vegetation, deciduous forest, evergreen forest, mixed forest, pasture/hay, row crop, and forested wetland. The webs were summarized by the number of

30x30 m cells classified in each vegetation association out of the total number of cells for each web, to obtain a percent vegetation type for each web (Table 2.1). Webs A, B, C, E, F, H, and I have evergreen forest as the dominant vegetation type. Web D has forested wetland as the dominant vegetation type and web G has mixed forest as the dominant vegetation type. Webs A, B, C, and I have evergreen forest as the dominant vegetation type and forested wetland as second dominant vegetation type. Similarly, webs E, F, and H can be grouped together for the two dominant vegetation types. In summary, webs on Oaky Woods WMA (A, B, I) are very similar in vegetation classification, while webs on Ocmulgee WMA (C, D, E, F, G, H) are more diverse. Web D is less like the other webs according to vegetation classification.

The slope, or maximum rate of change in elevation, from each cell to its neighbors in each web was calculated from the topographic map data. The output slope grid theme in ArcView® represents the degree of slope (e.g., 3 degree slope) for each cell location. Summary statistics for the slope of the webs were calculated (Table 2.2). The Digital elevation model (DEM) measured in meters above sea level was also used to describe the webs. Summary statistics for the DEM of webs were calculated (Table 2.3). The following arbitrary groupings can be made based on mean slope: group 1 (A and I), group 2 (B, C, E), group 3 (D, F, H). Webs A and D had the highest range in slope (indicating more variation in topography), while E and H had the lowest range in slope. The following arbitrary categorical groupings can be made based on mean elevation above sea level (meters): group 1 (A, E, I), group 2 (B, G, H), group 3 (C, F), and group 4 (D). Webs A, G, and I had the highest range in elevation (indicating more variation in meters above sea level), while H had the lowest range in elevation.

Field methods

Bears were captured and immobilized with a 2:1 mixture of ketamine hydrochloride (Ketaset) and xylazine hydrochloride (Rompun) at a dosage of 4.4 mg/kg of Ketaset and 2.2 mg/kg of Rompun, for estimated body weights by Georgia Department of Natural Resources personnel. Bears were captured in the study area using Fremont foot trap snares (Fremont 1986) in each of four trapping seasons, which extend from May through August each year. Culvert traps were used to trap nuisance bears and release the bears on Oaky Woods WMA. An upper pre-molar tooth for age estimation by cementum annuli analysis (Willey 1974), blood samples, and hair follicles were collected from each captured bear. Sectioning, staining, and aging of teeth were conducted by Matson Laboratories (Milltown, Montana). All bears were uniquely marked using a combination of collars, lip tattoos, and ear tags/streamers. Pertinent physiological data were recorded for each captured bear. Most bears were fitted with Advanced Telemetry Systems (Isanti, MN) radio transmitter collars (VHF, very high frequency) equipped with mortality signal sensors and motion sensors and four male bears received radio collars that contained Global Positioning technology and a mortality switch. All collars fitted to bears during the project were equipped with either a mechanical timer release (GPS) or a degradable release tab (VHF).

Barbed wire enclosures designed to obtain hair samples from individual bears entering the devices (Woods et al. 1999) were placed on Oaky Woods and Ocmulgee WMAs using trapping web arrays. A trapping web consists of lines with regularly spaced traps, which radiate from a central point, and has higher densities of traps or hair snares in the center (Anderson et al. 1983) (Figure 2.8). Nine trapping webs were placed in randomly selected locations covering most of the WMAs. Each trapping web consisted of 27 hair snares with three snares at the

center, and eight spokes, three rings, covering an area of ~ 7 or 16 km^2, depending on the location in the WMAs (Table 2.4). Web size was based on average female home range size in the CGP and average daily movement of bears (Cook 2007). Some webs had fewer snares if the web extended to private residences, or if the area was actively logged, burned, or flooded (so that the realized numbers of snares per web ranged from 22 to 35). In some cases, hair snares were placed outside but near web perimeters to monitor movement of individuals into the trapping web. Actual snare locations were recorded with Universal Transverse Mercator (UTM) coordinates (North American Datum 1987, Zone 17) using global positioning system (GPS) receivers using Garmin GPS units (Garmin International, Inc., Olathe, KS).

Hair snares in the trapping webs were monitored at least one primary period, and maximum of two primary periods from May to December, which consisted of three secondary sessions at 6-9 day intervals, with two to three simultaneously active webs considered to be independent from the other active webs. Some webs were monitored for two primary periods each year (2004, 2005, 2006). Within a primary period, the population is closed to births, deaths, immigration and emigration. The population from 1 April to 1 September (Summer), or from 1 September to 10 December (Fall) for each year is closed from births, deaths, immigration, and emigration. This summer primary period corresponds to the main trapping period the DNR used to capture and fit radiocollars to bears. The Robust Design (Pollock 1982) was used to allow for future analysis of combined estimated of abundance from closed periods and survival between open periods for the population. The Robust Design assumes the time period between primary periods is open to births, deaths and movement, and secondary periods, or short intervals within a primary period are assumed closed (Pollock 1982). Secondary periods from 6-9 days are replicated samples within the closed primary periods of each season. The Robust Design has the advantage of

sampling at two different temporal scales, which lead to more robust estimation of parameters, especially capture probability (Pollock 1982).

Barbed wire (4 point, 15.5 gauge) strands were placed 25 cm and 50 cm from the ground around 3-5 trees (10-30 m^2) and baited with corn in a perforated plastic bottle sprayed with anise oil (Figure 2.9). Irregularities in terrain, leading to high or low wire, were adjusted with debris on the ground. Each tree was flagged with brightly colored tape for public safety. Hair samples were removed from barbed wire with tweezers and placed into manila coin envelopes. Date, location, sample number, and strand (top or bottom) were recorded on each envelope. For the season of Summer 2005 and thereafter, area (defined as a group of hair samples in an area big enough for one bear to pass through) was also recorded as additional stratification of hair samples. The barbed wire and tweezers were sterilized between samples using a lighter for one to two seconds or until visible hairs were removed. A hair sample consisted of a sample on one barb on either the top or bottom strand, or two adjacent barbs on a strand. In cases of three adjacent barbs with hair, two samples were collected in arbitrary order (one barb in one sample, two adjacent barbs in the other). If there were no samples with more than 10 hairs, hair samples (one to nine hairs) with visible roots were collected. Hair samples from other species were also noted during each session.

Digital cameras utilizing a passive infra-red trigger system were used to monitor bait stations for marked or unmarked bears. Fifteen cameras were randomly placed among active webs at snare locations with a higher density of cameras at the center of a web, or near web perimeters. Cameras were secured to trees that are 3-5 m from the hair snare and aimed at the hair snare or 100 m from the web perimeter. Pictures from each camera were stored on digital memory cards and downloaded for analysis. Memory cards also stored the date and time of each

picture. Cameras in or near the trapping webs were monitored for three sessions at six to nine-day intervals, with charged batteries and memory cards replaced every session. The number of bear pictures and other species' pictures were recorded for each session. Pictures of unmarked bears taken two minutes between each picture were considered to be the same individual if physical characteristics are similar. Marked bears were individually identified if marks could be read.

Any time at least one hair snare within a web was baited the web was considered an active web. Active webs were monitored at least once a day, weather permitting, for bears with radiocollars. Pre-determined road routes that encircle and bisect the web were used to scan for all signals with a receiver and a whip antenna (Advanced Telemetry Systems, Isanti, MN) from vehicles during daylight and some night hours. The routes were selected to ensure that an observer would be able to detect a bear if the bear was in or near the web at least once during the route. A three-element yagi antenna (Advanced Telemetry Systems, Isanti, MN) was used to determine the direction of the collar in the field. If there was uncertainty whether the bear was in or out of the web, telemetry locations were estimated by the line that bisects the angle between two directions where the signal can just be heard (Kenward 1987). The azimuths were between 60º and 120º apart and collected within 20 minutes to increase accuracy of azimuth measurements. The azimuth range is best for triangulation purposes (White and Garrott 1990) and the short time period reduces the chance of large bear movements. If an observer was on the edge or outside of the web, and the direction of the bear was opposite the web, only one azimuth was obtained. If a bear were in the web, an observer would often be able to detect its frequency more than once during the web scan route. Locations of observers were recorded in Universal

Transverse Mercator (UTM) coordinates using global positioning system (GPS) receivers from Garmin GPS units (Garmin International, Inc., Olathe, KS).

Telemetry error was estimated using test collars placed throughout the webs in the study area. Webs were chosen to represent common topographic and vegetation conditions from the entire study area (see Tables 2.1, 2.2, 2.3 for vegetation data, elevation, and slope representation of each web). In all cases, locations of test collars were unknown to the observer. Web telemetry error was calculated for 10 observers (three from fall 2004, three from summer 2005, one from fall 2005, three from summer 2006). A separate telemetry data set was analyzed using two observers from summer 2004 from Cook (2007). One collar was placed in two to six webs in Oaky Woods and Ocmulgee WMAs during 2004-2006 (Table 2.5). Azimuths were obtained at five pre-selected stations at varied distances from the collars (0.2-2 km). Azimuth stations were repeated three times on separate days with summer and fall 2005, 2006 observers. Telemetry error was calculated as difference in the observed from the true azimuth based on observer location at a station and the known location of the test collar. Telemetry error, with telemetry observations of bears, will be used to determine if a bear is present in a web during the time periods when hair snares are baited.

Laboratory Methods

At least one hair sample per hair snare, web, session, season, and year occasion was selected for analysis, based on visual inspection of quality (i.e., visible roots with skin cells) and quantity (10 hairs). Additional samples were randomly selected, with more weight given to hair snares with more hair samples, to increase the chances of identifying additional unique bears. If possible, other areas or sections of the hair snare were selected than the original sample for the

additional samples. This follows the assumptions that: 1) more hair samples at a hair snare might lead to more individual bears, and 2) individual bears may leave hair samples in different locations at a hair snare. The sub-sampling technique aims to capture more unique individuals in the population. If only high-quality samples were selected, some hair snare, web, session, season, and year occasions would not be selected, which may bias population estimates (i.e., some bears may consistently leave lower quality samples than others). Budget and time constraints also precluded analyzing all hair samples.

After field collection, hair samples were stored in silica desiccant then transferred to a -20° C freezer. Prior to extraction and after field collection, blood and tissue samples were also stored in a -20° C freezer. Extraction of DNA from Georgia tissue samples was done with the DNeasy Kit (QIAGEN) and with one captured bear blood sample using the GenomicPrep DNA isolation kit (GE Healthcare). DNA from hair samples were extracted with Chelex100 (10% solution) (Promega), along with proteinase K (Phenix Research Products, QIAGEN) used for protein digestion that may inhibit PCR reactions (modified from Boersen 2001). The root portion (1 cm) from a maximum of 10 hairs per sample were cut and placed into 150 μl of Chelex 100 (10% solution) (Promega). The number of hairs and quality of sample were recorded. If the number of hairs was less than 10, the entire strand of hair was used in the sample. Low quality samples had little or no visible roots, and usually consisted of under-fur (thin) hairs. Medium quality samples were classified as samples with half of the hairs with roots visible and some guard hairs. High quality samples were classified by a majority of the hairs as guard hairs with most or all of the roots visible, and including visible skin cells. After roots were placed in the 10% solution Chelex 100 (Promega), 10 μl proteinase-K was added to digest excess protein. The hair samples were incubated at 65° C overnight (~8 hours). Samples were vortexed, and then

boiled at 100° C for 10 minutes. After removal, the samples were centrifuged at 10,000-12,000 rpm for 3 minutes. The supernatant was pulled off and placed into a clean tube, and stored at -20° C until PCR analysis.

PCR amplifications were performed in 10 μL volumes using Bio-Rad MyCycler thermal cyclers for both tissue and hair samples with 8 tetranucletide loci (UA-BM3-P1F04, UA-BM4-P1H06, UA-BM4-P2B06, UA-BM4-P2C10, UA-BM3-P1D05, UA-BM4-P2A06, UA-BM4-P2B08, and BM4-P2C02, hereafter named Bear 10Y, Bear 12Y, Bear 17G, Bear 19Y, Bear 30B, Bear 33B, Bear 35G, and Bear 36, respectively) previously described in Sanderlin et al. (2009). Loci Bear 10Y, Bear 12Y, Bear 17G, Bear19Y, Bear 30B, Bear 33B, and Bear 35G were directly labeled primers with the dyes NED (Y), HEX (G), and FAM (B). For comparison with known individuals from the CGP, eight microsatellite markers developed by Paetkau and Strobeck (1994) and Paetkau et al. (1995) were initially used for individual identification: G1A, G1D, G10B, G10C, G10L, G10M, G10P, and G10X. Final concentrations for optimizing reactions with unlabelled primers were 10 mM Tris pH 8.4, 50 mM KCl, 0.5 μM "pigtailed" primer (Brownstein 1996), 0.05 μM CAG or M13-reverse tagged primer (CAG or M13-reverse + primer), 0.45 μM dye labeled tag (HEX or FAM + CAG or M13-reverse), 1.5 mM $MgCl_2$, 0.5 mM dNTPs, 0.5 U Ampli*Taq* Gold DNA Polymerase (Applied Biosystems), and 50 ng DNA. Final concentrations for optimizing reactions with directly labeled primers were 10 mM Tris pH 8.4, 50 mM KCl, 0.5 μM upper directly labeled primer, 0.5 μM lower directly labeled primer, 1.5 mM $MgCl_2$, 0.5 mM dNTPs, 0.5 U Ampli*Taq* Gold DNA Polymerase (Applied Biosystems), and 50 ng DNA. We ran reactions using one touchdown thermal cycling program (Don et al. 1991), encompassing a 10.5 ^{o}C span of annealing temperatures (range: 60-49.5 ^{o}C).

For tissue samples, cycling parameters were: 21 cycles of 96° C for 20 s; highest annealing temperature for 30 s minus 0.5° C per annealing cycle; and 72° C for 1 min 30 s followed by 14 cycles of 96° C for 20 s; 50° C, for 30 s; 72° C for 1 min 30 s; and a final extension period of 10 min. at 72° C. For hair samples, cycling parameters were: 20 cycles of 96° C for 20 s; highest annealing temperature for 30 s minus 0.5° C per annealing cycle; and 72° C for 1 min 30 s followed by 30 cycles of 96° C for 20 s; 50° C, for 30 s; 72° C for 1 min 30 s; and a final extension period of 10 min. at 72° C. We checked PCR products for amplification and sized fragments using a 3730*xl* DNA sequencer (Applied Biosystems) with GENESCAN Rox500 fluorescent size standard (PE Applied Biosystems). Results were analyzed using GENEMAPPER software (Applied Biosystems) using the local Southern size-calling method.

Statistical methods

Observed and expected heterozygosity were calculated for each locus from the observed unique individual genotypes collected from hair snares using Cervus 2.0 (Marshall et al. 1998). GENEPOP 3.4 (Raymond and Rousset 1995) was used to test for genotypic linkage disequilibrium with *a posteriori* sequential Bonferroni correction to correct for multiple comparisons of markers (Rice 1989). The α level of significance is divided by the number of comparisons between markers to reduce pseudoreplication. The probability of identity (P_{ID}), or the probability that 2 randomly chosen individuals in a population will have identical genotypes (Paetkau and Strobeck 1994) was calculated over all loci with the observed unique individual genotypes collected from hair snares using the following formula:

$$\sum_i p_i^4 + \sum_i \sum_{j>i} (2 p_i p_j)^2 \qquad \text{(Equation 2.1)}$$

where p_i and p_j are the frequencies of the ith and jth alleles. The more conservative estimate with P_{IDsib}, or the probability of identity among siblings (Evett and Weir 1998), was also calculated using the following formula:

$$0.25 + (0.5\sum p_i^2) + [0.5(\sum p_i^2)^2] - (0.25\sum p_i^4)$$

(Equation 2.2)

where p_i is the frequency of the ith allele. The inbreeding coefficient, or within population heterozygote deficit (F_{is}), for the Paetkau and Strobeck (1994) and Paetkau et al. (1995) markers and Sanderlin et al. (2009) markers of known individuals was calculated using program FSTAT (Version 2.9.3) (Goudet 1995).

A minimum number of bears for each year (2003-2007) was calculated from known bears with radiocollars, and other captures of bears that were not marked. The unmarked bears from dead recoveries were also included. This information can be combined with the number of bears with radiocollars to obtain a minimum known number of bears per year (alive+dead).

We use a condensed version of telemetry data for model simplification in the full Bayesian model, described in the next section. Raw telemetry data consist of observations from radiocollared bears detected during vehicular travel with radio-equipped vehicles. Pre-determined routes encompassed, bisected, and were near the webs during sampling sessions. When a bear was detected during the vehicular scan, ground telemetry observations, including azimuths (angle from observer to bear), elevation above sea level, and level of gain, were conducted. Observer sampling error with telemetry may influence and bias conclusions of presence or absence of bears within a web with raw telemetry data, therefore this error should be included within the modeling procedure. The probability of presence in a web for each bear

observation was simulated from the combination of: 1) observer location points, and 2) estimates of azimuth error from spatial distributions of telemetry sampling error. The number of simulated locations in the web out of total number of simulated locations (n=10,000) was used as an estimate of the probability of the bear in the web for each bear and day observation in a secondary period. If this probability exceeded 0.50, the bear was classified as present ('1', and '0' otherwise) for that observation. Data were collapsed to a period of three weeks, with the assumption that the population was closed during the three-week sampling period for each web. Therefore, if a bear was detected at least once in a web over the three-week period, it was classified as a detection on that web.

The predicted true azimuth direction was simulated as the sum of the observed angle plus one draw from the von Mises distribution to simulate error in observer azimuth direction. The von Mises distribution is often used with circular data, like azimuth directions with possible values encompassing 360° (for example, see Figure 2.10). The probability density function of the von Mises distribution takes the following form:

$$\phi(\theta) = [2\pi \mathrm{I}_0(\kappa)]^{-1} e^{\kappa \cos(\theta - \mu_0)}$$

(Equation 2.3)

where the angles θ and μ_0 are between $-\pi$ and π, and standard deviation κ is greater than zero, and $\mathrm{I}_0(\kappa)$ is the modified Bessel function of the first kind and order. The predicted azimuth direction is:

$$\widehat{\theta} = \theta_{obs} + vonMises(\overline{\theta}_{error}, s^2)$$

(Equation 2.4)

The predicted distance from the observer to the bear was modeled from known distances to collars and recorded gain levels.

$$\hat{d} = \beta_0 + \beta_1 * gain + error$$

(Equation 2.5)

The full Bayesian Markov-Chain Monte Carlo (MCMC) models of the joint data structures were implemented using a combination of Gibbs and Metropolis sampling algorithms. Monte Carlo refers to estimation by simulation. Markov chains are a special type of stochastic process, where the future depends on the current state, but not past states. This is known as the 'Metropolis algorithm' first described by Metropolis and Ulam (1949) and Metropolis et al. (1953). Markov chains have the following properties of homogeneity, irreducibility, recurrence, stationarity, and ergodicity. Homogeneity is when the transition probabilities are independent of time. Irreducibility refers to a non-zero probability of reaching a state from any other state in the chain. States can be repeatedly selected with the property of recurrence. The marginal distribution is produced when multiplied by the transition kernel with stationarity. Ergodicity means that after many steps the marginal distribution of a Markov chain is the same at one step as all other steps.

The Metropolis algorithm was later generalized by Hastings (1970), and labeled as the Metropolis-Hastings algorithm. This special case of the Metropolis algorithm generates candidate state transitions from an alternative distribution, and uses an acceptance/rejection rule to converge to the specified distribution. The Metropolis algorithm uses a symmetric jumping distribution, while the Metropolis-Hastings algorithm is not limited to symmetry with the jumping distribution. The algorithm steps are listed below, following notation and summary of algorithm steps from Gelman et al. (2004).

1. First, select a starting point for parameter, θ^0, from either a starting distribution or reasonable initial values.
2. For t=1,… :

a) Sample a proposed value of the parameter, θ^*, from a jumping distribution at time t.

b) Calculate the ratio of densities or likelihoods of the parameter given y data as follows,

$$r = \frac{p(\theta^* \mid y)}{p(\theta^{t-1} \mid y)} \qquad \text{(Equation 2.6)}$$

c) Generate a uniform random variable, and accept the proposed value, θ^*, with probability min(r,1), and the previous value, θ^{t-1}, otherwise

Convergence to the target distribution with the Metropolis algorithm occurs because the sequence is a Markov chain with a unique stationary distribution and the stationary distribution equals the target distribution (Gelman et al. 2004). The Metropolis algorithm is useful for models that are not conditionally conjugate, i.e., the full conditional distribution kernels are not known distributions. However, the Metropolis algorithm can be slow. The Gibbs sampling algorithm offers a relatively fast alternative and is only appropriate for full conditionals that are kernels of known distributions.

Gibbs sampling, first named by Geman and Geman (1984), utilizes conditional distributions, where each parameter is conditioned on current values of the other k-1 parameters. By cycling through each parameter, conditioned on the current values of the other parameters, samples from the posterior distribution are generated.

To illustrate the scenarios in which Gibbs sampling would be useful, versus Metropolis-Hastings, here are two examples. First, consider a scenario where the likelihood the data given

the parameter is a binomial distribution, and the prior on p, the probability of success, is a beta distribution. The full conditional distribution of p is below:

$$[p \mid \bullet] \propto \binom{n}{\theta} p^{\theta}(1-p)^{n-\theta}\, p^{\alpha-1}(1-p)^{\beta-1} \propto p^{\theta+\alpha-1}(1-p)^{n-\theta+\beta-1} \quad \text{(Equation 2.7)}$$

This is the kernel of a Beta distribution with parameters $\theta+\alpha$ and $n-\theta+\beta$. This is an example of when Gibbs sampling would make sense, since the posterior can be directly sampled. However, consider the same binomial likelihood, but that p is constrained to the following form:

$$p = 1-(1-r)^{a} \quad \text{(Equation 2.8)}$$

So, the full conditional distribution of p is now:

$$[p \mid \bullet] \propto \binom{n}{\theta} (1-(1-r)^{a})^{\theta}(1-(1-(1-r)^{a}))^{n-\theta} \quad \text{(Equation 2.9)}$$

This does not have a known distributional form, thus Metropolis sampling from the posterior is the only option.

Reversible jump MCMC (RJMCMC) was also used for posterior simulation of parameters in the joint data structure model. Reversible jump MCMC was first introduced by Green (1995), and is useful when the dimension of the parameter space has a possibility of changing from one iteration to the next. The Markov chain samplers can jump between parameter subspaces of differing dimensionality in RJMCMC (Green 1995).

For each model, two chains of 50,000 iterations each and a burn-in period of 25,000 iterations were run with Python, version 2.5.2 (Python Software Foundation, http://python.org). No thinning interval was used. Each chain was selected from different combinations of initial parameter values to evaluate parameter convergence. The posterior iterations after the burn-in period from each chain were combined for output statistics and figures. The output for each

model included the median, 95% Bayesian credible interval (BCI), and histograms and traces of the posterior distributions. A full simulation study was conducted to assess model performance (Appendix A).

Statistical model

State-space models include both measurement and process error (Royle and Dorazio 2008). This is useful when multiple data sets are collected for inference on abundance, such as the following model incorporating three data structures of camera, telemetry and DNA hair snare data (refer to Table 2.6 for complete description of model notation, Figure 2.11). The biological motivation, assumptions for statistical distributions, and updating of parameters for the individual data components are described below, followed by the full Bayesian statistical model.

Spatial parameters of local abundance, N_i

We assume the true abundance distribution in the superpopulation follows a Poisson-Gamma process, where λ, the Poisson parameter, is the local density of bears and α and β, the Gamma parameters, control the amount of variability in abundance across the landscape. Due to low local abundance, and perhaps low sample size, the Poisson model may be more relevant to the study, thus efforts were focused on this less complex, null, model. However, we present the more complex model first, followed by the model used for this analysis. The Poisson distribution is often used to model count data, such as abundance, and allows for extra-Poisson variation in abundance, or overdispersion. The Poisson-Gamma process is used to control for local heterogeneity in abundance. Heterogeneity in local abundance can be a function of habitat covariates, environmental factors, or other unknown sources. The Poisson-Gamma process,

reparameterized as a negative binomial, has been used in ecological studies (Royle and Nichols 2003, Conroy et al. 2008).

The mixture of Poisson distributions that follow the gamma distribution results in a marginal distribution for N_i following a negative binomial distribution with parameters α and β (Gelman et al. 2004). Consider the vector of abundance $\{N_i\}$, i=1,…m, and the local density, $\{\lambda_i,\}$ i=1,…m. The spatial joint distribution of the data $\{N_i\}$, and the parameters λ_i, α, β is:

$$[\{N_i\},\lambda_i, \alpha, \beta]= [[\{N_i\}|\lambda_i][\lambda_i|\alpha, \beta][\alpha][\beta] \quad \text{(Equation 2.10)}$$

These are, respectively, Poisson, Gamma, and Gamma hyperprior distributions for α and β. Also, ν and ω are the parameters of the Gamma hyperprior distribution for α and δ and η are the parameters for the Gamma hyperprior distribution for β. Putting this together we get:

$$[\{N_i\},\lambda_i,\alpha,\beta] = \prod_{i=1}^{m}[\{Ni\}\mid\lambda_i]\prod_{i=1}^{m}[\lambda_i\mid\alpha,\beta] \propto \prod_{i=1}^{m}\left\{\frac{\lambda_i^{N_i}e^{-\lambda_i}}{N_i!}\right\}\prod_{i=1}^{m}\frac{\beta^{\alpha}}{\Gamma(\alpha)}\lambda_i^{\alpha-1}e^{-\beta\lambda_i}\frac{\omega^{\upsilon}}{\Gamma(\upsilon)}\alpha^{\upsilon-1}e^{-\omega\alpha}\frac{\eta^{\delta}}{\Gamma(\delta)}\beta^{\delta-1}e^{-\eta\beta}$$

(Equation 2.11)

To sample directly from the posterior distribution using Gibbs sampling, we must first derive the full conditional distributions. The full conditional distributions for the spatial parameters are:

$$[\lambda_i\mid\bullet] \propto \frac{\lambda_i^{N_i}e^{-\lambda_i}}{N_i!}\frac{\beta^{\alpha}}{\Gamma(\alpha)}\lambda_i^{\alpha-1}e^{-\beta\lambda_i} = \frac{\beta^{\alpha}}{N_i!*\Gamma(\alpha)}\lambda_i^{N_i+\alpha-1}e^{-\beta\lambda_i-\lambda_i}$$
$$\propto \lambda_i^{(N_i+\alpha)-1}e^{-\lambda_i(\beta+1)} \quad \text{(Equation 2.12)}$$

This is the kernel of the known Gamma distribution with parameters $N_i+\alpha$ and $\beta+1$, so the

posterior distribution can be sampled directly using Gibbs sampling. For the parameter α, the full conditional is:

$$[\alpha \mid \bullet] \propto \prod_{i=1}^{m} \frac{\beta^{\alpha}}{\Gamma(\alpha)} \lambda_i^{\alpha-1} e^{-\beta\lambda_i} \frac{\omega^{\upsilon}}{\Gamma(\upsilon)} \alpha^{\upsilon-1} e^{-\upsilon\alpha}$$
$$\propto \left[\frac{\beta^{\alpha}}{\Gamma(\alpha)}\right]^{m} \left[\prod_{i=1}^{m} \lambda_i^{\alpha-1}\right] e^{-m\omega\alpha-\beta\sum_{i=1}^{m}\lambda_i} \alpha^{\upsilon-1} \qquad \text{(Equation 2.13)}$$

This is not a known distribution, and requires the Metropolis-Hastings algorithm to sample from the posterior distribution. For the parameter β, the full conditional is:

$$[\beta \mid \bullet] \propto \prod_{i=1}^{m} \frac{\beta^{\alpha}}{\Gamma(\alpha)} \lambda_i^{\alpha-1} e^{-\beta\lambda_i} \frac{\eta^{\delta}}{\Gamma(\delta)} \beta^{\delta-1} e^{-\eta\beta}$$
$$\propto \beta^{m\alpha+m\delta-m} e^{-m\eta\beta-\beta\sum_{i}^{m}\lambda_i} \qquad \text{(Equation 2.14)}$$
$$\propto \beta^{(m\alpha+m\delta-m+1)-1} e^{-\beta(m\eta+\sum_{i}^{m}\lambda_i)}$$

This is a kernel of the known Gamma distribution with parameters ($m\alpha$+$m\delta$-m+1) and $(m\eta+\sum_{i=1}^{m}\lambda_i)$, so the posterior distribution can be sampled directly using Gibbs sampling.

If we assume local abundance is determined by only one density parameter, λ, the process is reduced to a Poisson process. The conjugate prior density for a Poisson process is the Gamma distribution (Gelman et al. 2004). Following Gelman et al. (2004), the posterior distribution for density, λ, is a Gamma distribution, which can be directly sampled from using Gibbs sampling:

$$[\lambda \mid \bullet] \sim Gamma(\alpha + \sum_{i=1}^{m} N_i, \beta + m) \ , \qquad \text{(Equation 2.15)}$$

where α and β are the parameters from the Gamma prior distribution, and m is the number of total possible webs. We chose a diffuse prior, a Gamma(0.001, 0.001), for the distribution.

Telemetry parameter

Telemetry data provides inference on the presence of a bear in a web, commonly referred to as occupancy, ψ, or the probability that a patch or sampling unit is occupied (MacKenzie et al. 2006). We are not directly estimating the probability of a patch occupied, but rather the number of bears in a patch. This can be used to indirectly estimate occupancy, where $N_i>0$ means the probability that a patch is occupied is one. The telemetry component consists of:

$$[\{V_{ik}\} \mid p_{w_i}, V][\{N_i\} \mid p_{w_i}][p_{w_i}], \qquad \text{(Equation 2.16)}$$

where V is the telemetry data consisting of the number of total bears collared during the year and season over all three sessions or occasions, and the individual bears detected on each web i (described below). The likelihood of the number of true bears on a web, N_i, given the total bears in a population, N_{tot}, and the probability of a bear on a web, p_{wi}, can be classified as a binomial distribution, or a series of independent Bernoulli trials where each trial is a bear with probability p_{wi} of being on the web. Similarly, the number of bears with collars on a web, $n_{collared,i}$, given the total number of bears with collars on during the sampling period, $N_{collared}$, can also be classified as a binomial distribution, with each bear with a collar having probability p_{wi} of being present on a web. This assumes that bears with and without collars have the same probability of being on a web. The conjugate prior for binomial distributions is a beta prior on the probability of a bear on a web. The full conditional distribution of the probability of a bear on a web, $p_{wi,}$ includes the product of two binomial distributions and a Beta(1,1) prior on the probability of a bear on a web:

$$[p_{w_i} \mid \bullet] \propto \binom{N_{collared}}{n_{collared,i}} p_{w_i}^{\,n_{collared,i}} (1-p_{w_i})^{N_{collared}-n_{collared,i}} \binom{N_{tot}}{N_i} p_{w_i}^{\,N_i} (1-p_{w_i})^{N_{tot}-N_i} p_{w_i}^{\,\alpha-1} (1-p_{w_i})^{\beta-1}$$

$$\propto p_{w_i}^{\,n_{collared,i}+N_i+\alpha-1} (1-p_{w_i})^{N_{collared}-n_{collared,i}+N_{tot}-N_i+\beta-1},$$

(Equation 2.17)

where $n_{collared,i}$ is the number of bears with collars on web i, $N_{collared}$ is the total number of bears with collars on during the sampling period, N_i is the number of true bears on web i, N_{tot} is the total bears the population, and α and β are the parameters for the beta prior on $p_{w,i}$. This is a kernel of a Beta distribution with parameters: $n_{collared,i}+N_i+\alpha$ and $N_{collared}-n_{collared,i}+N_{tot}-N_i+\beta$. Posterior prediction of p_w on webs not sampled is conducted by using a Beta ($N_j+\alpha$, $N_{tot}-N_j+\beta$).

Camera parameters

We used a model that links abundance and heterogeneous detection probabilities, known as the Royle-Nichols model (Royle and Nichols 2003) with the camera data. The probability of detecting occupancy d_i with the camera samples is a transformation of the individual probability of camera detection, r, and N_i, the abundance of bears on web i:

$$[d_i] = 1 - (1 - r)^{N_i} \qquad \text{(Equation 2.18)}$$

The probability of individual detection from cameras is assumed constant among bears and among webs. The conditional distribution of camera detections, Y_i, on web i, given the probability of detection, d_i, follows a binomial sampling model, where each camera is an independent Bernoulli trial of bear detection:

$$[Y_i \mid d_i] = \binom{j}{y_i} d_i^{Y_i} (1 - d_i)^{j - Y_i}, \qquad \text{(Equation 2.19)}$$

where j is the total number of cameras or sites on web i. Additionally, we assume that detection does not vary by occasion k, so j is condensed data consisting of the number of camera by occasion replicates in web i, and y_i is the number of bear detections over all cameras*occasions in web i in one season.

The conditional probability of occupancy, d_i, is a deterministic function of the stochastic r and N_i parameters. The full conditional distribution of r is:

$$[r \mid \bullet] \propto \prod_{i=1}^{w} \binom{j}{Y_i} (1-(1-r)^{N_i})^{Y_i} (1-r)^{N_i(j-Y_i)} \qquad \text{(Equation 2.20)}$$

This does not factor into a known distribution, and requires the Metropolis-Hastings algorithm for updating r from the posterior distribution (See Appendix B for details of algorithm).

Genetic data parameters

This component of the joint data structure model is based on the genetic error model with allelic dropout originally in Wright et al. (2009), with the exception of the calibration sample component. The calibration sample data consists of genotypes of tissue and/or blood, and hair samples from known individuals from the bear CGP, as originally described in Sanderlin (2009). The tissue samples are of higher quality with a lower probability of error than the hair samples, and can be used in conjunction with replicated hair samples from unknown individuals.

Dropout error probability, p

For true heterozygotes ($A_{il1} \neq A_{il2}$), where A is the allele at locus l for individual i, the probability of observing a true heterozygote is 1-p, while the probability of observing a homozygote is 0.5*p, since there are 2 ways that an allele can drop out. Following Wright et al. (2009), therefore, the probability of an observed genotype given the true genotype is as follows:

$$\Pr(G_{jlr}^{obs} \mid \mathcal{G}_{jl}) = \begin{cases} 1-p_l & A_{il1r}^{obs} \neq A_{il2r}^{obs} \\ 0.5p_l & A_{il1r}^{obs} = A_{il2r}^{obs} \end{cases} \qquad \text{(Equation 2.21)}$$

Since we are only considering allelic dropout, the probability of observing a homozygous individual at locus l, replicate r, given that the true individual at locus l is homozygous, is 1.

We assume that the calibration sample ($t=1,\ldots T,$ for tissue and blood samples and $h=1,\ldots H,$ for hair samples) is independent of the replicated hair samples from unknown individuals and that the allelic dropout probability is the same within the calibration samples and the replicated hair samples. Using the conjugate beta prior for allelic dropout of a binomial distribution, the error likelihood is the product of the two binomial likelihoods and beta prior. Following notation from Wright et al. (2009):

$$[G^{obs},C^{obs} \mid G,C,N,p] = \prod_{j=1}^{S}\prod_{l=1}^{L} I(G_{jl1} \neq G_{jl2}) \prod_{r=1}^{R}\left(\frac{p}{2}\right)^{I(G_{jl1r}^{obs}=G_{jl1r}^{obs})} (1-p)^{I(G_{jl1r}^{obs}\neq G_{jl1r}^{obs})}$$
$$\prod_{t=1}^{T}\prod_{l=1}^{L} I(C_{jl1} \neq C_{jl2}) \prod_{h=1}^{H}\left(\frac{p}{2}\right)^{I(C_{jl1r}^{obs}=C_{jl1r}^{obs})} (1-p)^{I(C_{jl1r}^{obs}\neq C_{jl1r}^{obs})} p^{\alpha}(1-p)^{\beta-1} \quad \text{(Equation 2.22)}$$

This reduces to a Beta($\alpha+w+w_c$, $\beta+W+W_c$) distribution, where w and w_c are the number of times the heterozygous loci originally seen in tissue/blood samples of the calibration sample or the samples, were genotyped as homozygous in any of R replicates. W and W_c are the total number of heterozygous loci across all n individuals that appeared in one of the S samples. Since this is a kernel of a known distribution, the posterior distribution of allelic dropout can be sampled using Gibbs updates.

True genotype matrix, G, and true sample histories, X

The true genotype matrix and true capture histories are updated using direct sampling, following Wright et al. (2009) (See Appendix C for a full description of how these matrices are updated). The true genotypes are updated by a combination of the error likelihood described above, and the probability of observing the specific genotype, given the true genotype frequencies in the population. The true sample histories are updated with the capture-history likelihood of proposed capture histories of compatible individual genotypes and the probability

of observing the observed genotype given the true genotype and error probability. Both sequences of updating require inserting proposed values of either the genotype at a specific locus and individual (genotype matrix), or proposed values of capture histories (capture history matrix) and evaluating the likelihood of the proposed values compared to other possible values.

Genotype frequencies, γ

Following Wright et al. (2009), the genotype frequencies are the kernel of the joint distribution of L independent Dirichlet random variables with parameters $\{y_{kj}+\alpha_{kj}\}$ of dimension l_j. Using uninformative priors, α_{kj}, of 1, the full conditional distribution of vector $\boldsymbol{\gamma}$ is:

$$[\underline{\gamma} \mid \bullet] = \prod_{j=1}^{L} \prod_{k=1}^{l_j} \gamma_{kj}^{y_{kj}+\alpha_{kj}-1} \qquad \text{(Equation 2.23)}$$

For a complete description of how these parameters are updated and derived, see Appendix C.

Capture probability from DNA hair snares, θ

Capture variation in closed mark-recapture models can be classified into three main categories: 1) heterogeneity (M_h), where each individual animal has a different probability of capture, or measurable individual attributes (e.g, group or individual covariates) 2) behavior (M_b), where animals captured have different probabilities of capture than animals not captured, either trap-happy or trap-shy, and 3) time (M_t), where capture probability can vary over trapping sessions (Pollock 1974, Otis et al. 1978, White et al. 1982). For the models presented in this chapter, the constant capture probability (M_0) over time, behavior and heterogeneity, and web was selected to reduce model complexity. However, there is evidence of behavior and time in

capture heterogeneity from closed capture models that assume no genetic error (see Appendix D for this analysis). Therefore, future models will include more complexity.

To update the constant capture probability after the genotype and capture history matrices are updated, the sufficient statistics of $u.$, or the unique number of individuals captured with DNA hair snares, and $n.$, the total number of times these individuals were captured over the three trapping occasions with DNA hair snares, are used. Capture mark-recapture (CMR) data consists of a series of independent Bernoulli trials, or animals, with probability of capture, θ. The full conditional likelihood of constant capture probability, using the conjugate Beta(1,1) prior for a binomial distribution is:

$$\begin{aligned}[\theta \mid \bullet] &\propto \frac{N_w!}{(N_w - u.)!}\theta^{n\cdot}\ (1-\theta)^{k(N_w)-n\cdot}\theta^{\kappa-1}(1-\theta)^{\upsilon-1} \\ &\propto \theta^{n.+\kappa-1}(1-\theta)^{kN_w-n.+\upsilon-1}\end{aligned}, \qquad \text{(Equation 2.24)}$$

where $n. = \sum_{i=1}^{w}\sum_{k=1}^{3} n_i$, or the total number of captures over the webs sampled for all three occasions, N_w is the true abundance of bears with webs sampled, k is the number of trapping occasions, and κ and υ are the capture probability priors. This is the kernel of a Beta distribution with parameters $n.+\kappa$ and $kN_w - n.+\upsilon$, thus the posterior distribution of θ can be sampled directly using Gibbs sampling.

Abundance of sampled areas (N_i)

The full conditional distribution of abundance on sampled areas (N_i) is the joint distribution of the three data structures and the spatial model of N. The full conditional likelihood is a combination of one Poisson from the spatial component, and two binomials from the camera and telemetry components, respectively, and a negative binomial from the genetic CMR data.

We also use a discrete uniform prior on N_i, with a lower limit of max($u_{\cdot i}$, $n_{collared,i}$, '1' if Y_i>0), and upper limit is the total number of genotype combinations of individuals over all loci. The full conditional likelihood is:

$$[\{N_i\} \mid \bullet] = \prod_{i=1}^{m} [\{Y_{ijk}\} \mid r, N_i][\{N_i\} \mid p_{w_i}][\{N_i\} \mid \lambda_i][\mathcal{G} \mid N_i, \gamma][X_{ik} \mid N_i, \theta_{ik}][\{N_i\}]$$

$$\propto \prod_{i=1}^{w} \left\{ \frac{\lambda_i^{N_i} e^{-\lambda_i}}{N_i!} \right\} \binom{j}{Y_i} (1-(1-r)^{N_i})^{Y_i} (1-r)^{N_i(j-Y_i)} \binom{N_{tot}}{N_i} (p_{w_i})^{N_i} (1-p_{w_i})^{N_{tot}-N_i} \frac{N_i!}{(N_i-u_{\cdot i})!} \theta^{n_{\cdot i}} (1-\theta)^{k(N_i)-n_{\cdot i}}$$

$$\propto \prod_{i=1}^{w} \left\{ \frac{\lambda_i^{N_i} e^{-\lambda_i}}{N_i!} \right\} \binom{j}{Y_i} (1-(1-r)^{N_i})^{Y_i} (1-r)^{N_i(j-Y_i)} \binom{N_{tot}}{N_i} (p_{w_i})^{N_i} (1-p_{w_i})^{N_{tot}-N_i} \frac{N_i!}{(N_i-u_{\cdot i})!} (\pi_0)^{N_i-u_{\cdot i}}$$

(Equation 2.25)

where π_0 is the probability of not being captured at least once over the three occasions (i.e., $\pi_0 = (1-\theta)^3$). A sequential update of N_i was used, where N_{tot} of the current accepted N_i s were used in N_{tot} from the telemetry portion, or probability of a bear on a web. The Poisson distribution with the current value of λ was used for posterior prediction of abundance for webs not sampled with the less complex spatial model. However, a negative binomial with updated spatial parameters of α and β (described in equations 2.9 and 2.10), would be used for posterior prediction of abundance on webs not sampled with the Poisson-gamma spatial model.

Based on the dimension of a proposed value of N^*, the genotype matrix G and the capture-history matrix are augmented (Tanner and Wong 1987) by N^*- N rows. Following Wright et al. (2009), the genotype matrix is augmented by sampling genotypes directly from multinomial distributions [$\mathcal{G}|\gamma$], with the constraint that the sampled genotype is not present in the population currently. The capture-history matrix is augmented with rows of zeros. If N^*<N, values must be deleted from the genotype and capture-history matrix. These individuals cannot appear in any of the observed samples. This joint full conditional for N is not a known

distribution and could potentially change matrix dimensions. Therefore, a reversible jump Metropolis-Hastings step is needed to update N (see Appendix B for details of the Metropolis-Hastings algorithm).

Unconditional population estimate of abundance

We want the unconditional estimate of abundance of bears in the target population of inference in central Georgia. The target population of inference encompasses the total area in which webs were sampled (see Figure 2.7). The minimal inference population is the WMA land (186 km^2), which includes both Ocmulgee and Oaky Woods, while the maximal inference population is the estimated range of black bears in central Georgia (~1200 km^2, Cook 2007). For this chapter, we will focus on the minimal inference population of the WMA land. This can be labeled the 'superpopulation'.

We have sample observations related to N_i under our sampling protocol, not $N_{tot,}$ where i is the individual web and *tot* is the superpopulation. Therefore, we must obtain posterior predictions of abundance from unsampled areas within the inference population from the heterogeneity parameters of abundance on sampled areas. One may assume random selection of webs, however, this is not entirely correct due to limitations of land ownership and other attributes of the WMA boundaries (rivers, roads, highways) that do not permit placement of web arrays. Our sample is part of the total set of possible web-sized areas in the inference population, or more formally:

$$N_{i=1,\ldots w} \cup N_{i=w+1,\ldots m},$$

where w is the total number of webs sampled and m is the total number of possible webs in the population area. The unconditional abundance of the superpopulation over all possible webs,

N_{tot}, is the sum of abundance over all sampled webs plus the predicted abundance from posterior simulation for unsampled webs using the Poisson-Gamma spatial model (described above) in the population range.

$$[N_{tot} \mid \bullet] \sim \sum_{i=1}^{w} N_i + \sum_{j=w+1}^{m} N_j, \qquad \text{(Equation 2.26)}$$

where w is the total number of webs sampled, m is the total number of possible webs in the population area, and *tot* refers to the superpopulation.

Full Bayesian model of joint camera, telemetry, and DNA hair snare data structures

The joint distribution of camera detection data $\{Y_{ijk}\}$, capture histories at hair snares $\{X_{ik}\}$, telemetry data $\{V_{ik}\}$, observed genotypes from DNA hair snares $\{G_{ikr}^{obs}\}$, and genetic calibration sample data $\{C, C^{obs}\}$ is:

$$[\{Y_{ijk}\},\{V_{ik}\},\{G_{ikr}^{obs}\},\{C\},\{C^{obs}\},\{X_{ik}\},\{N_i\},d_i,r,p_{w_i},p,G_{ikr},\mathcal{G},\gamma,\theta,\lambda,\alpha,\beta] =$$
$$\prod_{i=1}^{m}[\{Y_{ijk}\} \mid d_i][d_i \mid r,N_i][\{V_{ik}\} \mid p_{w_i},V][p_{w_i} \mid \{N_i\},N][\{N_i\} \mid \lambda_i][\lambda_i \mid \alpha,\beta][C_{obs} \mid p,C][G_{obs,ikr} \mid G_{ikr},p]$$
$$[\mathcal{G} \mid N_{tot},\gamma][X_{ik} \mid N_i,\theta][r][p][\alpha][\beta][\underline{\gamma}][\theta][N_i] \qquad \text{(Equation 2.27)}$$

where i is the individual web, k is the number of sessions or occasions, and m is the total number of web areas. Bayes theorem allows us to obtain the probability of abundance on web i, given the bear is on web i, from the probability that the bear is on web i, given the true number of bears on web i:

$$[p_{w_i} \mid \{N_i\}] = \frac{[\{N_i\} \mid p_{w_i}][p_{w_i}]}{[\{N_i\}]} \propto [\{N_i\} \mid p_{w_i}][p_{w_i}]$$

(Equation 2.28)

This leads to the joint distribution, where the only difference between Equation 2.28 and Equation 2.29 is the double underlined portion from the Equation 2.28 reverse conditioning:

$$[\{Y_{ijk}\},\{V_{ik}\},\{G_{ikr}^{obs}\},\{C\},\{C^{obs}\},\{X_{ik}\},\{N_i\},d_i,r,p_{w_i},p,G_{ikr},\mathcal{G},\gamma,\theta,\lambda,\alpha,\beta] =$$

$$\prod_{i=1}^{m}[\{Y_{ijk}\} \mid d_i][d_i \mid r,N_i][\{V_{ik}\} \mid p_{w_i},V]\underline{\underline{[\{N_i\} \mid p_{w_i}][p_{w_i}]}}[\{N_i\} \mid \lambda_i][\lambda_i \mid \alpha,\beta][C_{obs} \mid p,C][G_{obs,ikr} \mid G_{ikr},p]$$

$$[\mathcal{G} \mid N_{tot},\gamma][X_{ik} \mid N_i,\theta][r][p][\alpha][\beta][\underline{\gamma}][\theta][N_i] \qquad \text{(Equation 2.29)}$$

The Python code for the full model can be found in Appendix E.

Results

Data summary

Over 6 seasons from years 2003 to 2006, a total of 32 ‘webs’ (note: webs were sampled more than once, since there were 9 actual webs), or 830 hair snares were actively checked. A total of 4,180 hair samples over 2516 snare sessions (dates which a snare was ‘active’) were collected (Table 2.7). The number of snares with at least one hair sample was 1113. Some of these samples could contain feral hog hair, but not all samples were analyzed in the genetics laboratory. Some snares were not sampled for all three sessions due to river flooding or controlled burns, therefore the number of snares multiplied by three does not always equal the number of snare sessions

The total number of hair samples selected for genetic analysis was 1,487. These hair samples were collected at hair snares from 2003-2006, over six sample seasons. Of the 1487 hair samples selected, 1041 samples (70.0 %) had positive amplification for at least one locus. Of the 1041 samples with positive amplification for at least one locus, 42.7 % amplified at all 8 loci

selected for genetic identification (*n*=445). The samples that amplified at 7 loci (*n*=57) and 6 loci (*n*=66) could plausibly be used in further capture-recapture models. Models presented in this chapter only include samples with amplification at 8 loci. The samples with 6 and 7 loci with positive amplification have different probabilities of identity, and may match multiple samples that have information at all 8 loci.

Hair samples (*n*=203, or 19.5% of the total 1041 samples) were randomly selected from the hair samples that positively amplified for at least one locus to assess the genetic error in the DNA extraction, PCR, genotyping, scoring/binning of alleles, and database storage process. This process involved the selection of different hairs (but from the same physical sample as the initial sample) for DNA extraction, and may assess any mixed-sample errors. Samples were given a new genetic tag and treated as new hair samples in the whole process from extraction to scoring and database storage. Of the 203 hair samples selected for this assessment of genetic error, 180 samples (88.7 %) positively amplified for at least one locus. Additional samples (*n*=23, or 5.2% of the total 445 samples) were randomly selected to assess the PCR and re-genotyping error (not DNA extraction) from the samples that amplified at all 8 loci. This also involves scoring/binning of alleles and database storage of Genemapper data. There were six allelic dropout (ADO) events detected over all eight loci with the calibration data set, originally described in Sanderlin (2009) from known individuals (*n*=84) (Table 2.8). For the heterozygous samples from the first replicates with hair snare samples, the number of samples classified as homozygous with the second replicates varied over the following years and seasons: 2004 summer (*n*=16 samples), 2004 fall (*n*=9 samples), 2005 summer (*n*=29), 2005 fall (*n*=5), 2006 summer (*n*=5) (Table 2.8).

During 2003-2006, the number of camera samples of bear detections was 181 (note: individual cameras were used multiple times since there were only 15 physical cameras, and not all webs were monitored at the same time) with 530 camera sessions, or number of weeks in which the cameras were active and able to take photographs. There were 180 cameras with at least one picture of a bear (Table 2.9). Some cameras were not operational for all 3 sessions due to equipment failure, camera availability, or bear damage; therefore, the number of cameras multiplied by three does not always equal the number of camera sessions.

A total of 84 bears (53 M: 31F) were physically captured from 2003 to 2006. There were 16 recaptures (10 M: 6 F) from 2003 to 2006. There were a total of 14 recoveries of captured bears (12 M: 2 F). This summary includes the Sandersville male and North Carolina female bears, three untagged male bears (2003, 2004), one untagged female bear (2006), and two capture mortalities (one initial in 2004, one recapture in 2004) (2.10). Capture coordinates for initial and recaptured bears for 2003, 2004, 2005, and 2006 were spread out over the WMAs and surrounding land (Figures 2.12, 2.13, 2.14, 2.15, 2.16).

Telemetry error

The mean absolute value of telemetry error over all webs, observers, and years was 18.9 degrees, based on 360 stations from 10 observers (Figure 2.17). An analysis of variance (ANOVA) indicated no difference among azimuth error between years (df=1, p=0.929), observers (df=8, p=0.101), and webs (df=5, p=0.443) with an α significance level of 0.05.

Genetics

Tissue and blood samples from 83 bears (81 captured bears from 2003-2006, one capture mortality and one unmarked bear from a vehicle collision) were analyzed to determine if markers were adequate. The summaries reported here do not include the translocated female from North Carolina, known to be a non-resident of the central Georgia population. Seven of the eight loci amplified in at least one individual with the Paetkau markers. One locus, G10C, did not amplify well with any sample, so it was excluded from further genetic analyses. The observed number of alleles, number of heterozygotes and homozygotes are summarized, along with allele frequency distribution (Table 2.11) and the mean number of alleles observed per locus for the individuals that amplified was 2.25.

The North Carolina bear had unique alleles at the following Paetkau loci: G1A, G1D, G10L, G10P, G10X. Loci G1D and G10P were fixed in the central Georgia population with a sample of 82 and 78 known bears, respectively. Linkage disequilibrium tests with the Paetkau markers indicated that in central Georgia one loci pair (G1A vs. G10X, p=0.0004) had probability values smaller than the sequential significance level of 0.000476. Only one locus (G10M) had evidence of nonrandom mating (α=0.05) for the bears in central Georgia with the Hardy-Weinberg equilibrium test (refer to the p-values in Table 2.12). The overall probability of identity for all loci that amplified at 83 known bears from the central Georgia population was 0.00157, or 1 chance in 600 of randomly sampling 2 bears possessing identical genotypes. The probability of identity among siblings, or the more conservative estimate, was 0.051, or 1 in 20 chance of encountering matching genotypes in central Georgia among siblings.

There were 38 bears with unique genotypes, and 45 bears with overlapping genotypes, or matching genotypes with the loci that amplified with the 7 Paetkau loci. This does not

necessarily mean those 45 bears have matching genotypes, since not all loci amplified. There were no bears that had identical genotypes with the new Sanderlin et al. (2009) markers with the sample of 84 known bears from this analysis, which is a substantial proportion of the population for any specific year.

The overall inbreeding coefficient (F_{is}) was 0.165 for the CGP known individuals (n=83) using all of the Paekau markers, indicating an excess of heterozygotes with these markers. The overall F_{is} value for the CGP with all of the new markers and known individuals (n=84) was -0.019, compared to an overall F_{is} value of 0.010 with the CGP hair samples from hair snares (n=184 unique individuals), which show a small deficit and excess of heterozygotes, respectively.

For known individuals (n=84) with the new Sanderlin et al. (2009) markers, the observed number of alleles, number of heterozygotes and homozygotes are summarized, along with allele frequency distribution (Table 2.13) and the mean number of alleles observed per locus for the individuals that amplified was 3.75. Linkage disequilibrium tests with the Sanderlin et al. (2009) markers with known individuals indicated that in central Georgia no loci pairs had probability values smaller than the sequential significance level of 0.000435. No loci had evidence of nonrandom mating (α=0.05) for the bears in central Georgia with the Hardy-Weinberg equilibrium test (refer to the p-values in Table 2.14). The overall probability of identity for all loci that amplified at 84 known bears from the central Georgia population was 1.38×10^{-5}, or 1 chance in 72,500 of randomly sampling 2 bears possessing identical genotypes. The probability of identity among siblings, or the more conservative estimate, was 0.00547, or 1 in 200 chance of encountering matching genotypes in central Georgia among siblings.

Over all years from 2003 to 2006, a total of 184 unique individuals were identified from the observed genetic data from hair snares from the samples with data for all 8 loci (Table 2.15, Table 2.16). The observed number of alleles, number of heterozygotes and homozygotes are summarized, along with allele frequency distribution (Table 2.18) and the mean number of alleles observed per locus for the individuals that amplified was 5.38. Three loci (Bear17G, Bear36, Bear30B) had evidence of nonrandom mating (α=0.05) for the bears in central Georgia with the Hardy-Weinberg equilibrium test after Bonferroni correction (refer to the *p*-values in Table 2.19). The overall probability of identity for all loci that amplified with hair samples from central Georgia population was 1.31×10^{-5}, or 1 chance in 76,500 of randomly sampling 2 bears possessing identical genotypes. The probability of identity among siblings, or the more conservative estimate, was 0.00555, or 1 in 200 chance of encountering matching genotypes in central Georgia among siblings with these hair samples.

Error rates from joint model

The allelic dropout rates varied from season and year. In general, the allelic dropout rate decreased with newer samples and was greater in the summer than fall seasons. Summer 2004 had a median posterior estimate of allelic dropout rate over all loci of 0.052 (95% BCI: 0.034-0.076). Fall 2004 had a median posterior estimate of allelic dropout rate over all loci of 0.039 (95% BCI: 0.023-0.062). Summer 2005 samples had a median posterior estimate of allelic dropout rate over all loci of 0.076 (95% BCI: 0.054-0.102). Fall 2005 samples had a median posterior estimate of allelic dropout rate over all loci of 0.030 (95% BCI: 0.016-0.050). Summer 2006 had a median posterior estimate of allelic dropout rate over all loci of 0.027 (95% BCI: 0.014-0.045).

Population Size

The minimum number of bears known to be alive was calculated from bears with telemetry collars (Table 2.17). Using data from unmarked, but known-fate bears and live-captures of unmarked bears, the total known number of bears in the population per year, alive or dead, was also summarized (Table 2.17).

The median posterior abundance estimates of black bears from the WMAs for the CGP were higher in the summer compared to the fall seasons between 2004 and 2006 (Table 2.20, 2.21, 2.22, 2.23, 2.24). Summer 2004 had the highest median posterior abundance estimate of black bears out of all the seasons sampled with an estimate of 213 (95% BCI: 144-354) (Figure 2.18); however, all seasons had Bayesian credible intervals that covered all other Bayesian credible intervals. The lowest median posterior estimate of abundance of black bears out of all the seasons was in the Fall 2004 with an estimate of 106 (95% BCI: 72-179) (Figure 2.19). The other seasons had median posterior estimates of abundance of 184 (95% BCI: 137-266) (Figure 2.20), 131 (95% BCI: 91-207) (Figure 2.21), and 192 (95% BCI: 143-280) (Figure 2.22) for Summer 2005, Fall 2005 and Summer 2006, respectively.

In general, the constant CMR capture probabilities from DNA hair snares were low over all seasons (Tables 2.20, 2.21, 2.22, 2.23, 2.24), although the last two seasons had higher capture probabilities than the other seasons. The individual animal detection probabilities from camera data were consistently high over all seasons and years (Tables 2.20, 2.21, 2.22, 2.23, 2.24).

Discussion

Suitability of genetic markers

In general, bears tend to have low levels of genetic variation because of low population densities and effective population sizes (Paetkau and Strobeck 1994). These conditions may

increase the difficulty of uniquely identifying individuals in genetic capture-recapture studies. The Paetkau bear markers used in many other bear research studies were evaluated for the central Georgia population. These markers are known to be polymorphic in many bear populations, ranging from the southeastern U.S. to the northeastern and western United States, and even in other species, such as Brown bears (*Ursus arctos*) and polar bears (*Ursus maritimus*). Seven of the eight loci amplified, with only five of seven polymorphic. Thus the genotype at those two loci was identical for all bears sampled and varied at the remaining five loci. However, not all bears could be evaluated at all seven loci, due to low amounts of DNA in the samples or other laboratory inconsistencies. The number of bears, 84 from central Georgia, is a substantial sample of the population, thus similar genotypes are likely not due to a low sample size. Sampled bears from successive years, however, may be related, which could decrease the diversity seen in these samples.

The North Carolina bear had unique alleles at five out of the seven loci with the Paetkau markers and three of the eight loci with the Sanderlin et al. (2009) markers, which indicates there is a difference between residents and non-residents of the central Georgia population. This may also mean that the central Georgia bear population has low genetic diversity with these loci. The mean number of alleles observed, 2.25, is much lower than other bears in the southeastern U.S. using the same bear markers (Okefenokee Swamp ranged from 5-8 alleles per locus, Dobey et al. 2005, Tensas River National Wildlife Refuge, LA from Warrillow et al. 2001, mean=3.75). This supports the possibility of a population bottleneck in central Georgia. However, the new tetranucleotide markers had a higher average number of alleles per locus of 5.38 compared with the Paetkau markers. This number is comparable to other bear populations in the southeastern U.S.

There is evidence of linkage disequilibrium, even after sequential Bonferonni correction for one locus pair with the Paetkau markers but none with known individuals using the Sanderlin et al. (2009) tetranucleotide markers. The *p*-value (0.0004) is close to the predetermined significance level of 0.000476, so this should not be a big concern. There also was no evidence of non-random mating for this population with the tetranucleotide loci used in the current analysis. Of particular concern were the calculations of the overall probability of identity and probability of identity among siblings. That is, 1 chance in 500 of randomly sampling two bears possessing identical genotypes, and 1 in 18 chance of encountering matching genotypes in central Georgia among siblings with the five polymorphic loci with the Paetkau markers. These estimates of P_{ID} were inadequate for sampling a population with noninvasive techniques, since the ability of distinguishing individuals was so poor. Estimates of P_{ID} are theoretical in nature, thus, are not always accurate estimates of true P_{ID}(Waits et al. 2001). Waits et al. (2001) found that observed values of P_{ID} were much higher than the calculated theoretical values of P_{ID}. This happens if there is population substructure, non-random mating, many related individuals in the sample, or past events that disrupt Hardy-Weinberg equilibrium. Often, if these scenarios are present with a population, one is unable to detect it until a large number of samples are collected. These results provided impetus behind developing new markers for the bear population. The new tetranucleotide markers had 1 chance in 76,500 of randomly sampling two bears possessing identical genotypes, and 1 in 200 chance of encountering matching genotypes in central Georgia among siblings with the eight polymorphic loci used for the hair snare analysis.

None of the known individuals had identical genotypes with the new tetranucleotide markers, compared to only 38 bears with unique genotypes using the Paetkau markers. Since 84 known bears is a large sample, and likely a high percentage of the total number of individuals in

the population at any one time, the higher $P_{ID,sib}$ for the new tetranucleotide markers may not be a problem for the CGP. This provides evidence that noninvasive genetic methods were a valid sampling method for the CGP using the new tetranucleotide markers, despite lower genetic variability and allele counts.

Genetic error

There was an increase in genetic error from allelic dropout with older samples. Older samples tend to have more error and/or less DNA amplification success. Therefore, minimizing delays (<six months) between collection and DNA extraction maximizes amplification efforts (Roon et al. 2003). The DNA extraction of older samples occurred at the same time as newer samples, which increased the time between collection and extraction of older samples (>six months of between collection and extraction). DNA tends to degrade with time, and in particular with exposure to moisture or UV light (Lindahl 1993, Piggot 2004). Genetic error was also greater in summer than fall. Central Georgia experience hot and humid conditions in the summer, much more than the fall. Some noninvasive genetic studies document that warmer seasons have increased genetic error or reliability (Lucchini et al. 2002, Piggot and Taylor 2003). For example, wolf samples that were collected in the winter had higher-quality DNA than samples collected in the summer, or older samples (Lucchini et al. 2002).

Capture probability with DNA hair snares

The probability of detection for a black bear is influenced by several behavioral traits. Male black bears have a greater chance of encountering bait stations or being sited due to increased travel distances and large home ranges; and as a result, a greater chance of being

captured than female black bears (Hellgren and Vaughan 1989). However, we cannot distinguish between male and female bears in our sampling scheme. Noninvasive methods aim to reduce bias in capture rates with female and young age classes of bears. Depending on the capture method used, detection also may depend on age, with juveniles and cubs being less likely to be captured than adults. But, Kendall et al. (2009) document a substantial proportion of cubs and yearlings known to be present near DNA hair snares for Brown bears. Family groups, consisting of parent-offspring and siblings traveling together, are also a large source of nonindependent movement in bear populations (Kendall et al. 2009). Although, simulation studies indicate that this will cause minimal bias in population estimates (Miller et al. 1997, Boulanger et al. 2004). The current model also does not explicitly account for time, behavioral, or heterogeneity effects that may be present. There may indeed be time and behavioral capture effects with this population (Appendix D), which warrant further models.

Population estimates

Fall abundance estimates were lower than summer abundance estimates. This pattern is consistent with the cub mortality period, post-reproduction. The abundance estimates incorporate all age classes, although specific age classes cannot be determined through DNA hair traps. Telemetry data only captures presence of adult bears on webs. We can approximate the proportion of cubs in samples with hair and camera traps at the same location with camera occupancy data, which may warrant future development. The minimum estimates of abundance are well below the estimates of abundance from the joint data structure model, which should be expected. The abundance estimates presented in this chapter are for the WMA land only, and not for the entire region of central Georgia. Future models should include more information on the

spatial relationship to habitat (i.e., CAR models) and bear abundance, for posterior prediction of abundance on unsampled areas. These preliminary estimates should be used as initial estimates of abundance in population viability models and harvest decisions and additional management decisions.

Future models

The trapping web sampling design used in this study of the CGP is an extension of point transects and allows density to be directly estimated using Distance sampling methods (Anderson et al. 1983). Future models can incorporate Distance sampling methods in the joint full Bayesian model incorporating three data structures. The trapping web design also allows us to obtain estimates of capture-mark-recapture (CMR) data, as well as density estimates, which may improve estimates. The current model does not allow for bear movement among webs, which may occur within sampling periods. Thus, a movement model for individual bears from one sampling occasion to the next (i.e. random walk, average movement rates for females/males) could improve the probability of being on a web and telemetry portion of the model. Camera data do have additional information that could provide inference on abundance, rather than occupancy, such as the identity of individuals with collars, sex and/or age of unmarked individuals, and the minimum and maximum number of marked and unmarked bears.

Models that exclude areas that are predicted as unlikely to be occupied based on habitat models (Cook 2007) would improve estimates as well. The current model only includes WMA land. The current spatial Poisson model can be classified as a 'null' model for the CGP, where there is simply random variation of abundance, from one Poisson distribution, across the landscape. The next step would be to include the Poisson-Gamma process, which allows for

extra variation, or overdispersion, in abundance where each web would have a separate density parameter. This model does not explicitly include habitat covariates (i.e., distance to roads, vegetation characteristics, percent diversity in habitat, distance to rivers) that may influence species abundance. Conditionally autoregressive models (CAR) (e.g., Carlin and Banerjee 2003) provide a method of linking abundance to habitat covariates that likely exist with any animal population. CAR models, originally described by Besag (1974) are the fundamental regional cluster models. The proportional hazards portion of the CAR model assumes observed counts, *Y*, in a region *i* follow a spatial Poisson regression of the following form:

$$Y_i \mid \mu_i \sim Po(E_i e^{\mu_i}), \qquad \text{(Equation 2.30)}$$

where $\mu_i = \underline{x_i}'\underline{\beta} + \theta_i + \phi_i$ and E_i is expected number of occurrences in the region, x_i is a vector of region-level spatial covariates with the vector of parameter coefficients, $\underline{\beta}$ (as seen in Carlin and Banerjee 2003). The univariate spatially random variable, Φ_i, from equation 2.31, like survival of one animal species in region *i*, has a full conditional distribution of the following form:

$$\phi_i \mid \phi_{j \neq i} \sim N(\bar{\phi}_i, \frac{1}{\lambda n_i}), \qquad \text{(Equation 2.31)}$$

where $\bar{\phi}$ is the average of the neighboring values and *n* is the number of neighbors at region *i*

A gamma prior, with parameters α and β, is typically assumed for λ (Carlin and Louis 2000). Regional heterogeneity, θ_i, from equation 2.30, would be modeled as a random effect with an exchangeable normal prior (as seen in Carlin and Banerjee 2003):

$$\theta_i \overset{iid}{\sim} N(0, \frac{1}{\tau}) \qquad \text{(Equation 2.32)}$$

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Table 2.1. Percent of vegetation type for each web for the American black bear central Georgia population from 2004 to 2006 based on 30m x 30m resolution.

Web	A	B	C	D	E	F	G	H	I
Open water	0.0008	0.000109	0.009818	0.00248	0.004416	0.002243	0.004386	0.013868	0.000117
Transportation	0.0844	0.068481	0.061705	0.047919	0.026865	0.067476	0.066199	0.066842	0.058934
Utility swaths	0.0023	0	0	0.018007	0	0.017347	0.012147	0.028983	0.013915
Clearcut	#0.1530	#0.127398	0.061979	#0.113349	0.035083	0.105204	0.112153	0.065178	#0.080917
Deciduous	0.1216	0.081926	0.02545	0.053723	0.056428	0.066882	0.082327	0.057412	0.040926
Evergreen	*0.4025	*0.45543	*0.427326	**0.287465	*0.499387	*0.430051	**0.28315	*0.387602	*0.657858
Mixed forest	0.0537	0.122588	#0.083041	0.021082	**0.171001	**0.239958	*0.312639	**0.259603	0.041394
Pasture/hay	0	0	0	0	0.004416	0.006992	0.005398	0.001387	0
Row crop	0.0005	0.000492	0.069493	0.006945	0.096663	0.063848	0.121601	#0.119124	0.00152
Forested Wetland	**0.1809	**0.14292	**0.261079	*0.44903	#0.105741	#0.158565	#0.256967	0.06601	**0.10442

* indicates dominant vegetation type, ** indicates second dominant vegetation type, # indicates third dominant vegetation type

Table 2.2. Slope summary statistics (range, mean, standard deviation) for each web for the American black bear central Georgia population from 2004 to 2006.

Web	A	B	C	D	E	F	G	H	I
Range	13.5613	10.5547	10.9184	14.4636	8.2430	12.3128	11.6261	7.3924	10.0887
Mean	3.8165	2.4685	2.3323	1.7850	2.1287	2.8475	3.1347	1.7651	3.3189
sd	2.0783	1.5919	1.4755	2.2143	1.7253	1.8387	2.2211	1.1838	1.8901

Table 2.3. DEM (digital elevation model) in meters above sea level for each web for the American black bear central Georgia population from 2004 to 2006 summary statistics (range, mean, standard deviation).

Web	A	B	C	D	E	F	G	H	I
Range	70.9454	56.4680	52.6306	52.6458	55.8992	54.6838	66.7063	42.0025	67.2368
Mean	119.2861	96.6152	91.6718	77.7615	119.9789	93.0943	99.7679	100.7098	113.5859
sd	16.6140	10.9320	13.0387	12.7276	12.0218	11.4467	16.1277	8.0271	17.5940

Table 2.4. Summary of web area, rings, spacing between rings, average number of snares per web for years 2004 to 2006 for the American black bear central Georgia population, and average approximate density of snares per web.

Web	Area (km^2)	Rings	Spacing between rings (m)	Average number of snares/web	Average density of snares (snares/km^2)
A	12.6	4	500	35	2.778
B	15.9	3	750	26.4	1.66
C	15.9	3	750	23.3	1.46
D	15.9	3	750	25.3	1.59
E	7.1	3	500	24	3.38
F	15.9	3	750	22.5	1.42
G	15.9	3	750	25.5	1.6
H	7.1	3	500	22	3.1
I	7.1	3	500	26	3.66

Table 2.5. Summary of webs for the American black bear central Georgia population from 2004 to 2006 used for telemetry error calculations. Each cell represents the number of observers for each web and year combination. Cells marked with '*' indicated web and year combinations in which telemetry error calculations for observers were not conducted.

Web	2004	2005	2006
A	*	4	3
B	3	4	3
C	*	3	3
D	*	3	3
E	3	*	*
F	3	3	3
G	*	*	*
H	*	*	*
I	*	4	3

Table 2.6. Notation and definitions for terms in the multiple data structure (camera, hair snares, telemetry) Bayesian density model for the American black bear central Georgia population from 2004 to 2006. This model is only for one closed period, which consists of one season.

Term	Definition
i	Web, for i=1…9
j	Site (location of hair snare, or hair snare and camera), for j=1….$J(i)$
k	Occasion or session number, for k=1…3
d_i	Camera detection probability parameter for web i
r	Individual capture probability with cameras
Y_{ijk}	Camera occupancy data for web i, site j, occasion k (‘1’ if at least 1 bear is detected, ‘0’ otherwise)
N_i	True number of bears present on web i
α, β	Magnitude of spatial variation in the true number of bears
λ_i	Local heterogeneity in spatial distribution of true number of bears present on web i
V_{ikm}	Telemetry data which consists of the probability of marked bear m is present on web i, at occasion k
m	Identity of marked bear
γ	Allele frequency at locus L
G	An N_{tot} x L matrix of true genotypes
X	An N x S indicator matrix for which X_{ij}=1 if individual i appeared in sample j
θ_{ik}	Hair snare capture parameters for web i and occasion k
G	An S x L matrix of true genotypes of individuals appearing in S sample
$C_{obs,\ Ctrue}$	Observed and true genotypes in the calibration sample (an array of L x R)
$G_{obs,ijk}$	An S x L x R array of observed genotypes
p_{error}	Genetic error probability
S	Number of genetic samples
L	Number of microsatellite loci
R	Number of times genotyping was replicated
N_{tot}	Number of individuals in the population

Table 2.7. Hair snare data summary for the American black bear central Georgia population from 2003 to 2006.

Year	Seasons	Webs	Snares	Hair Samples[1]	No.of snare sessions[2]	Snares w/ hair detected
2003	1 (F/W)	1	27	134	121	48
2004	2 (S, F)	11	282	927	837	246
2005	2 (S, F)	14	362	1929	1081	561
2006	1 (S)	6	159	1190	477	258
TOTAL	6	32	830	4180	2516	1113

[1] Some samples may contain feral hog hair, thus bear hair samples may be fewer. Not all samples were analyzed within the laboratory.

[2] Some snares were not able to be sampled for all 3 sessions due to river flooding or controlled burns, therefore the number of snares x 3 does not always equal the number of snare sessions

Table 2.8. American black bear central Georgia population genetic data for assessment of genetic error from allelic dropout. Samples were collected from 2003 to 2006. Tissue and hair samples from known individuals (*n*=85) from the calibration sample data set were used to supplement replicate hair snare samples for each year by season combination, originally in described in Sanderlin (2009). Heterozygous samples with the first replicate and numbers of homozygous samples with the second replicate were used as a sample of allelic dropout from unknown hair samples.

Locus	Number of heterozygous samples								Number of homozygous samples							
	Bear 10Y	Bear 12Y	Bear 17G	Bear 19Y	Bear 30B	Bear 33B	Bear 35G	Bear 36	Bear 10Y	Bear 12Y	Bear 17G	Bear 19Y	Bear 30B	Bear 33B	Bear 35G	Bear 36
Calibration samples	35	36	51	42	46	46	42	37	1	0	1	0	1	2	1	0
2004 Summer	3	7	12	14	8	10	13	9	1	2	1	0	2	2	4	4
2004 Fall	4	4	6	6	6	7	10	3	1	2	1	2	0	1	1	1
2005 Summer	12	10	17	11	9	12	16	13	2	3	2	6	1	4	2	9
2005 Fall	2	4	8	6	4	7	7	7	0	0	1	0	0	1	0	3
2006 Summer	9	7	13	12	13	11	12	9	0	0	0	0	0	2	0	3
Total	65	68	107	91	86	93	100	78	5	7	6	8	4	12	8	20

Table 2.9. Camera data summary for the American black bear central Georgia population from 2003 to 2006.

Year	Cameras on webs	No. of Camera Sessions[1]	Cameras w/detections
2003	14	42	6
2004	59	176	23
2005	78	224	115
2006	30	88	36
TOTAL	181	530	180

[1] Some cameras were not operational for all 3 sessions due to equipment failure, camera availability, or bear damage; therefore, the number of cameras x 3 does not always equal the number of camera sessions

Table 2.10. Live captures, recaptures and recoveries of American black bears with the central Georgia population from 2003 to 2008. Note: this summary includes the Sandersville male (2005) and North Carolina female (2003), 3 untagged male bears (2003, 2004), 1 untagged female bear (2006), and 2 capture mortalities (1 initial capture in 2004, 1 recapture in 2004).

Year	Number of Live Captures			Number of Recaptures									Number of Recoveries		
				2003 initial capture			2004 initial capture		2005 initial capture		2006 initial capture				
	Total	Male	Female	Total	Male	Female	Male	Female	Male	Female	Male	Female	Total	Male	Female
2003	30	18	12	2	1	1	0	0	0	0	0	0	1	1	0
2004	19	13	6	7	3	2	1	1	0	0	0	0	2	2	0
2005	15	7	8	5	1	2	2	0	0	0	0	0	6	5	1
2006	20	15	5	2	0	0	1	0	1	0	0	0	2	2	0
2007	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0
2008	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
TOTAL	84	53	31	16	5	5	4	1	1	0	0	0	14	12	2

Table 2.11. Number of alleles (*A*), individuals analyzed at each locus (*N*), number of heterozygotes (N_{het}) and homozygotes (N_{hom}), observed heterozygosity (H_O), expected heterozygosity (H_E), and *p*-value for Hardy-Weinberg Equilibrium (HWE) test for the American black bear central Georgia population with known individuals (*n*=83) collected from samples from 2003 to 2006 with the Paetkau markers. Locus G10C did not amplify with any individuals, so data from this locus are not included in the table. A *p*-value for HWE cannot be calculated with monomorphic loci (G1D and G10P), marked with 'NA'.

Locus	*A*	*N*	N_{het}	N_{hom}	H_O	H_E	HWE *p*-value
G1A	4	82	57	25	0.695	0.676	0.623
G1D	1	82	0	82	0	0	NA
G10B	3	81	38	43	0.469	0.393	0.188
G10L	3	82	41	41	0.500	0.570	0.423
G10M	3	24	4	20	0.167	0.542	0.0001*
G10P	1	78	0	78	0	0	NA
G10X	3	68	29	39	0.426	0.514	0.023

* indicates significance after Bonferroni correction

Table 2.12. Observed alleles for each locus with more than one allele for known individuals, number of alleles observed (*n*), and frequency of alleles from the American black bear central Georgia population from samples collected from 2003 to 2006 with the Paetkau markers.

Locus	Allele	*n*	Frequency
G1A	183	21	0.128
	188	25	0.152
	190	79	0.482
	196	39	0.238
G10B	157	2	0.012
	161	120	0.741
	165	40	0.247
G10L	134	32	0.195
	136	97	0.592
	155	35	0.213
G10M	208	3	0.063
	210	28	0.583
	212	17	0.354
G10X	137	27	0.199
	139	89	0.654
	145	20	0.147

Table 2.13. Number of alleles (*A*), number of individuals analyzed (*N*), number of heterozygotes (N_{het}) and homozygotes (N_{hom}) for the American black bear central Georgia population with individuals (*n*=84) from known tissue samples from 2003 to 2006 with the Sanderlin et al. (2009) tetranucleotide markers.

Locus	*A*	*N*	N_{het}	N_{hom}	H_O	H_E	HWE *p*-value
Bear10Y	5	84	41	43	0.488	0.454	0.871
Bear12Y	3	84	48	36	0571	0.603	0.221
Bear17G	4	81	58	23	0.716	0.672	0.748
Bear19Y	4	80	48	32	0.600	0.658	0.225
Bear30B	4	84	53	31	0.631	0.612	0.924
Bear33B	4	82	52	30	0.634	0.631	0.795
Bear35G	4	83	47	36	0.566	0.532	0.462
Bear36	2	84	46	38	0.548	0.503	0.513

Table 2.14. Observed alleles for each locus and allele frequencies from the American black bear central Georgia population with known individuals (*n*=84) from tissue and blood samples collected from 2003-2006 with the Sanderlin et al. (2009) tetranucleotide markers.

Locus	Allele	*n*	Frequency
Bear10Y	238	3	0.018
	262	35	0.208
	290	1	0.006
	294	119	0.708
	298	10	0.060
Bear12Y	248	21	0.125
	256	79	0.470
	260	68	0.405
Bear17G	185	56	0.346
	193	47	0.290
	197	58	0.358
	201	1	0.006

Table 2.14 (continued)

Locus	Allele	*n*	Frequency
Bear19Y	356	34	0.213
	359	2	0.013
	371	65	0.406
	375	58	0.369
Bear 30B	439	47	0.280
	443	27	0.161
	447	90	0.536
	451	4	0.024
Bear 33B	272	83	0.506
	286	51	0.311
	292	22	0.134
	302	8	0.049
Bear 35G	216	1	0.006
	220	30	0.181
	224	106	0.639
	228	29	0.175
Bear 36	198	82	0.488
	207	86	0.512

Table 2.15. Number of hair snare genetic samples with data at all 8 loci for the America black bear central Georgia population from 2003 to 2006.

	Web[1]									
Year/Season	A	B	C	D	E	F	G	H	I	Total
2003 Fall	17	-	-	-	-	-	-	-	-	17
2004 Summer	33	5	-	-	7	-	19	-	6	70
2004 Fall	-	7	1	7	0	20	-	3	-	38
2005 Summer	28	10	3	4	-	16	9	11	20	101
2005 Fall	16	9	1	14	-	13	-	-	21	74
2006 Summer	42	35	1	7	-	32	-	-	28	145
Total	136	66	6	32	7	81	28	14	75	445

[1] Webs that were not sampled during the year and season combination are marked with a '-'.

Table 2.16. Number of unique individuals detected with genetic hair samples at all 8 loci for the American black bear central Georgia population from 2003 to 2006.

	Web[1]									
Year/Season	A	B	C	D	E	F	G	H	I	Total
2003 Fall	14	-	-	-	-	-	-	-	-	14
2004 Summer	21	5	-	-	6	-	8	-	5	45
2004 Fall	-	5	1	5	0	11	-	2	-	24
2005 Summer	14	8	3	4	-	14	8	5	10	66
2005 Fall	11	6	1	4	-	9	-	-	9	40
2006 Summer	18	12	1	5	-	20	-	-	9	65
Total	78	36	6	18	6	54	16	7	33	254

[1] Webs that were not sampled during the year and season combination are marked with a '-'.

Table 2.17. Minimum Known Alive in the American black bear central Georgia population from 2003 to 2007.

Year (date)	Number radiocollared[1]	Number censored[1,2]	Mortalities[1,2]	Total Other[3]	Total Known (alive+dead)	Minimum Known Alive
2003 (9/1)	25	3	0	5	30	26
2004 (9/1)	31	10	3	1	35	32
2005 (9/1)	26	17	5	9	40	26
2006 (9/1)	29	16	1	4	34	29
2007 (5/15)	21	5	2	2	25	21

[1] This summary includes the Sandersville male nuisance mortality, Altanta female and 2 capture mortalities (1 initial capture, 1 recapture)

[2] Number of censored and mortalities of bears with radiocollars indicates the number of bears censored from collar drops or lost collar and/or any mortality since the previous date and year (or the start of the study for the first record)

[3] Unmarked, but known-fate bears from capture mortalities, vehicle collisions, illegal harvest, and legal harvest. There are 2 captures of bears that were unmarked, but alive included in this column: a male bear in 2003 (9/1) (B-00) and a male bear in 2004 (9/1) (B-30).

Table 2.18. Number of alleles (*A*), number of individuals analyzed (*N*), number of heterozygotes (N_{het}) and homozygotes (N_{hom}) for the American black bear central Georgia population with individuals (*n*=184 unique individuals) from observed hair samples collected at hair snares from 2003 to 2006 with the Sanderlin et al. (2009) tetranucleotide markers.

Locus	*A*	*N*	N_{het}	N_{hom}	H_O	H_E	HWE *p*-value
Bear10Y	8	184	85	99	0.462	0.434	0.092
Bear12Y	4	184	113	71	0.614	0.607	0.104
Bear17G	8	184	122	62	0.663	0.684	0.004*
Bear19Y	4	184	113	71	0.614	0.659	0.059
Bear30B	4	184	104	80	0.565	0.594	0.522
Bear33B	7	184	100	84	0.543	0.616	<0.001*
Bear35G	4	184	112	72	0.609	0.532	0.084
Bear36	4	184	93	91	0.505	0.496	<0.001*

- indicates significance after Bonferroni correction

Table 2.19. Observed alleles for each locus and allele frequencies from the American black bear central Georgia population with unique individuals (*n*=184) from observed hair samples collected at hair snares from 2003-2006 with the Sanderlin et al. (2009) tetranucleotide markers.

Locus	Allele	*n*	Frequency
Bear10Y	217	2	0.0054
	238	11	0.0299
	262	64	0.1739
	270	2	0.0054
	286	1	0.0027
	290	5	0.0136
	294	269	0.7310
	298	14	0.0380
Bear12Y	248	48	0.1304
	252	4	0.0109
	256	133	0.3614
	260	183	0.4973
Bear17G	181	2	0.0054
	185	122	0.3315
	189	1	0.0027
	193	121	0.3288
	197	116	0.3152
	201	3	0.0082

Table 2.19. (continued)

Locus	Allele	*n*	Frequency
Bear 17G	205	1	0.0027
	213	2	0.0054
Bear19Y	356	91	0.2473
	359	2	0.0054
	371	149	0.4049
	375	126	0.3424
Bear30B	439	112	0.3043
	443	55	0.1495
	447	199	0.5408
	451	2	0.0054
Bear33B	268	4	0.0109
	270	7	0.0190
	272	201	0.5462
	274	3	0.0082
	286	97	0.2636
	292	47	0.1277
	302	9	0.0245

Table 2.19 (continued)

Locus	Allele	*n*	Frequency
Bear35G	216	2	0.0054
	220	82	0.2228
	224	233	0.6332
	228	51	0.1386
Bear 36	191	8	0.0054
	198	215	0.5842
	202	2	0.0054
	207	149	0.4049

Table 2.20. Parameter median, lower and upper 95% BCI for summer 2004 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
p	0.052	0.034	0.076
N_{tot}	213	144	354
r	0.009	0.004	0.019
θ	0.224	0.128	0.337
λ	15.255	9.895	25.382
N_1	27	21	39
N_2	9	5	19
N_3	15	7	29
N_4	15	7	29
N_5	10	4	21
N_6	15	7	29
N_7	17	12	30
N_8	15	7	29
N_9	12	6	24
N_{10}	15	7	29
N_{11}	15	7	29
N_{12}	15	7	29
N_{13}	15	7	29
N_{14}	15	7	29

Table 2.20. (continued) Parameter median, lower and upper 95% BCI for summer 2004 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
d_0	0.228	0.118	0.379
d_1	0.084	0.038	0.162
d_4	0.089	0.038	0.175
d_6	0.156	0.078	0.269
d_8	0.107	0.047	0.207
$p_{w,1}$	0.132	0.085	0.197
$p_{w,2}$	0.046	0.020	0.085
$p_{w,3}$	0.073	0.032	0.129
$p_{w,4}$	0.073	0.031	0.129
$p_{w,5}$	0.049	0.020	0.090
$p_{w,6}$	0.073	0.031	0.129
$p_{w,7}$	0.126	0.081	0.190
$p_{w,8}$	0.073	0.032	0.130
$p_{w,9}$	0.065	0.032	0.112
$p_{w,10}$	0.073	0.032	0.130
$p_{w,11}$	0.073	0.032	0.130
$p_{w,12}$	0.073	0.031	0.130
$p_{w,13}$	0.073	0.032	0.129
$p_{w,14}$	0.073	0.032	0.129

Table 2.21. Parameter median, lower and upper 95% BCI for fall 2004 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
p	0.039	0.023	0.062
N_{tot}	106	72	179
r	0.015	0.007	0.029
θ	0.213	0.119	0.324
λ	7.590	4.823	13.064
N_1	8	2	16
N_2	10	7	17
N_3	4	2	10
N_4	9	7	16
N_5	2	0	8
N_6	13	10	20
N_7	7	2	16
N_8	6	4	12
N_9	8	2	16
N_{10}	8	2	16
N_{11}	8	2	16
N_{12}	8	2	16
N_{13}	7	2	16
N_{14}	8	2	16

Table 2.21. (continued) Parameter median, lower and upper 95% BCI for fall 2004 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
d_2	0.141	0.069	0.255
d_3	0.063	0.024	0.136
d_4	0.136	0.067	0.243
d_5	0.030	0.000	0.101
d_6	0.175	0.089	0.302
d_8	0.090	0.041	0.180
$p_{w,1}$	0.075	0.021	0.158
$p_{w,2}$	0.130	0.075	0.209
$p_{w,3}$	0.045	0.014	0.098
$p_{w,4}$	0.127	0.072	0.206
$p_{w,5}$	0.021	0.002	0.068
$p_{w,6}$	0.128	0.073	0.205
$p_{w,7}$	0.075	0.021	0.159
$p_{w,8}$	0.081	0.039	0.146
$p_{w,9}$	0.075	0.021	0.158
$p_{w,10}$	0.075	0.021	0.159
$p_{w,11}$	0.075	0.020	0.157
$p_{w,12}$	0.075	0.021	0.158
$p_{w,13}$	0.075	0.021	0.157
$p_{w,14}$	0.075	0.021	0.158

Table 2.22. Parameter median, lower and upper 95% BCI for summer 2005 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
p	0.076	0.054	0.102
N_{tot}	184	137	266
r	0.037	0.023	0.055
θ	0.227	0.151	0.317
λ	13.165	9.331	19.376
N_1	18	13	26
N_2	14	9	21
N_3	5	3	11
N_4	10	6	18
N_5	13	6	23
N_6	19	13	28
N_7	16	10	25
N_8	10	5	17
N_9	13	10	21
N_{10}	13	6	23
N_{11}	13	6	23
N_{12}	13	6	23
N_{13}	13	6	23
N_{14}	13	6	23

Table 2.22. (continued) Parameter median, lower and upper 95% BCI for summer 2005 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
d_0	0.492	0.373	0.617
d_1	0.396	0.277	0.532
d_2	0.186	0.106	0.309
d_3	0.307	0.201	0.449
d_5	0.508	0.368	0.657
d_6	0.443	0.312	0.592
d_7	0.297	0.171	0.454
d_8	0.395	0.274	0.545
$p_{w,1}$	0.141	0.093	0.204
$p_{w,2}$	0.101	0.060	0.154
$p_{w,3}$	0.030	0.010	0.065
$p_{w,4}$	0.079	0.044	0.128
$p_{w,5}$	0.073	0.030	0.134
$p_{w,6}$	0.122	0.076	0.182
$p_{w,7}$	0.116	0.071	0.174
$p_{w,8}$	0.058	0.027	0.104
$p_{w,9}$	0.115	0.071	0.174
$p_{w,10}$	0.074	0.029	0.134
$p_{w,11}$	0.074	0.029	0.134

Table 2.22. (continued) Parameter median, lower and upper 95% BCI for summer 2005 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
$p_{w,12}$	0.074	0.029	0.134
$p_{w,13}$	0.074	0.029	0.134
$p_{w,14}$	0.073	0.030	0.134

Table 2.23. Parameter median, lower and upper 95% BCI for fall 2005 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
p	0.030	0.016	0.050
N_{tot}	131	91	207
r	0.111	0.067	0.164
θ	0.275	0.167	0.397
λ	9.376	6.143	15.028
N_1	15	11	22
N_2	10	6	17
N_3	2	1	6
N_4	8	5	14
N_5	9	3	18
N_6	13	10	21
N_7	9	3	18
N_8	9	3	18
N_9	9	6	15
N_{10}	9	3	18
N_{11}	9	3	18
N_{12}	9	3	18
N_{13}	9	3	18
N_{14}	9	3	18

Table 2.23. (continued) Parameter median, lower and upper 95% BCI for fall 2005 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
d_0	0.821	0.694	0.914
d_1	0.684	0.526	0.822
d_2	0.231	0.101	0.425
d_3	0.588	0.417	0.754
d_5	0.786	0.638	0.901
d_8	0.637	0.496	0.773
$p_{w,1}$	0.163	0.103	0.246
$p_{w,2}$	0.094	0.051	0.157
$p_{w,3}$	0.026	0.007	0.063
$p_{w,4}$	0.073	0.035	0.130
$p_{w,5}$	0.075	0.024	0.147
$p_{w,6}$	0.122	0.071	0.193
$p_{w,7}$	0.074	0.024	0.147
$p_{w,8}$	0.074	0.024	0.148
$p_{w,9}$	0.080	0.040	0.139
$p_{w,10}$	0.075	0.024	0.148
$p_{w,11}$	0.074	0.024	0.148
$p_{w,12}$	0.074	0.024	0.148
$p_{w,13}$	0.075	0.025	0.148
$p_{w,14}$	0.074	0.024	0.148

Table 2.24. Parameter median, lower and upper 95% BCI for summer 2006 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
p	0.027	0.014	0.045
N_{tot}	192	143	280
r	0.040	0.024	0.060
θ	0.308	0.206	0.413
λ	13.729	9.782	20.413
N_1	21	17	30
N_2	15	11	23
N_3	3	1	8
N_4	9	6	16
N_5	14	6	24
N_6	20	16	28
N_7	14	6	24
N_8	14	6	24
N_9	13	8	22
N_{10}	14	6	24
N_{11}	14	6	24
N_{12}	14	6	24
N_{13}	14	6	24
N_{14}	14	6	24

Table 2.24. (continued) Parameter median, lower and upper 95% BCI for summer 2006 of the American black bear central Georgia population.

Parameter	Median	95% Lower BCI	95% Upper BCI
d_0	0.583	0.434	0.727
d_1	0.470	0.336	0.611
d_2	0.111	0.038	0.246
d_3	0.302	0.194	0.440
d_5	0.563	0.415	0.706
d_8	0.410	0.259	0.585
$p_{w,1}$	0.175	0.119	0.247
$p_{w,2}$	0.097	0.059	0.151
$p_{w,3}$	0.017	0.003	0.047
$p_{w,4}$	0.067	0.035	0.112
$p_{w,5}$	0.074	0.030	0.133
$p_{w,6}$	0.137	0.088	0.202
$p_{w,7}$	0.073	0.031	0.133
$p_{w,8}$	0.074	0.030	0.132
$p_{w,9}$	0.095	0.055	0.149
$p_{w,10}$	0.074	0.030	0.133
$p_{w,11}$	0.073	0.030	0.133
$p_{w,12}$	0.074	0.030	0.133
$p_{w,13}$	0.074	0.030	0.132
$p_{w,14}$	0.073	0.030	0.133

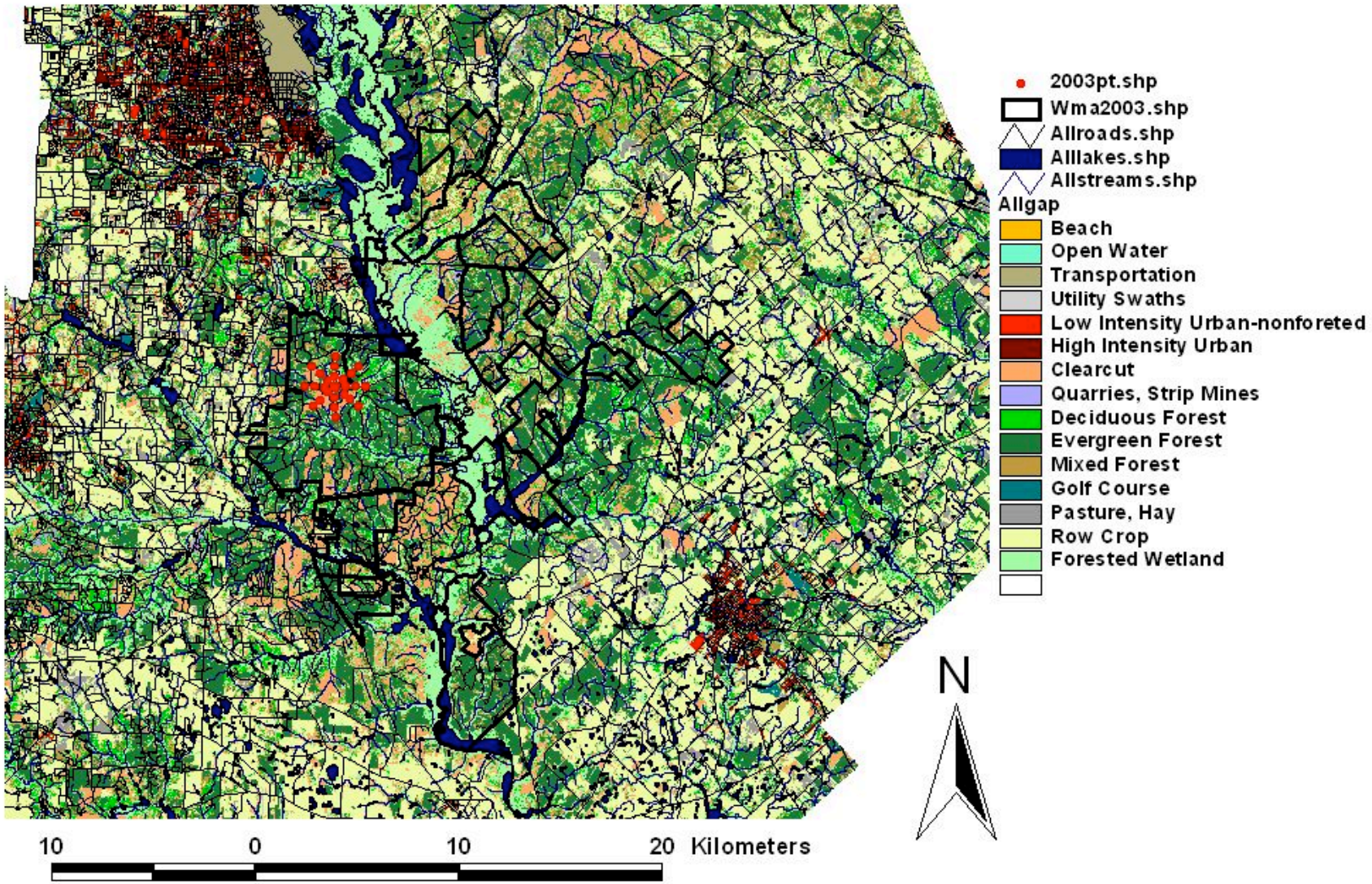


Figure 2.1. Hair snare locations for the American black bear central Georgia population during year 2003.

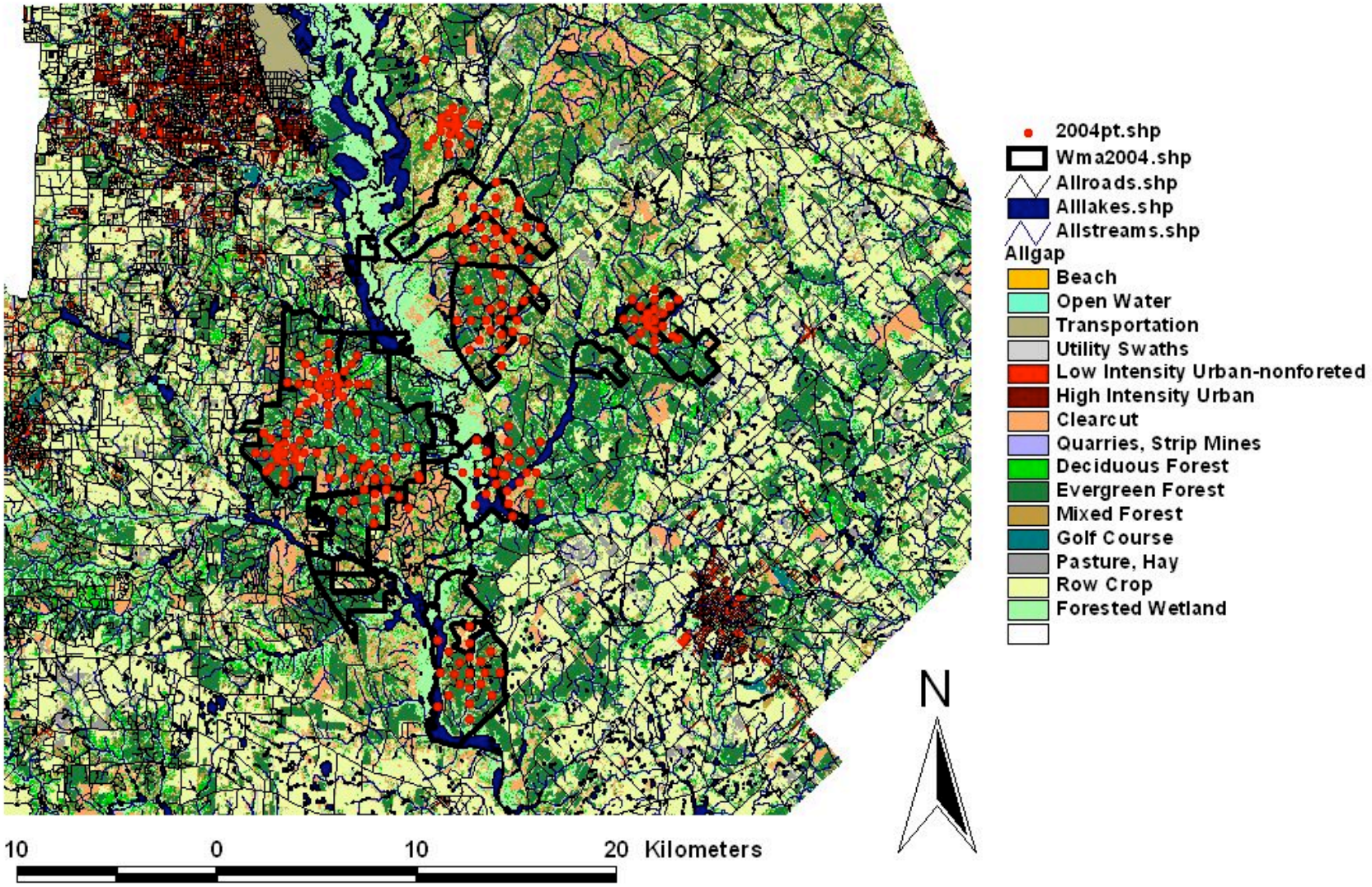


Figure 2.2. Hair snare locations for the American black bear central Georgia population during year 2004.

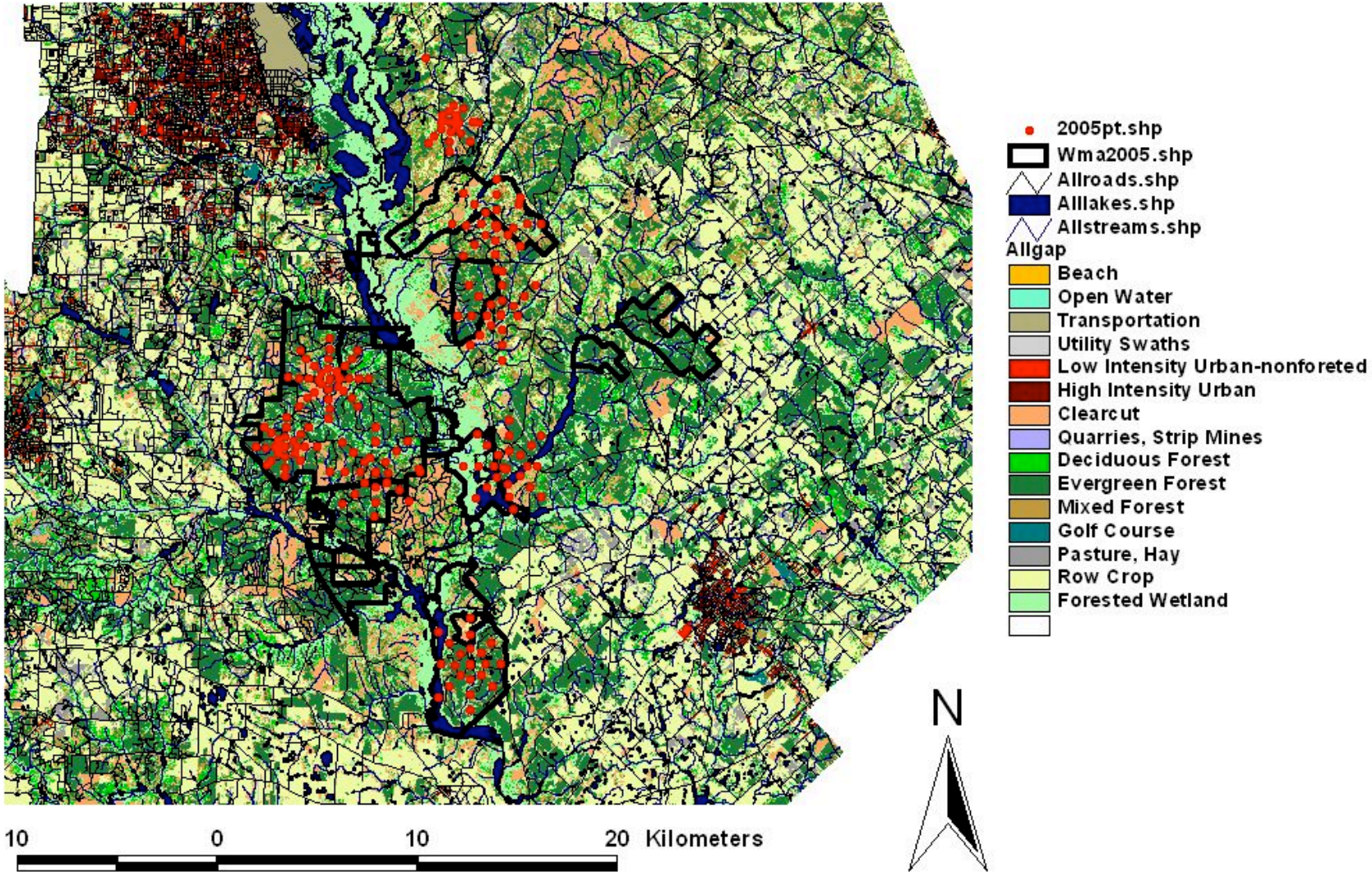


Figure 2.3. Hair snare locations for the American black bear central Georgia population during year 2005.

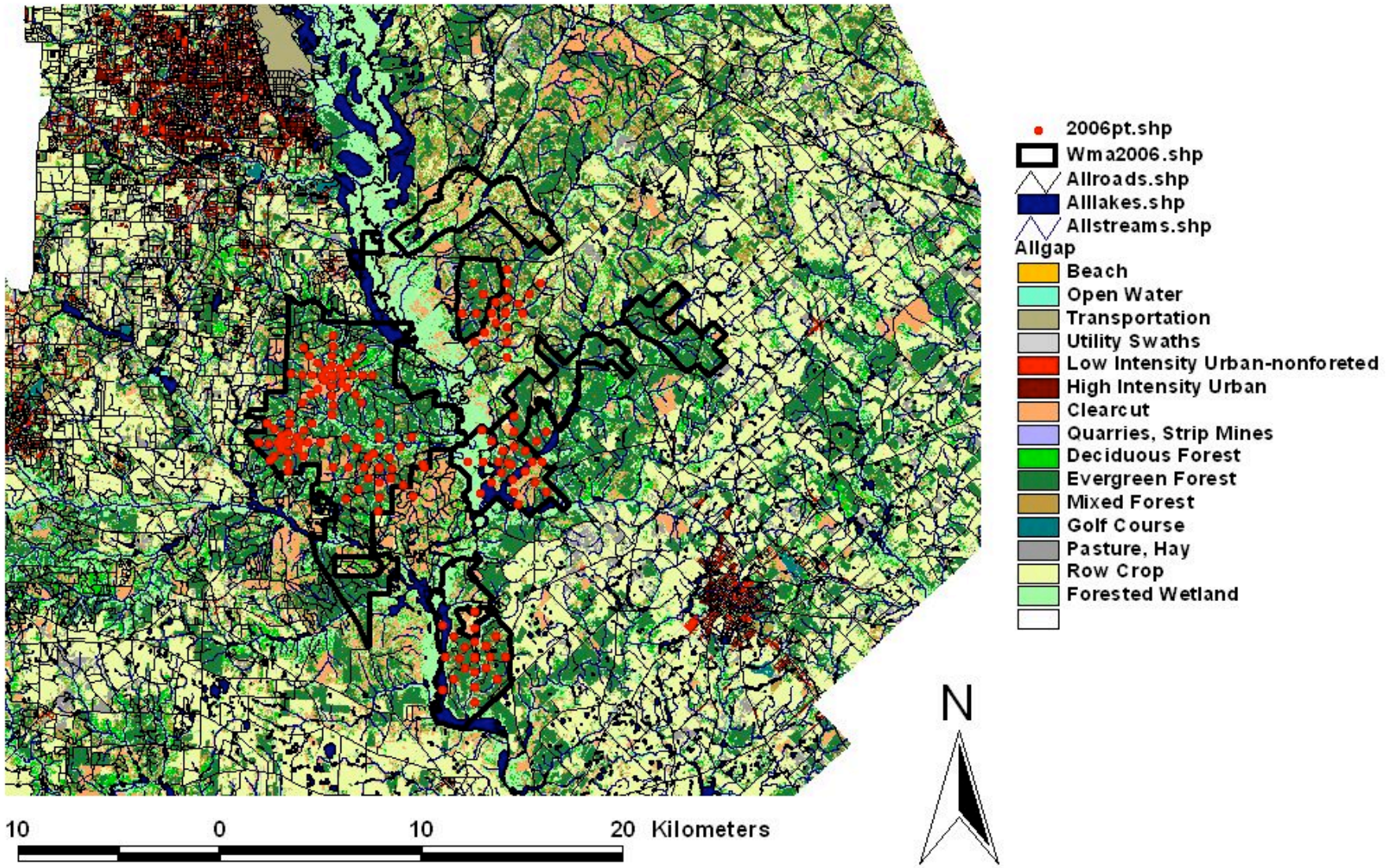


Figure 2.4. Hair snare locations for the American black bear central Georgia population during year 2006.

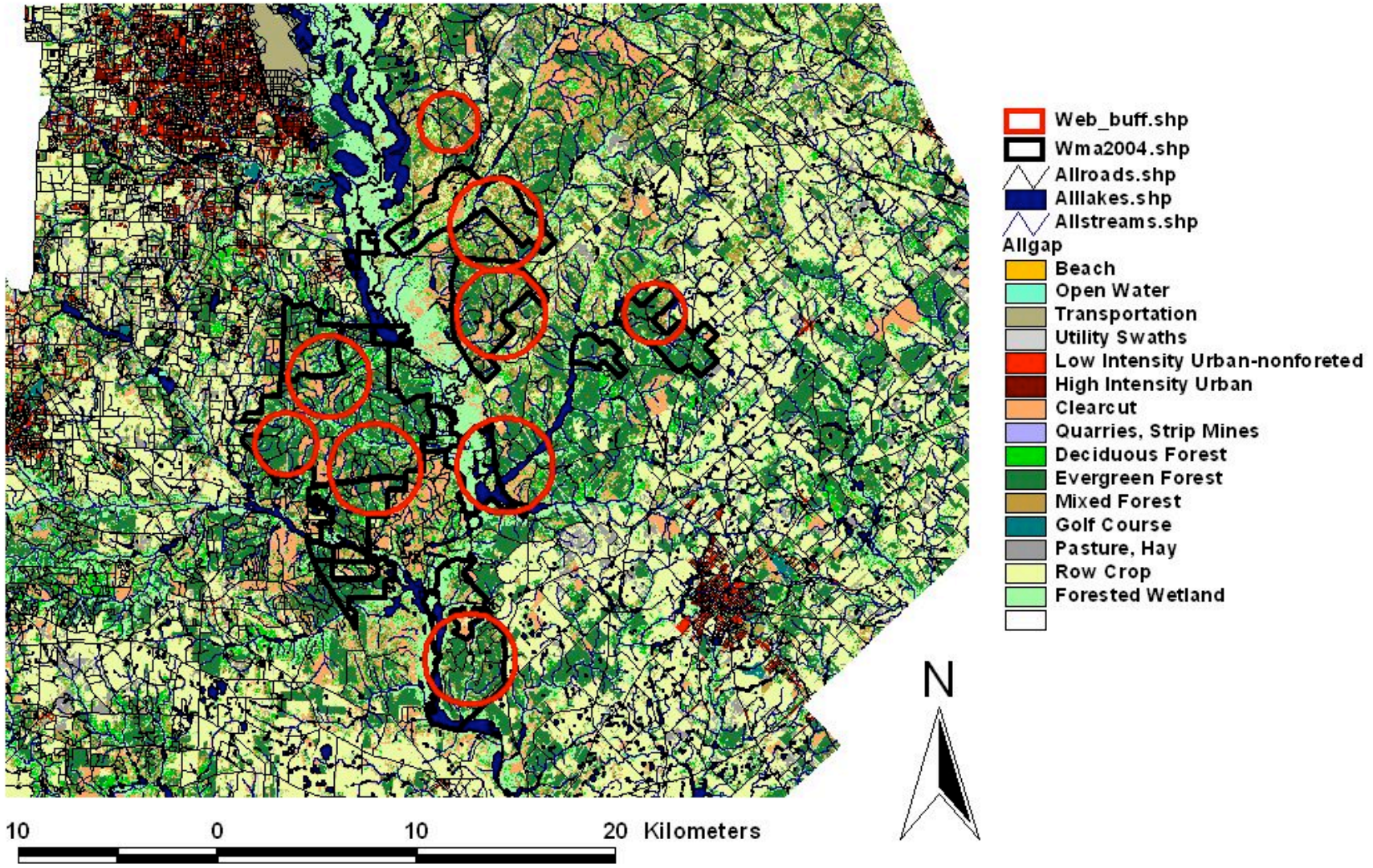


Figure 2.5. Web locations with 2004 boundaries for the American black bear central Georgia population with Gap data.

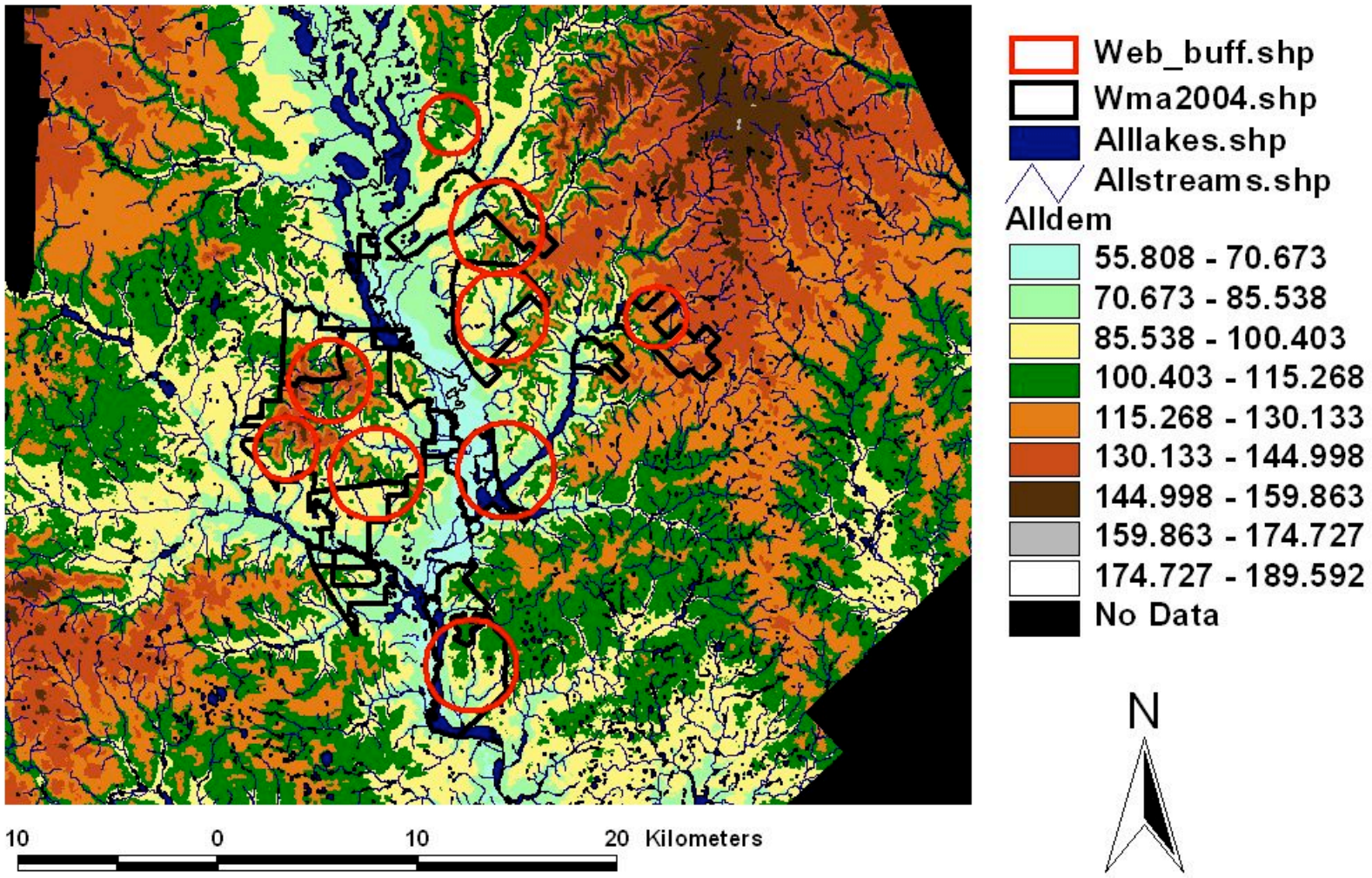


Figure 2.6. Web locations for the American black bear central Georgia population with DEM data (meters above sea level), 2004 boundaries.

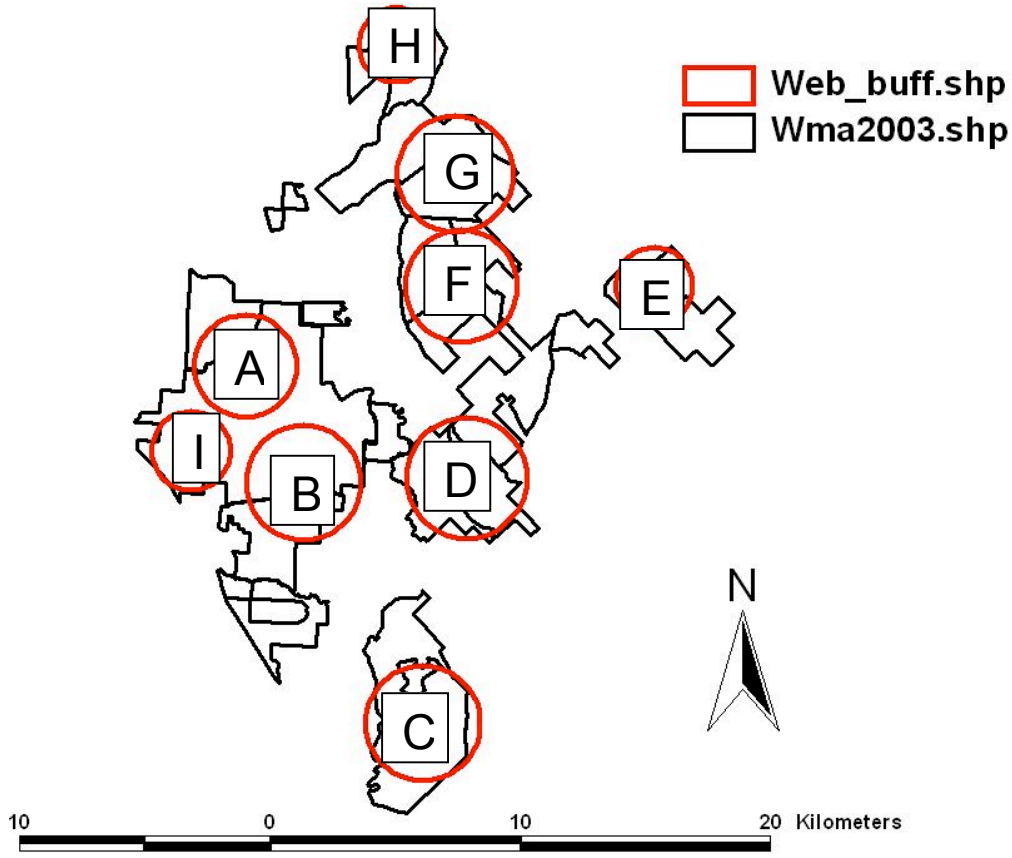


Figure 2.7. Web locations with 2003 boundaries from the American black bear central Georgia population.

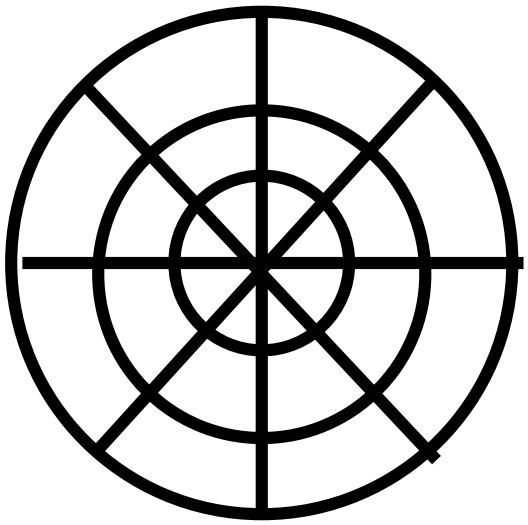


Figure 2.8. Trapping web with of 27 hair snares (located at the intersection of a circle and line) with 3 snares at the center covering an area of 7 or 15 km^2, depending on the location in the WMAs for the American black bear central Georgia population during the years 2003 to 2006.

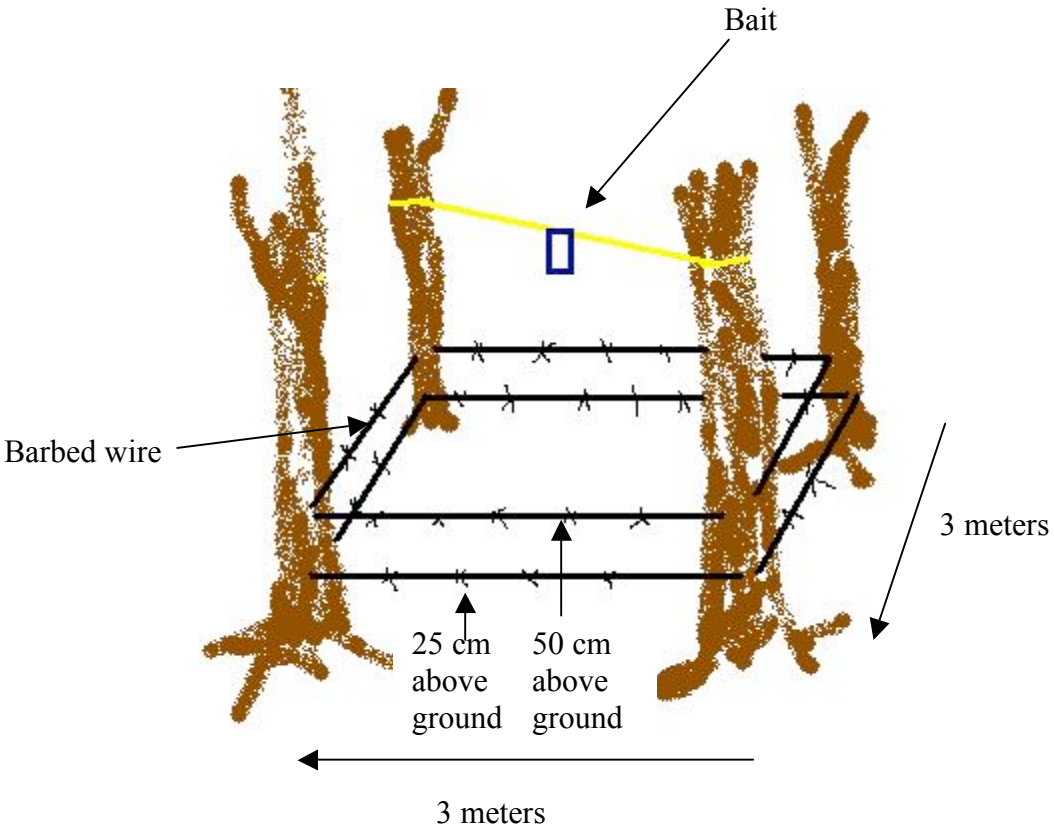


Figure 2.9. Barbed wire strands were placed 25 cm and 50 cm from the ground and baited with corn in a plastic bottle and anise oil to collect hair snare samples from the American black bear central Georgia population during the years 2003 to 2006.

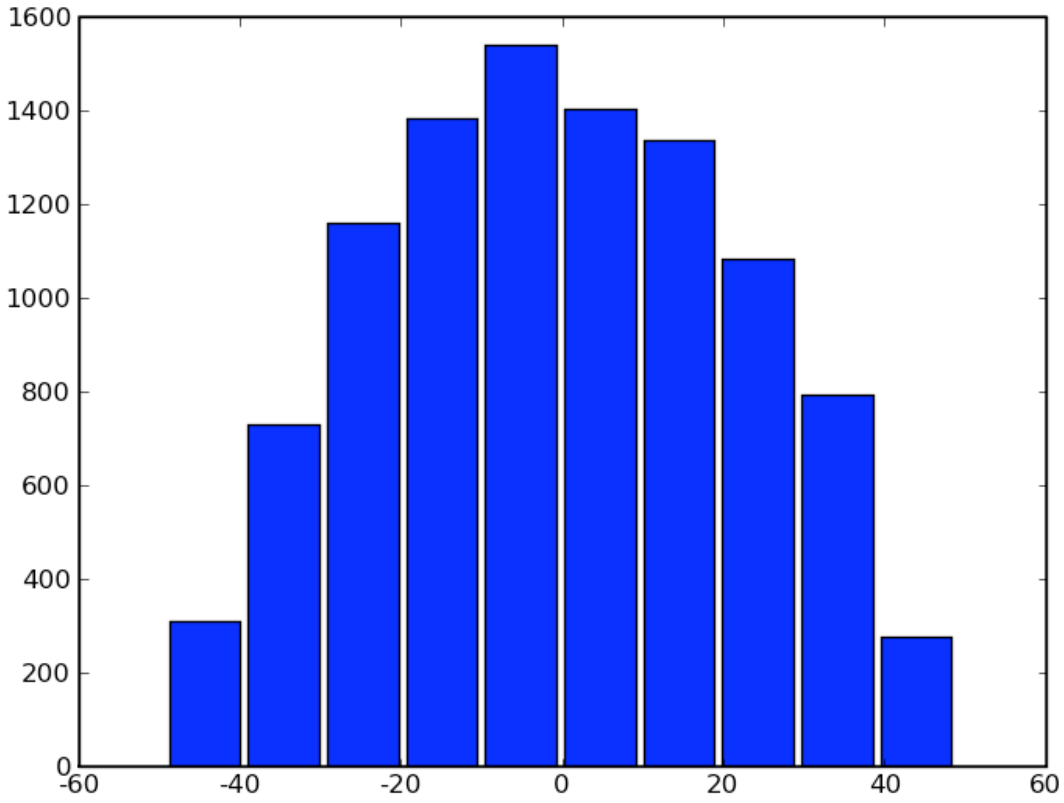


Figure 2.10. Histogram of the von Mises distribution with parameters θ=0, and κ=30.5 (n=10,000 samples). The distribution was simulated using Python, version 2.5.2 (Python Software Foundation, http://python.org) and an algorithm for the von Mises distribution (Best and Fisher 1979).

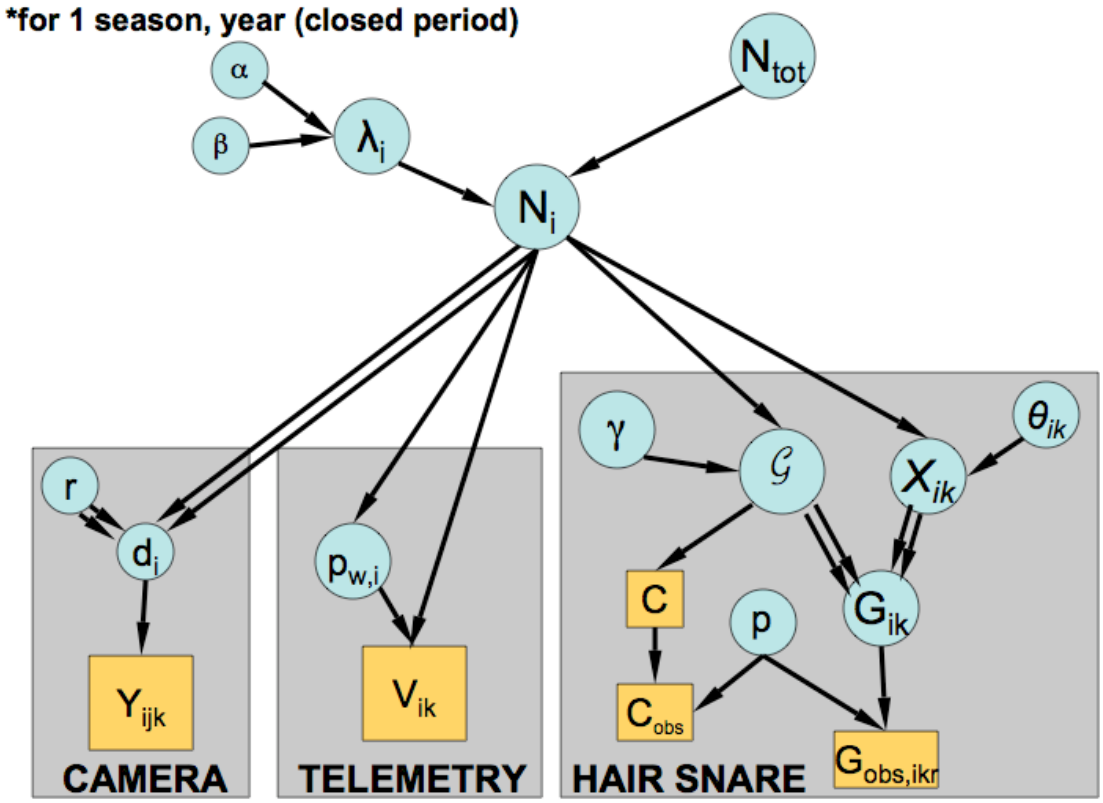


Figure 2.11. Diagram of the hierarchical model incorporating the three data structures: camera, telemetry, and hair snare. This model is for population abundance of American black bears in the central Georgia population for the years 2004 to 2006.

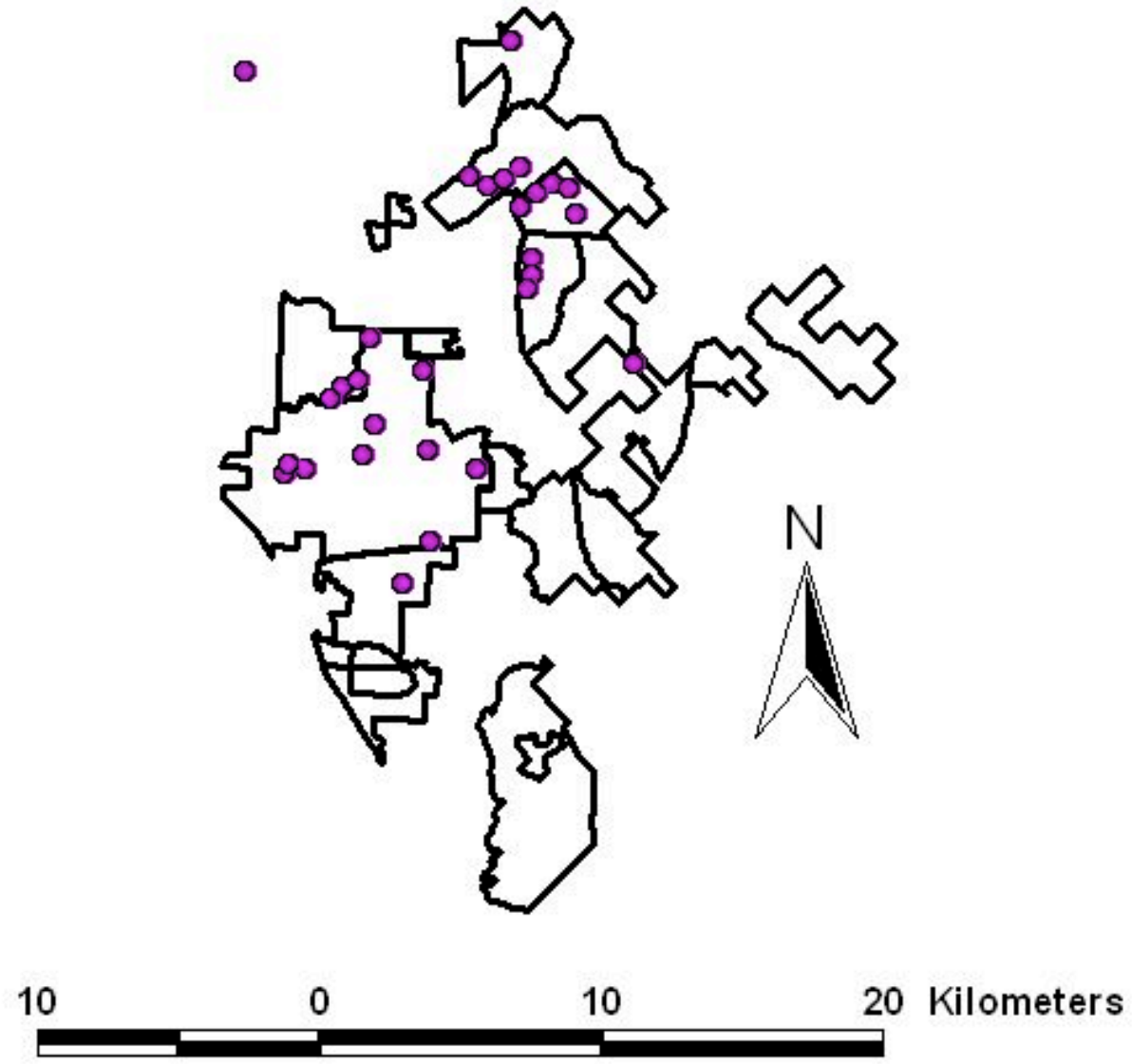


Figure 2.12. Initial and recapture coordinates for American central Georgia population black bears from 2003.

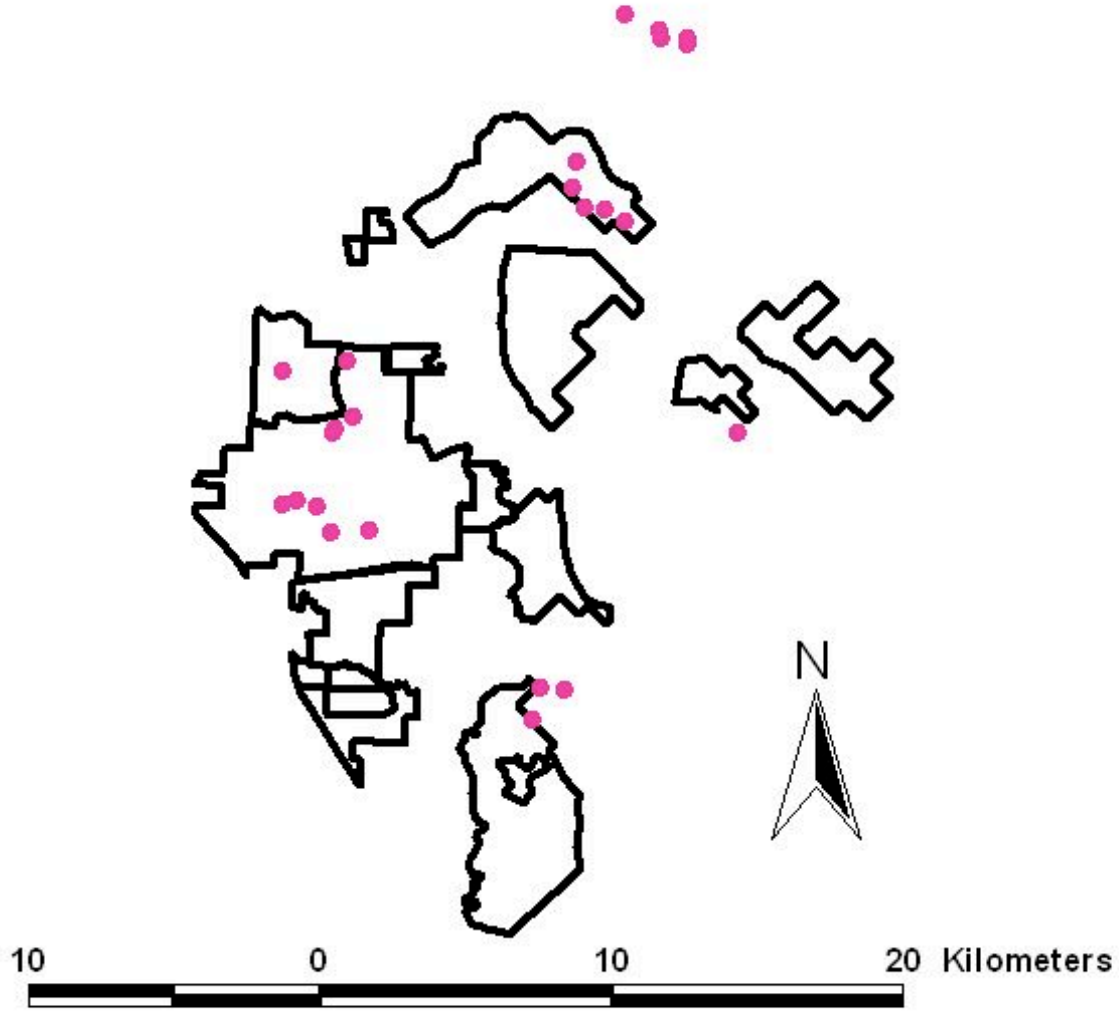


Figure 2.13. Initial and recapture coordinates for American central Georgia population black bears in 2004.

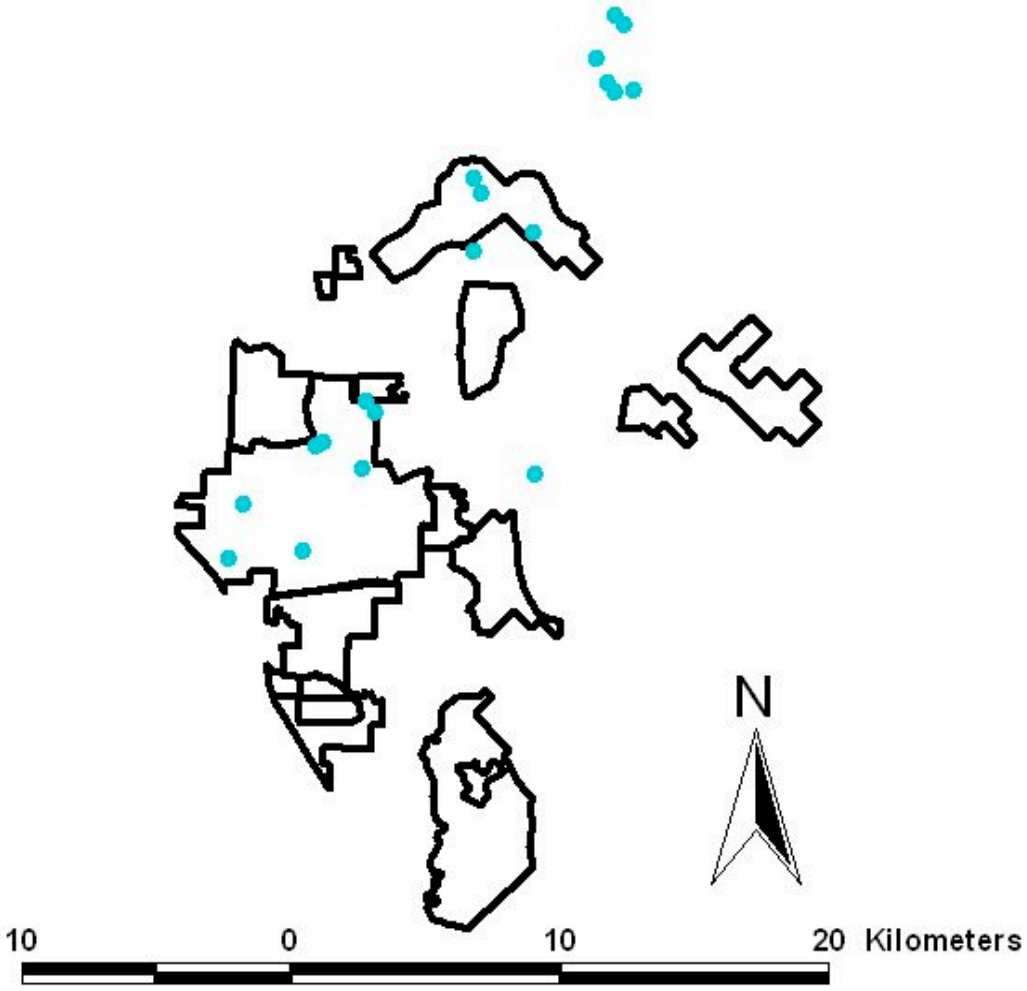


Figure 2.14. Initial and recapture coordinates for central Georgia population American black bears in 2005

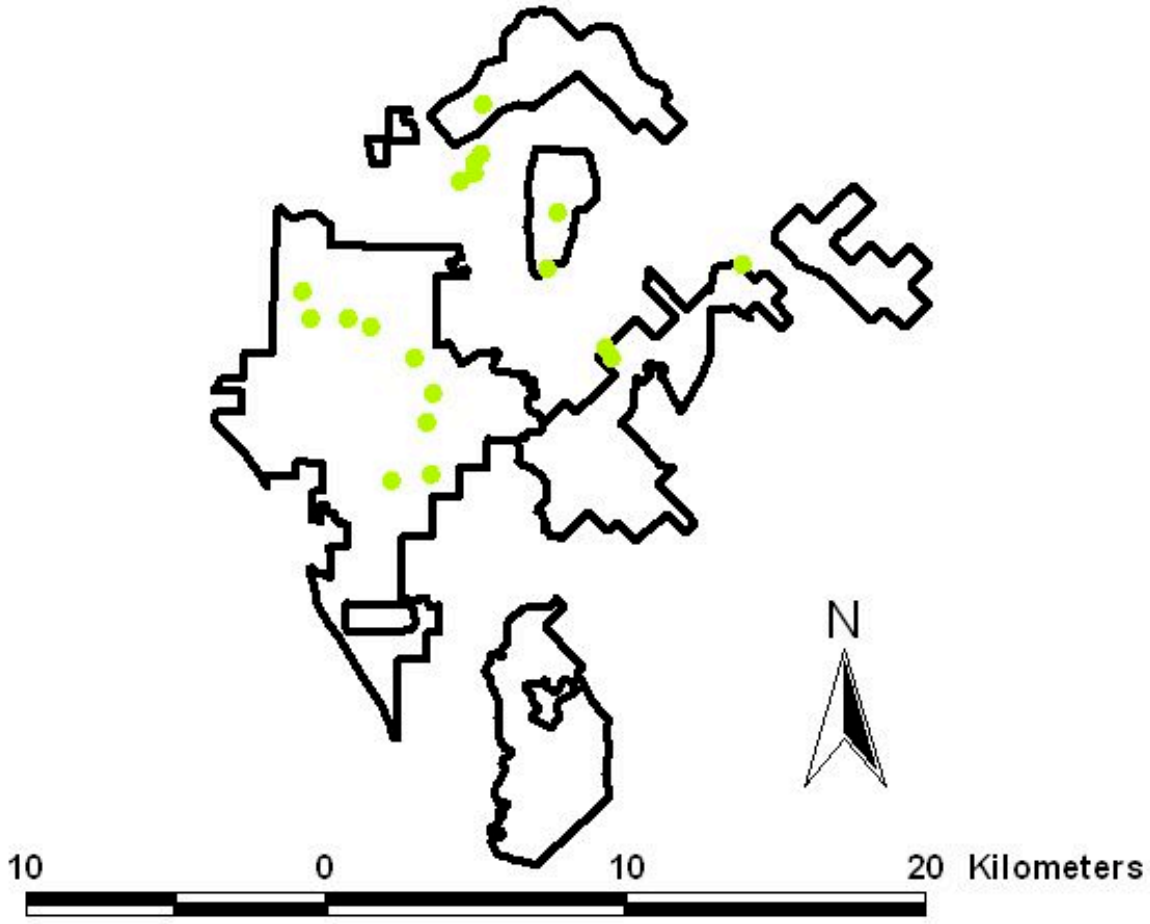


Figure 2.15. Initial and recapture coordinates for central Georgia population American black bears in 2006.

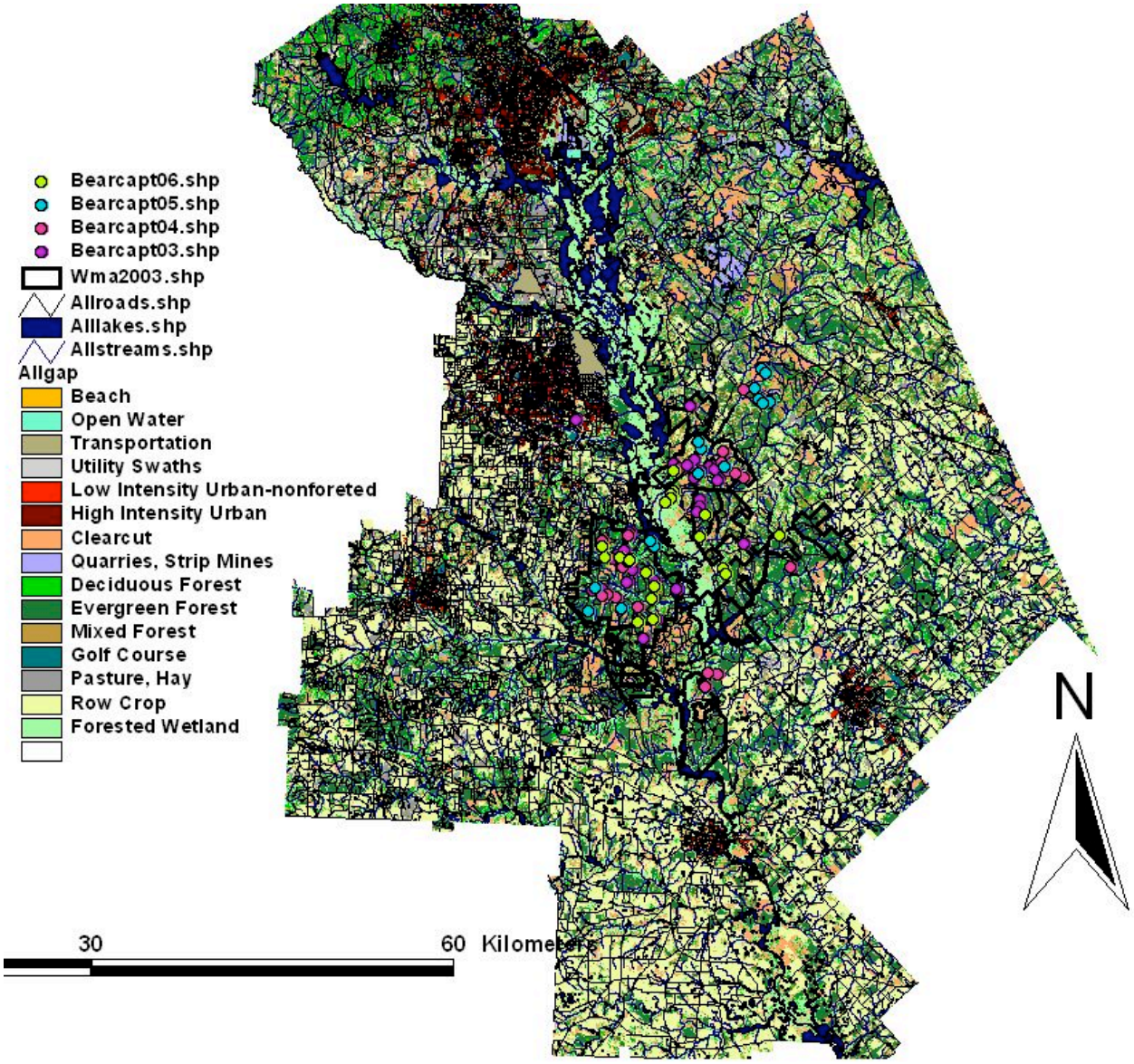


Figure 2.16. Capture coordinates for years 2003-2006 of initial and recaptured American central Georgia population black bears.

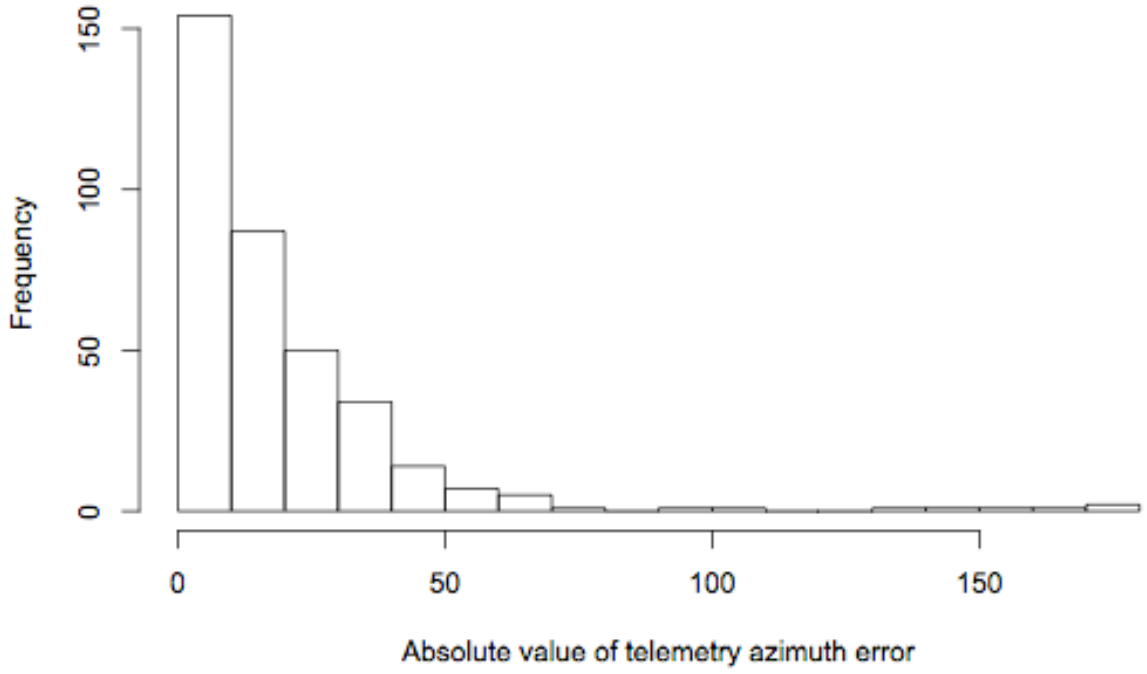
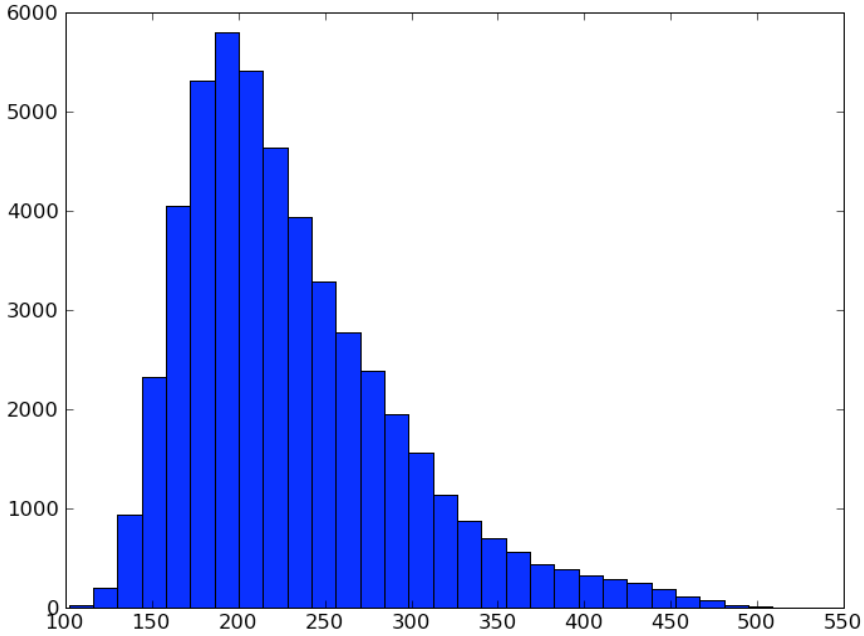


Figure 2.17. Telemetry error for 10 observers for the central Georgia population American black bear study from years 2003-2006 (*n*=360 stations). Angle error (x-axis) indicates the absolute value of the difference between the true angle and the observed angle at a specific station in a web.

a)



b)

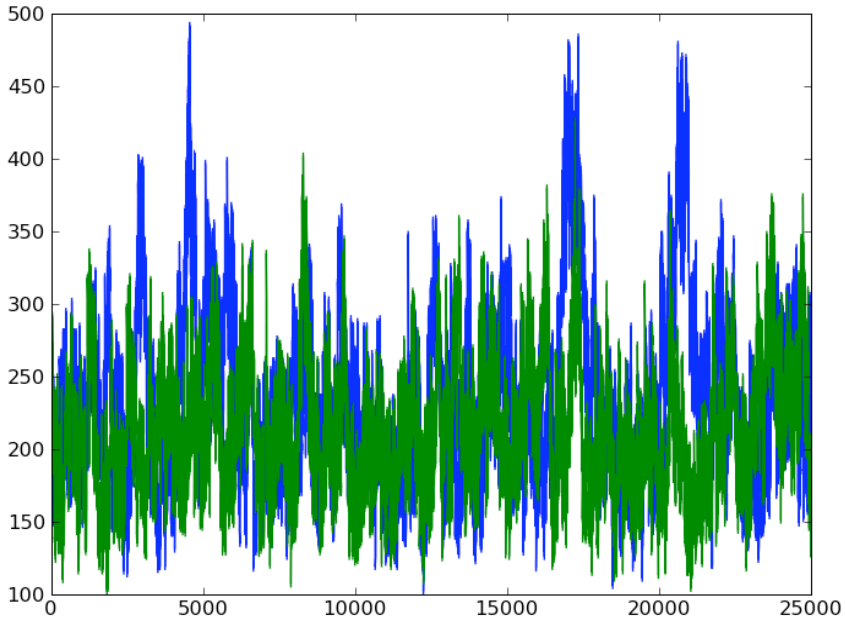
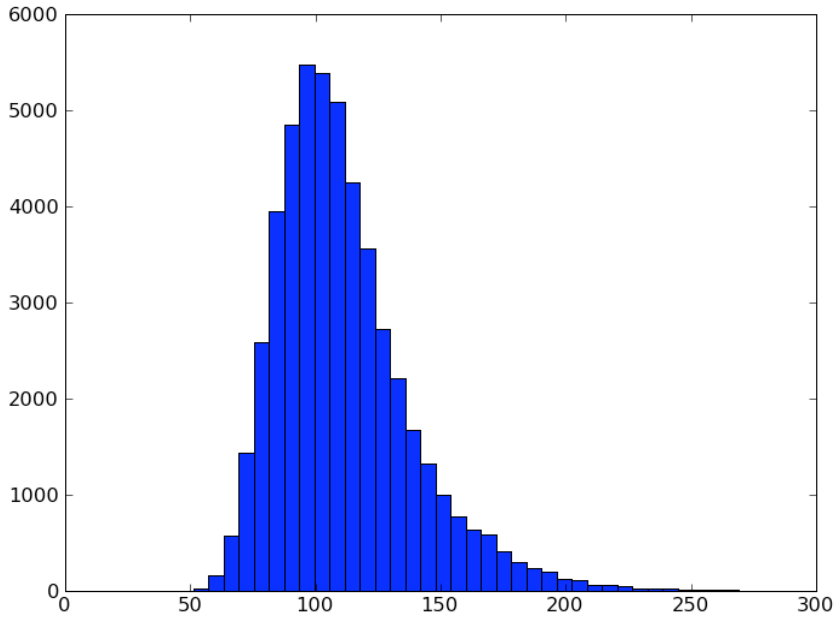


Figure 2.18. Posterior distribution of total abundance (a) and trace (b) in year 2004, summer season for the American black bear central Georgia population from 2 chains of 50,000 MCMC iterations (25,000 burn-in period for each chain).

a)



b)

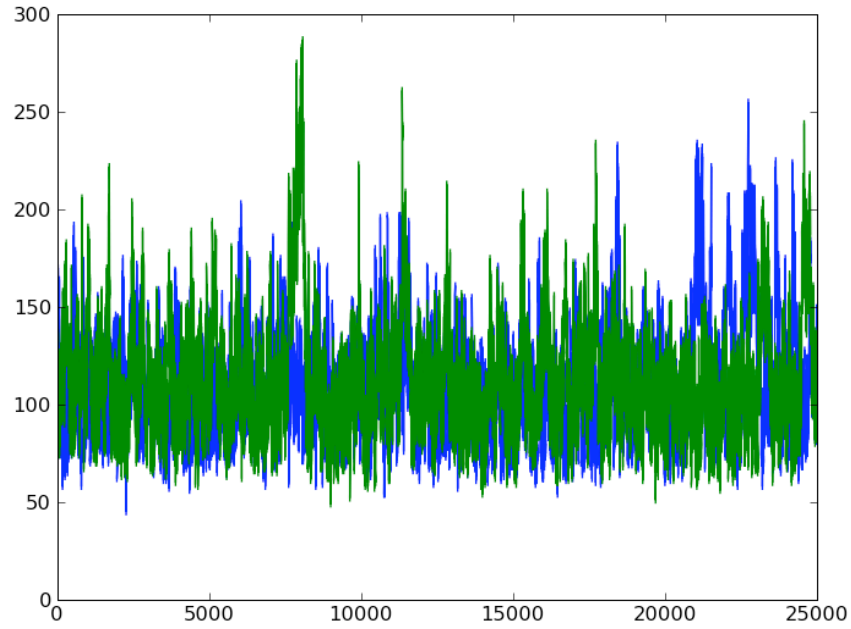
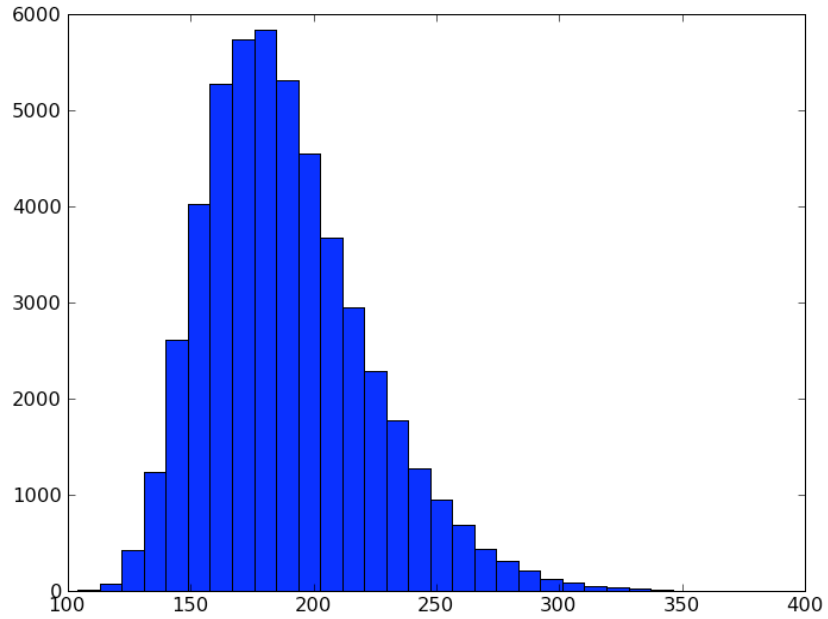


Figure 2.19. Posterior distribution of total abundance (a) and trace (b) in year 2004, fall season, for the American black bear central Georgia population from 2 chains of 50,000 MCMC iterations (25,000 burn-in period for each chain).

a)



b)

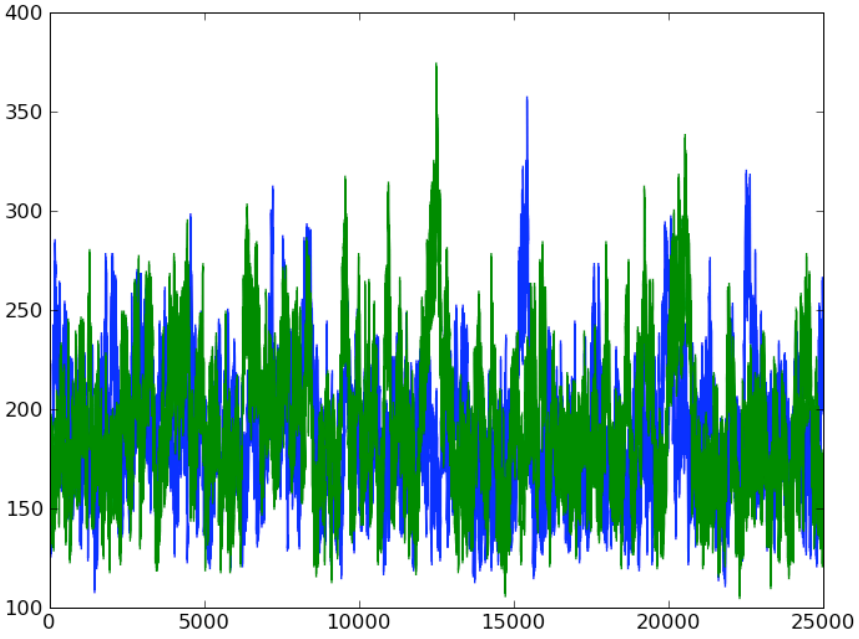
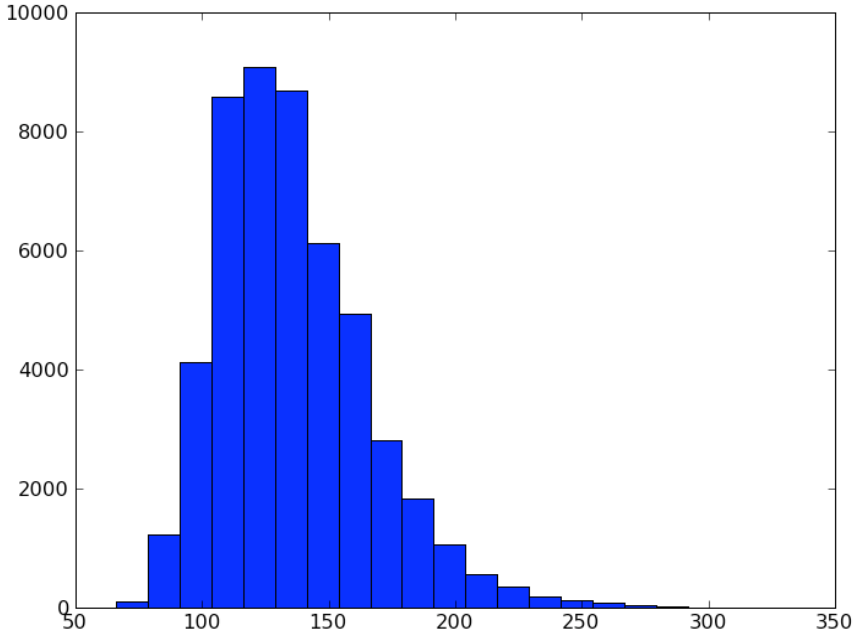


Figure 2.20. Posterior distribution of total abundance (a) and trace (b) in year 2005, summer season for the American black bear central Georgia population from 2 chains of 50,000 MCMC iterations (25,000 burn-in period for each chain).

a)



b)

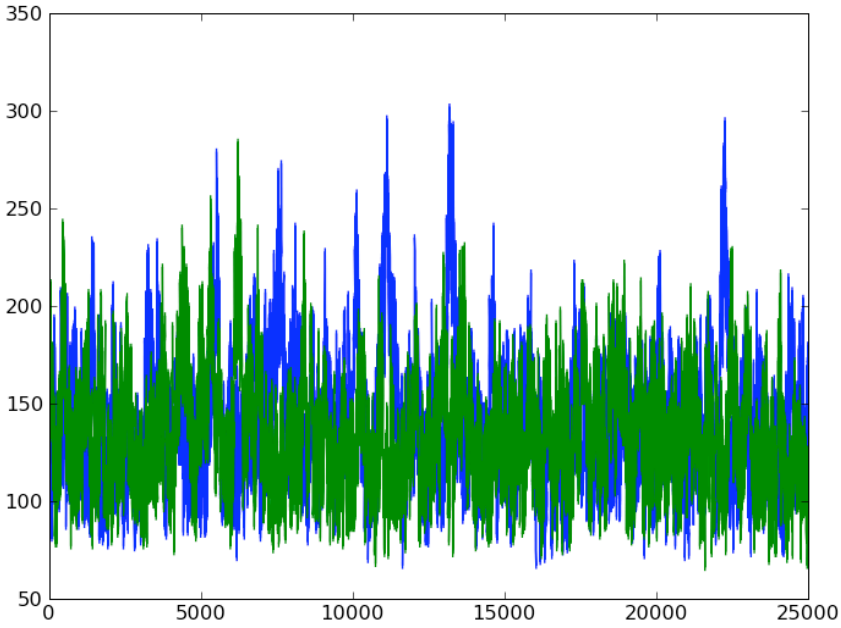
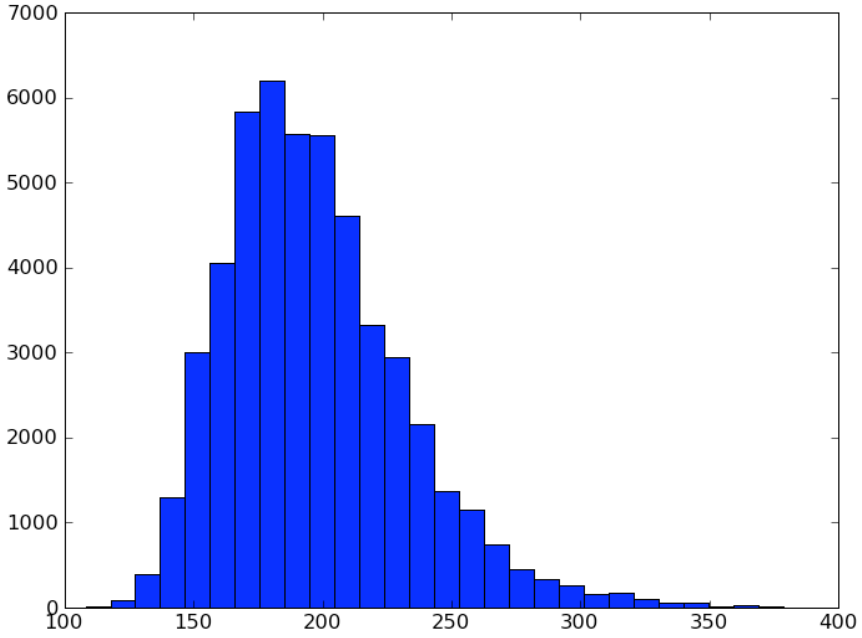


Figure 2.21. Posterior distribution of total abundance (a) and trace (b) in year 2005, fall season, for the American black bear central Georgia population from 2 chains of 50,000 MCMC iterations (25,000 burn-in period for each chain).

a)



b)

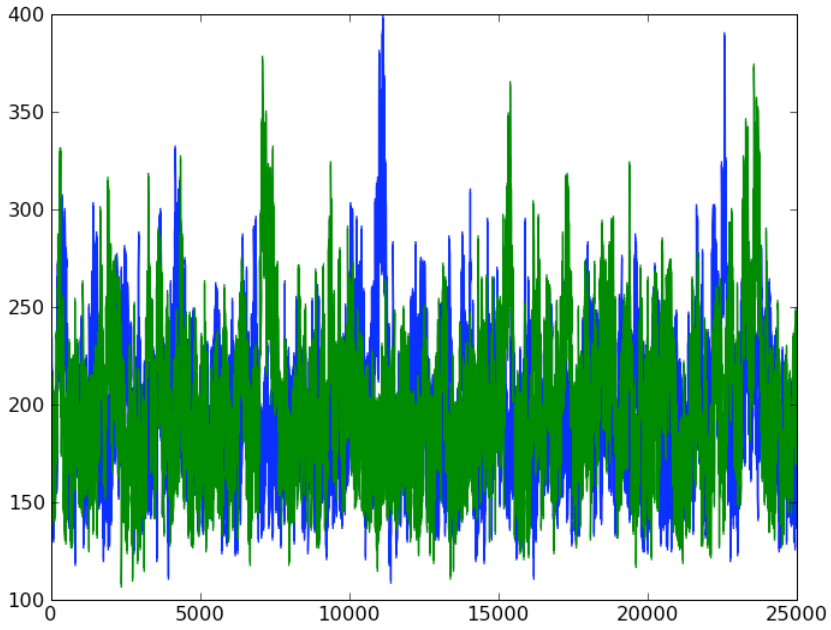


Figure 2.22. Posterior distribution of total abundance (a) and trace (b) in year 2006, summer season, for the American black bear central Georgia population from 2 chains of 50,000 MCMC iterations (25,000 burn-in period for each chain).

CHAPTER 3

ESTIMATION OF SURVIVAL AND REPRODUCTION DEMOGRAPHIC PARAMETERS FOR CENTRAL GEORGIA BLACK BEARS [1]

[1] Sanderlin, J. S., M. J. Conroy, et al. Submit to Journal of Wildlife Management.

Introduction

Population viability models require information on survival and reproduction in a population. These components provide information on the numbers of individuals that are added or deleted from a population. The age and sex ratio of a population are also integral parts of a population viability model. The current age distribution at the current time *t*, along with survival and reproduction, predicts the future population size at time *t+1*. For example, consider two populations of equal total population size and with the same survival and reproductive rates in all age classes. One population has a higher proportion of young age classes than the other population. The first population will have a future population size that is larger, and a larger rate of population growth than the second population with a higher proportion of older age classes. Age stability and stationarity analyses can be conducted, but several assumptions are necessary (*e.g.*, sampling probabilities are constant over time, sex, and age classes), and the data to construct these models are often difficult to collect (Williams et al. 2002). Unbalanced sex ratios in populations may have genetic implications based on effective population size (Caballero 1994, Woodworth et al. 1994) and population growth (Brook et al. 2000), or be indicators of competition for resources (Hamilton 1967, Clark 1978).

Survival

Survival estimates reported from black bear populations in the eastern United States, specifically southeastern populations, tend to be high, with higher survival estimates in females than males (Table 3.1). Reported causes of adult mortality include: legal harvest, illegal harvest, vehicle collisions, nuisance mortalities, cannibalism, natural causes, research handling, and unknown sources. Eastern black bear populations have cub survival estimates ranging between

62 and 75% (Wathen 1983, Smith 1985, McLean 1991). Causes of mortality for bear cubs include: abandonment in dens, natural accidents, disease, death of the mother, vehicle collisions, hunting, research handling of cubs (Elowe and Dodge 1989), and unique to the southeast, drowning in tree dens and other complications from flooded habitats (Smith 1985). Of the possible causes of cub mortality listed previously, most cases are commonly attributed to food abundance and the nutrition of parturient females (Wathen 1983), which could cause cub abandonment in dens, disease, and mortality of the mother. Subadult bears are more likely to disperse from a population, and may have lower survival rates than adults. Reported mortality rates for subadults vary between 15 to 35% annually (Bunnell and Tait 1985). In conclusion, there are three main age classes for bears: cub, subadult, and adult. As a result of the reported differences in mortality, for predictive population modeling, it is important to consider these three stages of survival.

Reproduction

In the eastern part of North America, black bears often live in habitats consisting of deciduous or mixed forests, which provide energy and nutrient-rich foods, such as berries and mast (Bunnell and Tait 1985). The average litter sizes per study, not necessarily per year, range from 2.15 to 2.74 from several studies, with an average of 2.42 among all the summarized studies (reported in Bunnell and Tait 1985). In the eastern United States, specifically southeastern populations, mean litter sizes per study range from 1.4 to 2.98 (Table 3.2). Growth rates in the eastern United States are generally faster than western populations, ages of first reproduction are younger, and breeding interval is about 2 years (Bunnell and Tait 1985).

Reported ages of first reproduction in the eastern United States, specifically southeastern populations, range from 3 to 5.2, with mean birth intervals ranging from 2 to 2.4 (Table 3.2).

Most female bears in North Georgia do not produce litters until age 4, and average about 2.59 cubs per female every other year (Carlock et al. 1983). The female bears in the other two populations from Georgia tend to reach an earlier age of maturity than the northern Georgia bears. Female bears in Southeast Georgia, based on examination of reproductive tracts, have the capability to breed at 2.5 years (Abler 1985), and litter sizes range from 1-4 cubs per sow ($\bar{x}$=2.1) (Dobey et al. 2005).

A population viability model can be constructed from survival and reproduction estimates with both deterministic and stochastic population models. Deterministic models require assumptions of constant survival and reproduction over time, no environmental or demographic stochasticity, and equal sampling probabilities over time, sex, and age classes. Demographic and environmental stochasticity are often important components of population viability models, because populations rarely meet all the assumptions of deterministic models. Previous chapters have focused on abundance estimation for the central Georgia population. The population abundance is an important component in a population viability model. However, these quantities alone do not necessarily provide information on the viability of a population. The finite rate of population growth per-capita λ over one year indicates if a population is increasing (λ>1), decreasing (λ<1), or is constant (λ=1). Without additional information on other vital rates, the reasons for the population increasing, decreasing, or remaining constant are unknown. For example, a population may have a high abundance, but decreasing survival and low reproduction, which may lead to an unsustainable population. Conversely, populations of smaller population size may have high rates of survival and high reproductive output, leading to

a sustainable population. To properly manage populations with conservation applications or harvest management, all vital rates should be assessed in a population viability model. The goal of this chapter is to assess the demographic rates of survival and reproduction in the central Georgia population, and include them in a population viability model. Given the demographic rates and population viability analysis, an additional goal is assess the feasibility of an increase in harvest for the black bear CGP.

Field Methods

Physical Capture

Bears were captured in the study area using Fremont foot trap snares (Fremont 1986) for four trapping seasons (May-August). Bears were immobilized with a 2:1 mixture of ketamine hydrochloride (Ketaset) and xylazine hydrochloride (Rompun) at a dosage for estimated body weights by Georgia Department of Natural Resources personnel. Culvert traps were used to trap and release nuisance bears to Oaky Woods WMA. An upper pre-molar tooth for age estimation by cementum annuli analysis (Willey 1974), blood samples, hair follicles, and physiological data were collected from each captured bear. Sectioning, staining, and aging of teeth were conducted by Matson Laboratories (Milltown, Montana). All bears were uniquely marked using a combination of collars, lip tattoos, and ear tags/streamers. Most bears were fitted with Advanced Telemetry Systems (Isanti, MN) radio transmitter collars (VHF, very high frequency) equipped with mortality signal sensors and motion sensors and four male bears received radio collars that contained Global Positioning technology and a mortality switch. All collars fitted to bears during the project were equipped with either a mechanical timer release (GPS) or a degradable release tab (VHF).

Telemetry observations

Telemetry bear signals were obtained by scanning all signals with the receiver and a whip antenna (Advanced Telemetry Systems, Isanti, MN) from vehicles. Department of Natural Resources personnel monitored radiocollared bears at least once per week to determine the status of bears (alive, dead, or dropped collar) from the motion and mortality sensors equipped with the radio transmitter collars. Any radio collar with a mortality signal was located within 1-2 days using first a whip antenna (Advanced Telemetry Systems, Isanti, MN) from vehicles to locate the general area of the collar, and then a 3-element yagi antenna (Advance Telemetry Systems, Isanti, MN) to determine the specific location of the collar in the field. Once the collar was located, and a death had occurred, the cause of death was determined from visual inspection or via necropsy. If the cause of death could not be determined, the cause was classified as 'unknown'. The location of either the dropped collar or bear mortality was recorded with a Garmin GPS unit (Garmin International, Inc., Olathe, KS) using Universal Transverse Mercator (UTM) coordinates.

Dead recoveries of unmarked bears

Physiological data (e.g., age, weight, sex), when possible, were collected within 1 day (usually immediately) of reporting for dead recovery bears from legal kills and vehicle collisions by Georgia Department of Natural Resources personnel. Dead recoveries also included illegal kills detected by Georgia DNR. If the fate of a bear could not be classified, the cause of death was considered as 'unknown'.

Reproduction and den observations

One method of obtaining estimates of reproduction is with female den observations. Other methods include field counts of cubs, examining the corpora lutea or taking note of placental scars. Georgia DNR personnel monitored female bears during the winter months for den activity with radiotelemetry by first scanning telemetry from all radioed bears with a receiver and whip antenna (Advanced Telemetry Systems, Isanti, MN) from vehicles, and then taking locations with a 3-element yagi antenna (Advanced Telemetry Systems, Isanti, MN). From February to March, visual inspection of dens was conducted by first locating the den with a whip antenna (Advanced Telemetry Systems, Isanti, MN) from vehicles, and then a three-element yagi antenna (Advance Telemetry Systems, Isanti, MN) was used to locate the specific location of the den. To minimize the risk of den abandonment, personnel approached dens as quietly as possible. Reproductive status was determined by visual observation or listening for young at den sites.

Additional estimates of reproduction were based on data from cementum layers in the teeth extracted from physical capture, or known-fate at encounter bears. A thinner layer, or reduced deposition, in the tooth section is an indicator of a year during which a female black bear successfully reared a cub(s). This has been documented for female black bears in northern Minnesota (Rogers 1975) and central Arizona (Carrel 1980). Cementum characteristics vary greatly among black bear populations and individuals, therefore, not all teeth can be reconstructed for reproductive history (Matson Laboratories, Milltown, MT).

Statistical Analysis and Modeling

Age and Sex Ratios

Two separate medians and 95% CI and distributions of ages for females and males were calculated from: 1) physically captured bears (including capture mortalities), and 2) known-fate at encounter bears (i.e. illegal kills, legal kill, vehicle collisions). To determine whether the sex ratio differed from 1:1, the z-test for comparing binomial proportions was used. Differences in age by sex and age by weight for both sexes were tested with the nonparametric Kruskal-Wallis test (Gottfried 1971) using the program R (R Development Core Team 2008). The median weight and 95% CI for females and males was also calculated. The median and 95% CI and distribution of ages for both sexes for all years (2003-2006) of physical captures were also calculated to show any changes in age distribution within the study period. All graphics were produced in program R (R Development Core Team 2008).

Reproduction

The median and 95% CI of the breeding interval and age of first reproduction were calculated from cementum layers in the teeth extracted from physical captured or unmarked dead recovery bears. The natality rate or reproduction rate (b), or the number of cubs per adult female per year, was calculated by dividing the average litter size by the mean interval between reproduction events, or the interbirth interval (Stringham 1980, Bunnell and Tait 1985). Since this quantity is composed of two independent means with respective variances, the variance of the reproduction rate with mean values can be approximated. An empirical variance was obtained through bootstrap simulation using 500,000 iterations in a Python program, version

2.5.2 (Python Software Foundation, http://python.org) of litter size from a Poisson distribution with the mean from central Georgia bears and a weighted mean from other eastern black bear studies. A Poisson distribution is commonly used to simulate reproduction events or other forms of count data. Next, an interval between reproduction events was simulated from a log-normal distribution with mean and coefficient of variation (*CV*) from the central Georgia bears and the weighted mean from other eastern black bear studies. A log-normal distribution ensures the interval values will be positive, since negative intervals are impossible. We also assume a normal distribution of intervals between reproduction events. Finally, the litter size was divided by the interval between reproduction events. The variance of the distribution of values over the 500,000 iterations was the approximate variance used in further modeling. The weighted means were weighted with normalized weights of sample size of the specific studies, w_i, (i.e., $\sum_{i=1}^{n} w_i = 1$), calculated by:

$$\bar{x} = \sum_{i=1}^{n} w_i x_i \ ,$$

with sample standard deviation,

$$\sigma(\bar{x}) = \sqrt{\sum_{i=1}^{n} w_i^2 \sigma_i^2}$$

Survival estimation from radiotelemetry data

Annual survival for both sexes was estimated using the Kaplan-Meier product-limit model, allowing staggered entry and censoring (Pollock et al. 1989) with weekly time intervals. The estimated survival function was calculated as:

$$\hat{S}(t) = \prod_{j|a_j<t}\left(1 - \frac{d_j}{r_j}\right),$$

$\hat{S}$ is the probability of survival, d_j is the number of deaths at time a_j, r_j is the number of animals at risk at time a_j, a_j is a particular time of death, and t is the week after the initiation of the study period each year (Pollock et al. 1989). Estimates of variance were calculated as:

$$\text{var}\left[\hat{S}(t)\right] = \frac{\left[\hat{S}(t)^2\right]\left[1 - \hat{S}(t)\right]}{r(t)}.$$

Then, 95% confidence intervals were calculated from the estimated probability of survival and its respective variance. The Kaplan-Meier estimator is based on the following assumptions: 1) all animals were sampled randomly, 2) survival times were independent for individual animals, 3) capturing or radiocollaring animals did not influence future survival, 4) censoring mechanisms were random, and 5) survival functions for newly marked animals were the same as for previously marked animals (Pollock et al. 1989). The log-rank test (Pollock et al. 1989) was used to compare overall survival rates by sex. The overall annual survival rates were calculated using the geometric mean over all years, where $\hat{S}(t)$ is the weekly survival estimate for all weeks in the study, and years is the total number of years for the study:

$$\hat{S}_{year} = \hat{S}(t)^{1/years}$$

Survival estimation from age-structure data

Survival can also be estimated from age distribution data, either from age-specific (horizontal life tables) or from time-specific (vertical life tables). If the population is at a stable age distribution and stationary (or λ is known for each year of observation), vertical life tables can be used to calculate age-specific survival rates. Additionally, sampling probability is

assumed constant over time and among age classes. The age structure data from initial physical captures and stochastic estimates of λ (see next section for calculation) were used to calculate a combined survival estimate for both sexes of sub-adults (age two) and adults (age three and over). A sub-adult survival rate was not calculated for age one individuals because sampling bias may occur with this age group (i.e., leg snares are more likely to catch larger, and thus older bears). The approach of Udevitz and Ballachey (1998) was used to calculate maximum likelihood estimates (MLE) of age-specific survival from age-structure data. They show that the MLE of survival at age *i* is:

$$\widehat{S}_i = \frac{x_{i+1}(t)\lambda}{x_i(t)},$$

where *x* is the number of individuals in the specific age class *i*, and λ is the known population growth rate. Udevitz and Ballachey (1998) show that the variance of survival estimate can be derived from the delta method, with the additional variance of λ, if λ is independently estimated:

$$\widehat{\text{var}}(\widehat{S}_i) = [\widehat{S}_i^2 / n(t)][1/\widehat{c}_i(t) + 1/\widehat{c}_{i+1}(t)] + (\widehat{S}_i / \widehat{\lambda})^2 \text{ var}(\widehat{\lambda}),$$

where $n(t)$ is the sum of all individuals in each age class, and $c(t)$ is the estimate of age class proportion.

Population viability analysis

The survival and reproduction estimates, age ratio, and sex ratio from the central Georgia population were the main components of the population viability model. When necessary, values from other bear populations in the Eastern United States, specifically cub and subadult survival and reproduction estimates, were pooled together to use in the overall population viability model. Projections of population growth, or the finite range of population growth (λ), were calculated using matrix models and stochastic simulations.

A population projection matrix is a matrix consisting of age-specific survival (S_i) for age class i, and reproduction (F_i), where F represents the fecundity or number of young produced by survivors that were in cohort i at time t. This matrix can be used, along with current abundances at each age class to project the future population size of each age class. The population projection matrix we use has the standard form for the three age classes of cubs (age 0), subadults (ages 1 and 2), and adults (ages 3 and over). Under this scenario, the fecundity and survival of the one and two year sub-adult age classes are equal (i.e., $F_1=F_2$ and $S_1=S_2$). The standard form of the post-breeding model for the CGP bear population is:

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \end{bmatrix} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & S_3 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix},$$

where i indicates the age-specific class in years, S_i represents age-specific survival, N_i represents the number of individuals in an age class, and F_i represents the number of young produced by survivors in the specific age class at time t. Fecundity (F_i) is calculated by multiplying the reproduction rate (b_i) described above by the age-specific survival (S_i) and the proportion of females in the age class (sex ratio).

The stable age distribution and λ were calculated for the CGP bear population using the population projection matrix. The dominant eigenvalue represents λ and the eigenvector associated with the dominant eigenvalue represents the stable age distribution (Caswell 2001). The stable age distribution is when individuals in all age-classes expand exponentially at the same per capita rate of growth (Caswell 2001). Values of λ greater than one indicate population growth; while λ values less than one indicate population decline. Values of λ equal to one after

the stable age distribution is attained indicate the population size is not changing. A population would require λ values greater than one to sustain harvest.

Stochastic simulations of population growth for the bear CGP included as many parameter estimates from data collected in the CGP as possible. Random survival rates were generated from a beta distribution, with parameters α and β (described below), to constrain the random variables on the interval between zero and one and to allow modeling of heterogeneity. The survival rates were generated using the first two moments with survival mean and coefficient of variation (*CV*) estimates. The survival mean ($\bar{x}$) and sample variance (v), where $v=(CV\bar{x})^2$, can be used to approximate a prior Beta distribution with the first two method-of-moments estimates. The two parameters (α, β) for the Beta distribution are approximated by the following: 1) $\alpha = \bar{x}\left(\frac{\bar{x}(1-\bar{x})}{v}-1\right)$, and 2) $\beta = (1-\bar{x})\left(\frac{\bar{x}(1-\bar{x})}{v}-1\right)$. Sex-specific survival rates and sex-ratios were used for each age class. Random recruitment was generated using a log-normal distribution, given mean estimates of reproduction rate and *CV*. The log-normal distribution restricts random values to be positive and still maintain a normal distribution. Two scenarios were used, one including reproductive values from bootstrap simulations and survival estimates from the CGP only and one with reproductive values from bootstrap simulations of derived parameters and survival estimates from multiple eastern black bear population studies. Initial population size of both sexes was generated from the sample of radio-tagged bears from the CGP pooled across all years, as a representative sample of the population age and sex ratio. Population growth was monitored for 50 years, using 10,000 replications of the stochastic simulation process. The number of times that the population went extinct for 50 years out of the total 10,000 replications was calculated as percent extinction probability.

Harvest analysis

We assume a constant additive mortality hypothesis of harvest for models (Anderson and Burnham 1976). The additive mortality hypothesis assumes as harvest mortality increases, the total annual mortality increases proportionately. Annual survival probability (*S(t)*) would be modified by the harvest rate (*h(t)*) in the following manner:

$$S(t)=S_0[1-h(t)]$$

A few scenarios of increased harvest (1%, 2%, 3%) were selected for analysis. These absolute percentage increases in harvest are equivalent to harvest of 1-2 additional bears per harvest percentage. The current harvest of bears in the CGP is about one bear every year to two years. We also assume harvest would be targeted towards adults, so only adult survival probabilities were modified. Stochastic simulations, described above, of population growth with the extra parameter of harvest rate were used to determine if the harvest rate is sustainable (i.e., average λ over all replications is equal to or greater than one after a reduction in survival from harvest occurs). The extinction probability over 50 years was also calculated for the increased harvest scenarios.

Comparison with abundance data

To assess the validity of demographic parameters used in the population viability analyses, the values of λ from the PVA were compared to apparent rates of change based on the yearly estimates of abundance of the WMA properties from the DNA hair snare, camera, and telemetry model of abundance. Two λ values were calculated from one summer (mid-May-August) to the next summer (mid-May-August) in 2004 to 2005 and 2005 to 2006. This corresponds to the post-reproduction period for each year. The values of λ were calculated from

the MCMC posterior distributions from chapter 2 of total abundance for years 2004, 2005, and 2006. Distributions, median values, and 95% Bayesian Credible Intervals (BCI) of λ were calculated using Python, version 2.5.2 (http://www.python.org).

Results

Data summary of physical captures

From 2003 to 2006, 84 bears (53M: 31F) were captured (Table 3.3). There were 16 recaptures (10M: 6 F) from 2003 to 2006. There were a total of 14 recoveries, or known-fate from the captured bears (12 M: 2 F) from 2003 to 2008. This summary includes the Sandersville male (2005) and North Carolina female (2003), 3 untagged male bears (2003, 2004), 1 untagged female bear (2006), and 2 capture mortalities (1 initial capture in 2004, 1 recapture in 2004). There were a total of 31 bears in the dead recovery data set for age and weight distribution analyses (Table 3.4). Successful den observations for 3 female bears in 2004, 3 females in 2005, 3 females in 2006, and 3 females in 2007 were made (Table 3.5).

Age and sex ratio

The North Carolina female and Sandersville male were removed from this analysis. The initial capture data set included all live-capture bears with radiocollars (50 M: 30 F), live-captures without collars (1 M: 2 F), cub captures with live-capture bears (1 M: 2 F), and capture mortalities (2 M: 1 F). Age and/or weight measurements were not available for all individuals from this data set; hence the discrepancies between total sample sizes reported below. The bear sex ratio from initial captures was 1.56 M: 1 F (n=89) and differed from 1:1 (z=2.014, p=0.044). The age distribution of females (n=34) differed from males (n=54) ($\chi^2_{05} = 7.168$, df=1,

p=0.007). The median age of females (*n*=34) from initial captures was 6.0 years (95% CI: 4.4-6.7), ranging from 0.5 to 14 years, and the median age of males (*n*=54) from initial captures was 3.0 (95% CI: 0.6- 6.7) years, ranging from 0.5 to 11 years (Figure 3.1, Figure 3.2). The median initial capture body mass of females (*n*=33) was 55.6 kg (95% CI: 50.8-59.8) and for males (*n*=51) was 81.6 kg (95% CI: 80.4-106.5) (Figure 3.3, Figure 3.4). The distribution for female age by weight for initial captures had less variation as age increased than males (Figure 3.3, Figure 3.4).

The median age for both sexes (*n*=31) from 2003 initial captures was 5.0 years (95% CI: 4.5- 6.6), ranging from 1 to 14 years (Figure 3.5). The median age for both sexes (*n*=19) from 2004 initial captures was 2.0 years (95% CI: 2.6- 5.1), ranging from 1 to 10 years (Figure 3.6). The median age for both sexes (*n*=15) from 2005 initial captures was 5.0 years (95% CI: 3.5-6.1), ranging from 1 to 11 years (Figure 3.7). The median age for both sexes (*n*=23) from 2006 initial captures was 2.0 years (95% CI: 2.0- 4.0), ranging from 0.5 to 10.5 years (Figure 3.8). The age distribution from 2003 to 2006 did not differ much from year to year (Figure 3.9).

The data set for dead recovery bears included illegal kills (0 M: 2 F), legal harvest (0 M: 1 F), and bears from vehicle collisions (13 M: 7 F). Again, age and/or weight measurements were not conducted on some individuals in the data set; hence the discrepancy below in total sample sizes. The median age of females (*n*=8) from known-fates was 4.5 years (95% CI: 1.6-11.4), ranging from 0.5 to 18 years, and the median age of males (*n*=12) from known-fates was 4.0 years (95% CI: 0.6- 8.6), ranging from 0.5 to 12 years (Figure 3.10, Figure 3.11). The median known-fate at encounter body mass of females (*n*=3) was 68.5 kg (95% CI: 49.2-96.2) and for males (*n*=5) was 117.9 kg (95% CI: 47.7- 142.2).

Reproduction

The total number of female bears age 3 or older is 30, however, only 15 bears age 3 or older had reproduction data (50 %). The mean age of first reproduction based on data from cementum annuli was 4.3 years (n=15, 95% CI: 4.0-4.7). The mean breeding interval per female, based on data from cementum annuli, was 2.1 (n=8, 95% CI: 1.9-2.4). There were 12 successful observations of dens out of 20 total observations in central Georgia for years 2004-2007. The average number of cubs per female litter observed was 1.8 (n=12, 95% CI: 1.1-2.4) (Figure 3.12). This was used to calculate reproduction rate pooled over all years of den observations and age classes. Due to small sample size and inconsistent effort, alternative approaches were also used to estimate reproduction rate.

Two values of natality rate or reproduction rate (b), or number of cubs per adult female per year, were calculated. The first estimate of reproduction rate was calculated from the mean estimate of litter size from den observations and the mean interbirth interval from the cementum annuli from bears in central Georgia from this study. Reproduction rate was determined directly through simulation using these two means, but we also report the means and distributions of litter size and interbirth interval for comparison to other eastern black bear populations.

The first estimate of reproduction rate from this study is 0.845 cubs per adult female per year (95% CI: 0.843-0.847) (Figure 3.13). The second estimate of reproduction rate was calculated from an analysis of 22 studies (including the CGP) of weighted mean litter size ($\bar{x}_{wt}$=2.45, CV=0.003), weighted by the normalized weights of study litter sample size, and 7 studies (including the CGP) of weighted mean interbirth interval ($\bar{x}_{wt}$ =2.15, CV=0.003),

weighted by the normalized weights of study sample sizes (Table 3.6, Table 3.7, Figure 3.14). The second estimate of reproduction rate is 1.139 cubs per adult female per year (95% CI: 1.137-1.141).

Survival estimation from telemetry data

Survival was estimated using the non-parametric Kaplan-Meier approach with a staggered entry design on marked bears (*n*=81, M=51, F= 30) starting 31 March 2003 and ending 23 June 2008 (273 weeks) for females and ending 5 November 2007 (240 weeks) for males, in weekly time intervals. The ending weeks for males and females differed because there were no more male bears with collars after 5 November 2007 due to censoring or mortalities, but a few female bears still had collars. The North Carolina bear (female) and Sandersville bear (male), and 1 unmarked male bear were not included in the survival analysis. The North Carolina and Sandersville bears were not considered residents of the central Georgia population. The overall annual survival estimate was 0.845 (95% CI: 0.754-0.937) for males and 0.861 (95% CI: 0.746-0.976) for females (Figure 3.15, Figure 3.16). Annual survival rates varied from 0.754 to 1.000 for males between the years of 2003 to 2007, and from 0.237 to 1.000 for females between the years of 2003 to 2008 (Table 3.8). The difference between female and male survival functions was statistically significant using the log-rank test of significance (χ^2_{1df}=5.70, p=0.017). The main source of mortality for bears with radiocollars was vehicle collision (Table 3.9).

Survival estimation from age-structure data

Under the assumption of age stability during the period of 2003 to 2006, an adult (ages 3 and older) and sub-adult (age 2) survival estimate was calculated from the vertical table of initial

physical capture age structure data (n=88). The mean sub-adult survival estimate was 0.622 (95% CI: 0.568-0.676) and the adult survival estimate was 0.610 (95% CI: 0.565- 0.654), under the assumption of λ_s from mainly CGP data equal to 0.788 (see next section for calculation of λ_s). The mean juvenile sub-adult estimate was 0.879 (95% CI: 0.830 -0.929) and the adult survival estimate was 0.862 (95% CI: 0.837- 0.887), under the assumption of λ_s from eastern black bear populations equal to 1.114 (see next section for calculation of λ_s).

Population viability analysis

Estimates of cub survival rate were calculated from an analysis of three eastern bear population studies ($\bar{x}$=0.632, CV=0.034) (Table 3.10). Both sexes were pooled in this age class due to low sample size. Estimates of sub-adult survival rate were calculated from an analysis of four eastern bear population studies, specifically, a study conducted on a population in Florida and Georgia (Dobey et al. 2005) ($\bar{x}_{females}$=0.863, $CV_{females}$=0.019, $\bar{x}_{males}$=0.543, CV_{males}=0.124) (Table 3.11). Additional estimates of adult survival rate, weighted by normalized weights of study sample sizes, were calculated from an analysis of five eastern bear population studies, including the CGP ($\bar{x}_{wt,females}$ =0.909, $CV_{females}$=0.002, $\bar{x}_{wt,males}$=0.767, CV_{males}=0.009) (Table 3.12). Demographic parameter estimates for the population viability analysis included estimates mainly from the CGP (Table 3.13) and estimates pooled from eastern black bear populations (Table 3.14).

Projections of population growth, or λ, were calculated using matrix models and stochastic simulations. The stable age distribution and the deterministic population growth (λ_d) were calculated for the CGP bear population using the population projection matrix. Both sexes

were pooled for all age classes, so average estimates of survival were used in the projection matrix. Two projection matrices were used:

1) with reproduction values from the CGP only,

$$A_1=\begin{bmatrix} 0 & 0 & 0 & 0.845 \\ 0.632 & 0 & 0 & 0 \\ 0 & 0.700 & 0 & 0 \\ 0 & 0 & 0.700 & 0.853 \end{bmatrix}$$

2) with reproduction values from the analysis from eastern black bear populations,

$$A_2=\begin{bmatrix} 0 & 0 & 0 & 1.139 \\ 0.632 & 0 & 0 & 0 \\ 0 & 0.700 & 0 & 0 \\ 0 & 0 & 0.700 & 0.838 \end{bmatrix}$$

The first projection matrix had a λ_d of 1.047, with a stable age distribution of 0.289 cubs, 0.174 sub-adults (age class 1), 0.117 sub-adults (age class 2), and 0.420 adults. The second projection matrix had a λ_d of 1.076, with a stable age distribution of 0.323 cubs, 0.190 sub-adults (age class 1), 0.123 sub-adults (age class 2), and 0.364 adults.

Stochastic simulations of population growth (λ_s) for the bear CGP included as many parameter estimates from the CGP as possible. Two scenarios were used, one including reproductive values from bootstrap simulations and adult survival estimates of the CGP only (Table 3.13) and one with reproductive values from bootstrap simulations of derived parameters and adult survival estimates from eastern black bear populations (Table 3.14). The λ_s for the first scenario was 0.788 (95% CI: 0.783-0.793) over 10,000 replications of 50 years each (Figure 3.17). The mean final population size was 71 (95% CI: 0- 448) with 54.1 % of the replications resulting in extinction after 50 years (Figure 3.18). The λ_s for the second scenario was 1.114 (95% CI: 1.114- 1.115) over 10,000 replications of 50 years each (Figure 3.19). The mean final

population size was 6,006 (95% CI: 1,059-15,092) with 0.0001 % of the replications resulting in extinction after 50 years (Figure 3.20).

Harvest analysis

Stochastic simulations of population growth for the bear CGP included as many parameter estimates from the CGP as possible. A few scenarios of increased harvest (0%, 1%, 2%, 3%) were selected as possible scenarios. Two sets of parameter estimates were used, one including reproductive values and adult survival estimates from the CGP only and one with reproductive values and adult survival estimates from eastern black bear populations. The λ_s for the CGP only had values between 0.544 and 0.788 (Table 3.15). Harvest cannot be sustained with the CGP mean lambda of 0.788 (95% CI: 0.783-0.793) over 10,000 replications of 50 years each (Figure 3.17). All values of increased harvest had λ_s less than one, which indicates increased harvest is unsustainable under this scenario.

The λ_s for the analysis derived from estimates from eastern black bear populations had values between 1.090 and 1.114 (Table 3.15). The parameters that differed from this set and the CGP only data set were adult survival and reproductive values, which may indicate key parameters for population viability analyses since harvest sustainability was very different under the two parameter sets. All scenarios of increased harvest rate had confidence intervals with a lower limit above one, which indicates increased harvest is sustainable up to 3% with these parameter values. However, with a 7 % increase in harvest, under these parameter values, the mean λ_s was 0.999 (95% CI: 0.996-1.002) with 14.1 % of the replications resulting in extinction after 50 years. This indicates that a 7 % percentage of increase in harvest would be unsustainable.

Comparison with abundance data

Two values of λ from apparent rates of change were calculated, one from summer 2004 to summer 2005, and the other from summer 2005 to summer 2006. From summer 2004 to summer 2005, the median value of λ was 0.861 (95% BCI: 0.484-1.478) (Figure 3.21). From summer 2005 to summer 2006, the median value of λ was 1.043 (95% BCI: 0.641-1.677) (Figure 3.22). The BCI coverage overlapped the values calculated in the population viability analysis.

Discussion

Age and Sex Ratio

The sex ratio of captured bears and unmarked, but known-fate bears differed from 1:1, with more males than females captured or detected. This is common in bear studies, and has been documented in other eastern U.S. black bear populations (Table 3.16). Male black bears have a greater chance of encountering bait stations or being sighted due to increased travel distances and large home ranges; and as a result, a greater chance of being captured than female black bears (Hellgren and Vaughan 1989). Male bears typically have larger home ranges (Garshelis and Pelton 1981, Rogers 1987), and disperse further than females for a variety of reasons, such as aggression (Pelton 1982), food shortage (Rogers 1987), and avoidance of inbreeding (Rogers 1987). Therefore, an apparent sex ratio difference from this study does not necessarily indicate a true sex ratio difference, only that a sex ratio difference exists in the sample of bears, which primarily consist of captured bears. Biases may exist in the dead recovery bears as well. Sampling efforts and study design should attempt to mitigate these differences if one of the main goals is to estimate the true sex ratio. Techniques, such as sex-identification (Taberlet et al. 1993) with DNA from hair snares placed within the size of a bear

female home range, increase the capture probability of female bears and provide a more reliable view of the population sex ratio. Sex-identification with genetic data does have associated errors (Bradley et al. 2001).

Male bear behavior also leads to lower survival probabilities, thus leading to an age structure in males that is younger than females. The bears in central Georgia had a significant difference between the female age distribution and the male age distribution, with females having a larger mean age at first capture. The variation in female age was much larger than males, with the oldest female detected at 18 years of age. The distribution of age frequencies did not vary much from year to year (mean age range over all years: 3.0-5.6), suggesting that the population may be at a stable age structure. Hellgren (1988) suggests that exploited bear populations have mean ages of less than 4 years of age and are less than 55% adults, and unexploited bear populations have mean ages greater than 6 years and greater than 60% adults. With a limited hunting season (1 day per year) in central Georgia, one might *a priori* classify the population as unexploited. The Georgia DNR documented four cases of illegal kills during the course of the study (one marked male bear, two unmarked female bears, one unmarked and unknown sex bear) of the central Georgia bear population. This number is likely an underestimate for the total number of illegal kills, due to low detection rates. The overall mean age of bears initially captured was 4.4, which means the bear CGP can neither be classified as an exploited or unexploited bear population using Hellgren's rule (1988) described above. The overall mean age for both sexes of the bears initially captured is similar to other populations in the southeastern U.S. (Table 3.17).

Reproduction

Reproduction estimates (i.e. age of first reproduction, breeding interval, and ages at which female reared cubs) were based on data from female teeth. These estimates were based on the assumption that information reported from Mattson's Laboratory was accurate. However, eight of the fifteen individual female bears with ages at which cubs were recorded as successfully reared were classified as "layer thinning for this year cannot be determined with certainty". Also, 7 out of 15 individual female bears had layer thinning for years in which years could not be judged because "criteria were absent, indistinct, or ambiguous". This means that possible breeding intervals for these ages were not evaluated. Carrel (1992) reported a few cases in which no light staining cementum was visible for very old females, leading to a source of error in aging old females. However, unlike den observations, reconstruction of reproduction data from females indicates successful cub rearing and accounts for cub mortality (a female's resources would not be allocated to cub rearing if the cub dies, thus the ring for that year would not be thin or indicate a 'cub year'), so it is an approximation of reproduction (Carrel 1992).

The mean age of first reproduction and mean breeding interval for central Georgia, based on the bears sampled, were similar to other estimates of these parameters in the southeastern region of the U. S. (Table 3.2). The mean number of cubs per litter observed during den visits was low compared to other populations in the southeastern U.S. (Table 3.2). It is important to note that most of the sample sizes for the other research studies in the table were much higher, so this difference may be due to a higher degree of variation in small sample sizes. However, if this estimate is representative of the population, it is evidence of a low reproduction rate, an important parameter for predicting population viability models.

Survival

Behavioral traits of male bears, such as increased rates of dispersal and large home ranges, may be responsible for observed lower rates of survival, as outlined in the discussion section on age and sex ratio. Similarly, the female annual survival rate was significantly higher than the male annual survival rate with the radiocollared bears in central Georgia. The combined sex annual survival rate is similar to other populations in the southeastern U. S. (Table 3.1). All causes of mortality observed in other studies, were also observed in central Georgia, including a possible case of cannibalism. The highest sources of mortality with known bears from this population were anthropogenic in nature (vehicle collisions and illegal kills).

The adult survival rate from age-structure data with the λ_s from eastern black bear populations was similar to the adult survival rate of both sexes calculated from radiotelemetry data. If the assumption of a stable age structure is true for this analysis, this suggests that the population may have a λ closer to the eastern black bear population estimate, than the one with mainly CGP data. The age-structure data analysis of survival also suggests little difference between adult and sub-adult estimates, however, only age class two individuals were included in this analysis due to inconsistent sampling effort of the younger age class. It is likely that the estimate is lower since sub-adults tend to have lower survival rates.

Population viability and harvest analysis

We did not have data for two main components (cub and sub-adult survival estimates) of the population viability analysis. Therefore, these estimates were based on studies of other populations of black bears in the eastern United States. These reproduction data have limited value, due to low sample sizes and the associated biases of the types of data. The sensitivity to

population growth and harvest analysis was evaluated with demographic estimates primarily from the CGP, as well as estimates from bear populations in the eastern United States. The CGP demographic estimates of reproductive rate were lower than estimates from other populations, which may just be a reflection of small sample size from reproduction data or, alternatively, it could be evidence of an area of concern for this population. Also, the CGP sample size from radiotelemetry data of adult female survival was not too low (n=30), and was about 5% lower than the weighted female survival mean from black bear populations in the eastern United States. This could also indicate an area of concern for this population compared to other populations in the eastern United States. Both scenarios of demographic parameters led to deterministic population growth estimates that were increasing, but just by a small amount. This indicates that reproduction and adult female survival estimates are an integral component of the health of the population, and future sampling efforts should focus on obtaining a better estimate of the reproduction demographic rate.

All values of increased harvest for the CGP produced $\lambda_s < 1.0$, which indicated increased harvest at any level with reproduction and adult survival estimates based on the CGP data would be unsustainable. The λ_s for the analysis derived from estimates from eastern black bear populations had values greater than one. All scenarios of increased harvest rate (below an increased harvest of 7%) had confidence intervals with a lower limit above one, which indicates increased harvest is sustainable with these parameter values. The conclusions from the two data sets are very different, which may indicate that the CGP is sensitive to the parameters that differ between the two data sets. The parameter values that differed from the two data sets were adult survival, particularly adult female survival, and reproductive values. Future sampling efforts in the CGP should focus on estimating reproduction and cub and sub-adult survival rates to reduce

uncertainty in the population viability analysis. Additional monitoring of female adult survival would also be ideal. Since there is uncertainty in these key parameter values, the most conservative and recommended course of action is not to increase harvest in the CGP.

The BCI coverage from apparent rates of change, calculated from the posterior distributions of total abundance from chapter 2, overlapped the values calculated in the population viability analysis. This indicates that the values used in the population viability analysis are reasonable and are consistent with the apparent rates of change in abundance. Therefore, the conclusions based on increased harvest rates will also be consistent with the values of apparent rate of change from abundance models. In conclusion, future sampling efforts in the CGP should focus on estimating reproduction and cub and sub-adult survival rates and abundance to reduce uncertainty in the population viability analysis and apparent rate of change from abundance models (see Chapter 2 discussion regarding abundance of age class models).

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Table 3.1. Survival estimates reported from American black bear populations in the eastern US.

Location and Source	Sample size	Adult (>1 yr) annual survival rate	Sources of mortality
Great Dismal Swamp, E. Virginia and N.E.. North Carolina (Hellgren and Vaughn 1989) [a]	46	0.59 M, 0.87	LK,C, V, IK (suspected),N, R
White River NWR, Arkansas (Smith 1985) [a]	26	0.95	LK, U
Gum Swamp (Martorello 1998) [a]	29	0.83 (0.70-0.96)	LK, U
Big Pocosin (Martorello 1998) [a]	23	1.00 (0.88-1.00)	none
Camp Lejeune MCB, NC (Brandenburg 1996) [a]	16	0.71 (0.56-0.87)	V, LK, IK, NAT
White Rock, Dry Creek (Clark 1991) [a]	31	0.977	NAT, V, IK, LK, N

[a] physical capture and telemetry , [b] physical capture, [c] apparent annual mortality rate, [d] roadkill and illegal kill

* indicates subadult mortality rate

LK= legal harvest, IK= illegal harvest, C= cannibalism, NAT= natural causes, N= nuisance, V= vehicle collision, R= research handling, U= unknown

Table 3.1 (continued)

Location and Source	Sample size	Adult (>1 yr) annual survival rate	Sources of mortality
GSMNP (McLean 1991) [b]		0.78	LK, IK, C, V, R,NAT,U
Cherokee and Pisgah National Forest (Mclean 1991) [b]		0.7	LK, IK, V, R
Southeastern GA (Abler 1985) [c]	43	0.82 M, 0.68 F	
Southeastern NC (Hamilton 1978) [c]	66	0.72 M, 0.84 F	
Okefenokee Swamp, GA (Dobey et al. 2005) [a]	68,10F*, 6M *	0.89 (0.83-0.95	LK, IK, NAT, V, N
Ocmulgee River, central GA (Grahl 1985) [d]	39	0.95	V, IK
Osceola National Forest, FL (Dobey et al. 2005) [a]	21 , 9 *	0.97 (0.92-1.00)	LK, IK, NAT, V, N

[a] physical capture and telemetry , [b] physical capture, [c] apparent annual mortality rate, [d] roadkill and illegal kill

* indicates subadult mortality rate

LK= legal harvest, IK= illegal harvest, C= cannibalism, NAT= natural causes, N= nuisance, V= vehicle collision, R= research handling, U= unknown

Table 3.2. Reproduction estimates of eastern American black bear populations. Litter size methods are: D (den observations), FC (field count), CL (corpora lutea), and P (placental scars)

Location and Source	State	Litter size method	*N* litters	Mean Litter size	Age of first breeding	Mean interbirth interval
White River NWR (Smith 1985)	AK	D	10	2.3	4	2.4
Dry Creek (Clark 1991)	AK	D	20	2.25 (0.22)		
White River (Clark 1991)	AK	D	17	1.41 (0.12)		
Florida (Harlow 1961)	FL	FC	10	2.2		
Osceola National Forest, FL (Dobey et al. 2005)	FL	D	22 (32 bears)	2.08 (0.14)		
Southeastern GA (Abler 1985)	GA	CL	5	2		
Okefenokee Swamp, GA (Dobey et al. 2005)	GA	D	34 (72 bears	2.1 (0.11)		
Ocmulgee River, central GA (Grahl 1985)	GA	FC	5 females	2		

Table 3.2 (continued)

Southeastern NC (Hamilton 1978)	NC	CL, P	11	2.4		
North Carolina (Collins 1973)	NC	CL	30	1.8	4.2	2
Camp Lejeune MCB (Brandenburg 1996)	NC	D	4	2.5		
Northeast Pennsylvania (Alt 1989)	PA		211	2.98		
GSMNP, CNF_Cherokee National Forest (Wathen 1983)	TN, NC	D	19	2.58	5.2 (n=6)	2.15
GSMNP (McLean 1991)	TN, NC	D	81 *, 23**	1.96 *, 1.96 **	4.82 (n=11)	2.39 (n=18)
Cherokee and Pisgah National Forest (Mclean 1991)	TN, NC	D	32 *, 11**	2.25 *, 1.91 **	3.6 (n=10)	2.2 (n=5)
Virginia (Stickley 1961)	VA	D	19	2.63		
Shenandoah NP (Carney 1985)	VA		21	2		2.3
Shenandoah NP (Kasbohm 1994)	VA		26	2.31		
Great Dismal Swamp (Hellgren and Vaughn 1989)	VA, NC	D,CL	12	2.1	3	2
West Virginia (Alt 1989)	WV		41	2.73		

* cubs, ** yearlings

Table 3.3. Live captures, recaptures and recoveries from American black bears in central Georgia. Note: this summary includes the Sandersville male (2005) and North Carolina female (2003), 3 untagged male bears (2003, 2004), 1 untagged female bear (2006), and 2 capture mortalities (1 initial capture in 2004, 1 recapture in 2004).

	Number of			Number of Recaptures								Number of		
Year	Live Captures			2003		2004		2005		2006		Recoveries		
	Total	M	F	Total	M	F	M	F	M	F	M	F	Total	M	F
2003	30	18	12	2	1	1	0	0	0	0	0	0	1	1	0
2004	19	13	6	7	3	2	1	1	0	0	0	0	2	2	0
2005	15	7	8	5	1	2	2	0	0	0	0	0	6	5	1
2006	20	15	5	2	0	0	1	0	1	0	0	0	2	2	0
2007	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0
2008	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
TOTAL	84	53	31	16	5	5	4	1	1	0	0	0	14	12	2

Table 3.4. Dead recovery bears from the American black bear central Georgia population (15 M: 11 F) included in the age distribution analysis. Additional unmarked bears were also included (2 M: 3F). The bears are summarized below by mortality cause or unmarked/no mortality and year of tooth extraction or estimated age.

Year	2001		2002		2003		2004		2005		2006		2007		
Mortality Cause or Unmarked live capture	M	F	M	F	M	F	M	F	M	F	M	F	M	F	TOTAL
Capture mortality					2					1					3
Vehicle collision	1		1		2	2		1	3	4	4		2		20
Illegal kill								1		1					2
Legal harvest										1					1
Unmarked live capture					1	1					1	2			5
TOTAL	1	0	1	0	5	3	0	2	3	7	5	2	2	0	31

Table 3.5. central Georgia population den observation data of American black bears from 2004 to 2007. An '*' indicates the bear ran away before the resting location could be determined, and a '+' indicates the estimate was based on the number of cubs heard making noise.

Year	Location	Bear	Observed	Cubs	cub age	Cub weight (kg.)
2004		20	1	4	6 weeks	
2004		25	1	2	6 weeks	
2004		26	1	2	6 weeks	
2005		27	1	0		
2005		37	1	2		
2005		43	1	2		
2005		44 *	0			
2005		48 *	0			
2006	OW	13	1	3 (1M, 2F)	6 weeks	1.36-1.7
2006	Perry	18	1	0		
2006	Twiggs	62	1	1-2 +		
2007		25 *	0			
2007		75 *	0			
2007	OC	16	1	1	yearling	
2007	N. of 96	65	1	2	6 weeks	
2007		78 *	0			
2007		84 *	0			
2007	OW	76	1	2 (2F)	4 weeks	0.91-1.13
2007		58	0			
2007		61	0			

Table 3.6. Reproduction estimates of American black bear populations in the eastern United States used in analysis from multiple studies of mean litter size. The litter size methods include: D (den observations), FC (field count), CL (corpora lutea), P (placental scars).

Study	State	Litter size method	*N* (Litters unless marked F)	Mean litter size
Central GA (this study)	GA	D	12	1.8
White River NWR (Smith 1985)	AK	D	10	2.3
Dry Creek (Clark 1991)	AK	D	13	2.38
White River (Clark 1991)	AK	D	14	1.36
Florida (Harlow 1961)	FL	FC	10	2.2
Osceola National Forest, FL (Dobey et al. 2005)	FL	D	22 L, 104 F	2.1
Southeastern GA (Abler 1985)	GA	CL	5	2
Okefenokee Swamp, GA (Dobey et al. 2005)	GA	D	34 L, 72 F	2.1
Ocmulgee River, central GA (Grahl 1985)	GA	FC	5 F	2
Southeastern NC (Hamilton 1978)	NC	CL, P	11	2.4
North Carolina (Collins 1973)	NC	CL	30	1.8
Camp Lejeune MCB (Brandenburg 1996)	NC	D	4	2.5
Northeast Pennsylvania (Alt 1989)	PA		211	2.98
GSMNP, CNF_Cherokee National Forest (Wathen 1983)	TN, NC	D	19	2.58

Study	State	Litter size method	*N* (Litters unless marked F)	Mean litter size
GSMNP (McLean 1991)	TN,NC	D	83	1.99
Cherokee and Pisgah National Forest (Mclean 1991)	TN,NC	D	34	2.24
Virginia (Stickley 1961)	VA	D	19	2.63
Shenandoah NP (Carney 1985)	VA		21	2
Shenandoah NP (Kasbohm 1994)	VA		26	2.31
Great Dismal Swamp (Hellgren and Vaughn 1989)	VA, NC	D,CL	12	2.1
West Virginia (Alt 1989)	WV		41	2.73
GSMNP (Eiler et al. 1989)	TN, NC	D	22	2.59

Table 3.7. Reproduction estimates of American black bear populations in the Eastern United States used in analysis from multiple studies of mean interbirth interval. The litter size methods include: D (den observations), FC (field count), CL (corpora lutea), P (placental scars).

Study	State	Litter size method	*N* (Litters)	Mean interbirth interval
Central GA (this study)	GA	D	12	2.1
White River NWR (Smith 1985)	AK	D	10	2.4
North Carolina (Collins 1973)	NC	CL	30	2
GSMNP, CNF_Cherokee National Forest (Wathen 1983)	TN, NC	D	19	2.15
GSMNP (McLean 1991)	TN,NC	D	83	2.39
Shenandoah NP (Carney 1985)	VA		21	2.3
Great Dismal Swamp (Hellgren and Vaughn 1989)	VA, NC	D,CL	12	2

Table 3.8. Annual survival estimates, variance, standard error (*SE*), and 95% confidence intervals for male and female American black bears from the central Georgia population using the Kaplan-Meier approach with the staggered entry design for years 2003 to 2008.

	Males				Females			
Year	Survival estimate	Survival variance	Survival *SE*	Survival 95% CI	Survival estimate	Survival variance	Survival *SE*	Survival 95% CI
2003	0.908	0.004	0.067	(0.777-1.000)	1.000	0.000	0.000	(1.000-1.000)
2004	1.000	0.000	0.000	(1.000-1.000)	1.000	0.000	0.000	(1.000-1.000)
2005	0.851	0.005	0.072	(0.711-0.992)	0.909	0.004	0.060	(0.792-1.000)
2006	0.875	0.004	0.065	(0.749-1.000)	1.000	0.000	0.000	(1.000-1.000)
2007	0.754	0.010	0.100	(0.558-0.950)	1.000	0.000	0.000	(1.000-1.000)
2008	N/A	N/A	N/A	N/A	0.237	0.011	0.103	(0.034-0.439)
Overall	0.845	0.002	0.047	(0.754-0.937)	0.861	0.003	0.059	(0.746-0.976)

Table 3.9. Sources of mortality for radiocollared bears in the central Georgia American black bear study. Other sources of mortality include: 2 capture mortalities (censored from analysis at capture mortality), 1 nuisance bear (removed from analysis entirely), 1 illegal kill, 1 possible case of cannibalism and 2 unknown causes of death.

Year	Number of mortalities	Number of vehicle collisions	Number of male mortalities	Number of female mortalities
2003	1	0	1	0
2004	2	0	2	0
2005	6	5	5	1
2006	2	1	2	0
2007	2	1	2	0
2008	1	0	0	1
TOTAL	14	7	12	2

Table 3.10. Studies with estimates of American black bear cub survival used in the central Georgia population population viability analyses.

Location and Source	Data type	*N*	Survival rate
MA (Elowe & Dodge 1989)	Direct observation	41 (21M, 20F)	0.38 M, 0.8 F
Bunnell and Tait (1985)	Literature review		0.70-0.75
GSMNP (Eiler et al. 1989)	Direct observation	29	0.621

Table 3.11. Studies with estimates of sub-adult American black bear survival used in the population viability analyses for the central Georgia population. Data types include: PC (physical capture) and T (telemetry)

Location and Source	Data type	*N*	Survival rate
Osceola National Forest, FL (Dobey et al. 2005)	PC, T	9 F	0.95
Okefenokee Swamp, GA (Dobey et al. 2005)	PC, T	10 F, 6 M	0.94 F, 0.63 M
MA (Elowe & Dodge 1989)	Direct observations	8 M, 16 F	0.25 M, 0.8125 F
Bunnell and Tait (1981)	Literature review		0.65-0.85

Table 3.12. Studies with estimates of adult American black bear survival used in the population viability analyses for the central Georgia population. All study data types were from physical captures and telemetry. Dashed lines indicate survival estimates for males were not available for that particular study.

Location and Source	N_f	Female survival rate (95%CI)	N_m	Male annual survival rate (95%CI)
Great Dismal Swamp, VA, NC (Hellgren and Vaughn 1989)	24	0.87	22	0.59
White Rock, Dry Creek, AK (Clark 1991)	31	0.977	-	-
Okefenokee Swamp, GA (Dobey et al. 2005)	41	0.88 (0.81-0.95)	11	0.76 (0.57-0.96)
Osceola National Forest, FL (Dobey et al. 2005)	21	0.98 (0.94-1.00)	-	-
CGP (this study)	30	0.861 (0.746-0.976)	51	0.845 (0.754-0.937)

Table 3.13. Demographic parameter estimates primarily from the central Georgia population of American black bears used in population viability analyses. The initial population sizes were pooled over all years of physical captures of the central Georgia population. An equal sex-ratio was used in all analyses.

Age class	Age Class	N	N_m	N_f	Male survival[2,3,4], S_m (CV)	Female survival[2,3,4], S_f (CV)	Reproduction Rate[1], b	Mean litter size[1]	Mean breeding interval[1] (CV)
Cubs	0	3	1	2	0.632 (0.034)	0.632 (0.034)	0	0	0
Sub-adults	1	7	6	1	0.543 (0.124)	0.863 (0.019)	0	0	0
Sub-adults	2	19	13	6	0.543 (0.124)	0.863 (0.019)	0	0	0
Adults	3	59	34	25	0.845 (0.055)	0.861 (0.068)	0.845	1.79	2.1 (0.06)

[1] Estimates were calculated from central Georgia population data (n=12 observations of litters, n=8 females' breeding intervals)

[2] Cub estimate was calculated from eastern black bear studies (n=3 studies)

[3] Sub-adult estimates were calculated from eastern black bear studies (n=4 studies)

[4] Adult survival was calculated from central Georgia population Kaplan-Meier estimates from telemetry data (n=81 bears)

Table 3.14. Demographic parameter estimates primarily from eastern American black bear studies, including the central Georgia population, used in population viability analyses. The initial population sizes were pooled over all years of physical captures of the central Georgia population. An equal sex-ratio was used in all analyses.

Age class	Age Class	N	N_m	N_f	Male survival[2,3,4], S_m (CV)	Female survival[2,3,4], S_f (CV)	Reproduction Rate[1], b	Mean litter size[1]	Mean breeding interval[1] (CV)
Cubs	0	3	1	2	0.632 (0.034)	0.632 (0.034)	0	0	0
Sub-adults	1	7	6	1	0.543 (0.124)	0.863 (0.019)	0	0	0
Sub-adults	2	19	13	6	0.543 (0.124)	0.863 (0.019)	0	0	0
Adults	3	59	34	25	0.767 (0.009)	0.909 (0.002)	1.137	2.45	2.15 (0.003)

[1] Estimates were calculated from a collection of eastern black bear populations (*n*=22 studies of mean litter size, *n*=7 studies of breeding intervals)

[2] Cub estimate was calculated from eastern black bear studies (*n*=3 studies)

[3] Sub-adult estimates were calculated from eastern black bear studies (*n*=4 studies)

[4] Adult estimates were calculated from eastern black bear studies (*n*=5 studies)

Table 3.15. Increased harvest rate scenarios with stochastic simulations (n=10,000 replications) of λ_s using reproduction data from the American black bear central Georgia population only and from eastern American black bear populations.

Increase in harvest rate	λ_s (95 % CI) for CGP only	% extinct for CGP only	λ_s (95% CI) from eastern black bear populations	% extinct from eastern black bear populations
0%	0.788 (0.783-0.793)	0.542	1.114 (1.114-1.115)	0.0001
1%	0.704 (0.699-0.710)	0.683	1.107 (0.107-1.108)	0.0003
2%	0.615 (0.610-0.620)	0.814	1.100 (1.099-1.100)	0.0011
3%	0.544 (0.540-0.549)	0.892	1.090 (1.089-1.090)	0.0034

Table 3.16. Sex ratio of American black bears in research projects from the eastern United States. The data types include: physical captures (PC) and harvest data (H).

Location and Source	State(s)	Data type	Sample size	Sex ratio (M:100 F)
Great Dismal Swamp (Hellgren and Vaughn 1989)	VA, NC	PC	101	237
White River NWR (Smith 1985)	AR	PC	64	156
White Rock, Dry Creek (Clark 1991)	AR	PC	113	88
Osceola National Forest (Dobey et al. 2005)	FL	PC	78	160
Southeastern GA (Abler 1985)	GA	PC, H	43	72
Okefenokee Swamp (Dobey et al. 2005)	GA	PC	127	149
Ocmulgee River (Grahl 1985)	GA	PC	22	340
Southeastern NC (Hamilton 1978)	NC	PC, H	66	194
Gum Swamp (Martorello 1998)	NC	PC	136	116
Big Pocosin (Martorello 1998)	NC	PC	77	88
GSMNP (McLean 1991)	TN, NC	PC	312	92
Pisgah National Forest (Mclean 1991)	TN, NC	PC	26	133
Cherokee National Forest (McLean 1991)	TN, NC	PC	43	96

Table 3.17. Age structure of eastern United States American black bear populations. All data types are from physical captures, unless specifically noted.

Location and Source	State	Sample size	$\bar{x}_{total}$ (sd)	$\bar{x}_f$ (sd)	$\bar{x}_m$ (sd)
Great Dismal Swamp (Hellgren and Vaughn 1989)	VA, NC	100 (30F:70M)	4.2 (0.3)	4	4.2
Big & Montgomery Islands (White 1996)	AR	12 (4F:8M)		8.5	4.5
White Rock, Dry Creek (Clark 1991)	AR	113 (53M:60F)		4.68 (0.44)	4.58 (0.57)
Osceola National Forest (Dobey et al. 2005)	FL	78 (30F:48M)	3.3 (0.28)	3.4 (0.45)	3.2 (0.36)
Ocala NF (McCown et al. 2004)	FL	126 (40F:86M)		4.8	4.4
Okefenokee Swamp (Dobey et al. 2005)	GA	127 (51F:76M)	3.8 (0.21)	4.5 (0.33)	3.3 (0.25)
Ocmulgee River (Grahl 1985) [1]	GA	39 (6F:33M)		6.1	4.8
Camp Lejeune MCB (Brandenburg 1996)	NC	15 (12F:3M)	5.7 (1.45)	5.9 (1.17)	9.875 (10)
Gum Swamp, Big Pocosin (Martorello 1998)	NC	123	4.2 (0.22)		
GSMNP (McLean 1991)	TN, NC	437 (254M:183F)	4.52 (2.704)	5.28 (3.224)	3.92 (2.1)

Pisgah National Forest (Mclean 1991)	TN, NC	56 (30M:26F)	3.86 (2.631)	4.46 (3.256)	3.33 (1.84)
Cherokee National Forest (McLean 1991)	TN, NC	66 (39M:27F)	3.74 (2.037)	3.28 (1.761)	4.06 (2.171)

[1] Data from vehicle collisions and illegal kills were also included into these reported means

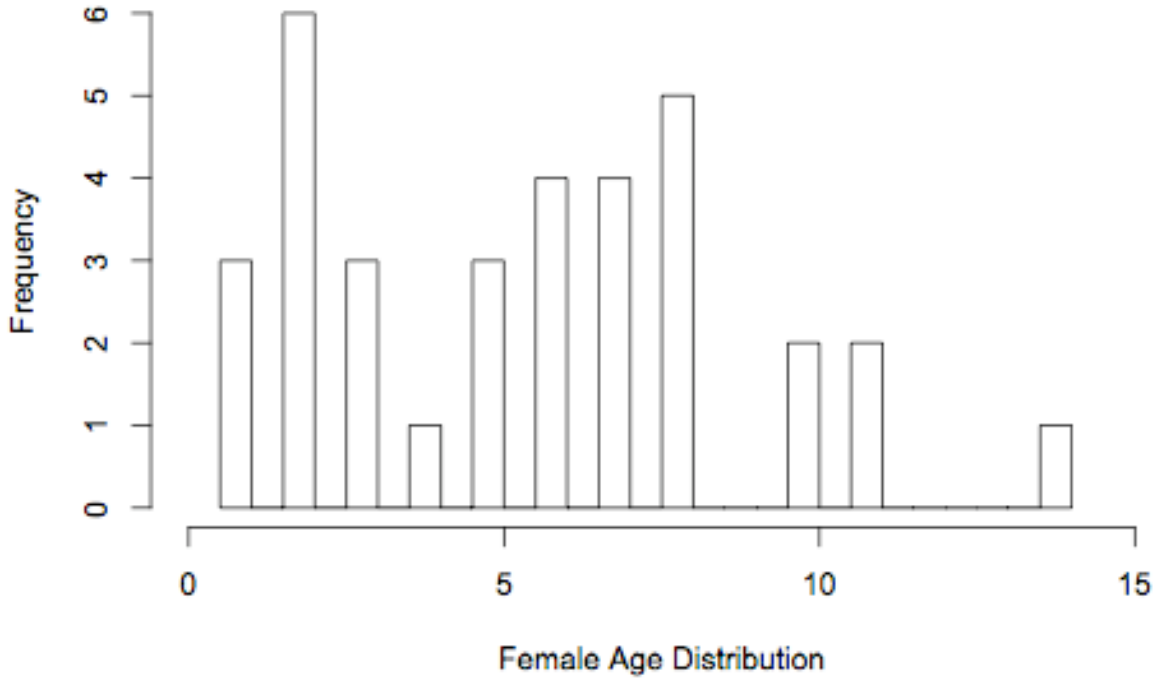


Figure 3.1. Age frequency of female American black bears at initial capture in Middle Georgia, 2003-2006.

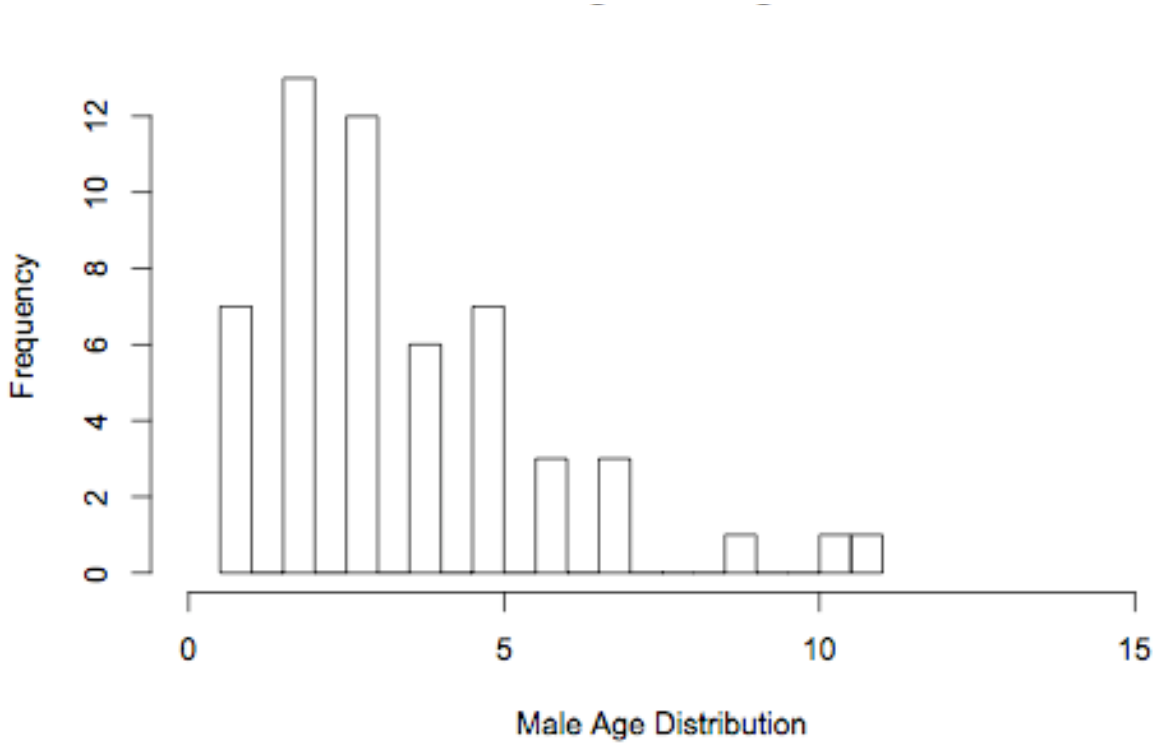


Figure 3.2. Age frequency of male American black bears at initial capture in Middle Georgia, 2003-2006.

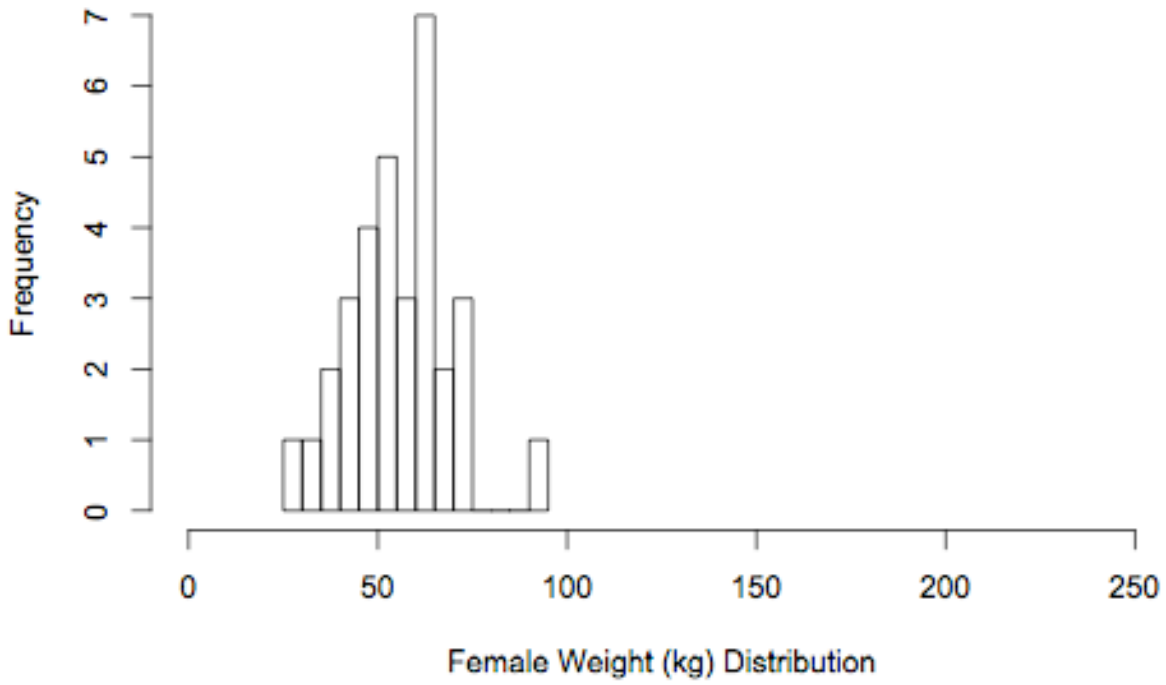


Figure 3.3. Body mass (kg) of female American black bears at initial capture from Middle Georgia, 2003-2006.

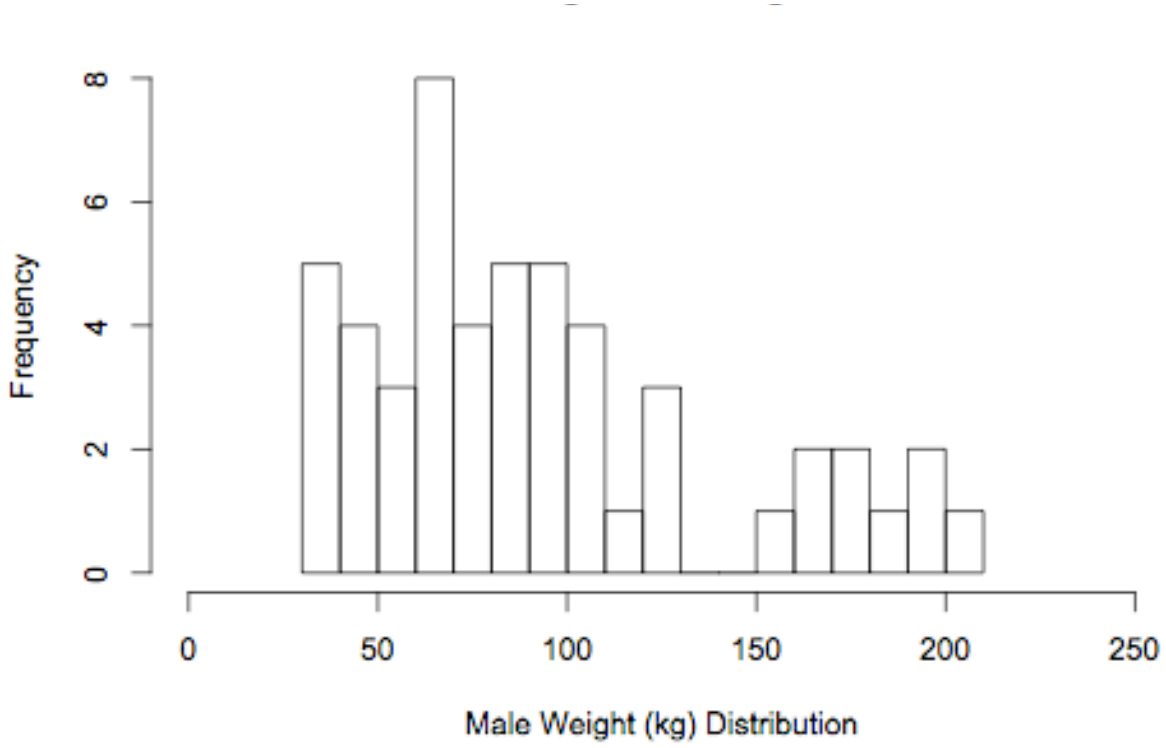


Figure 3.4. Body mass (kg) of male American black bears at initial capture from Middle Georgia, 2003-2006.

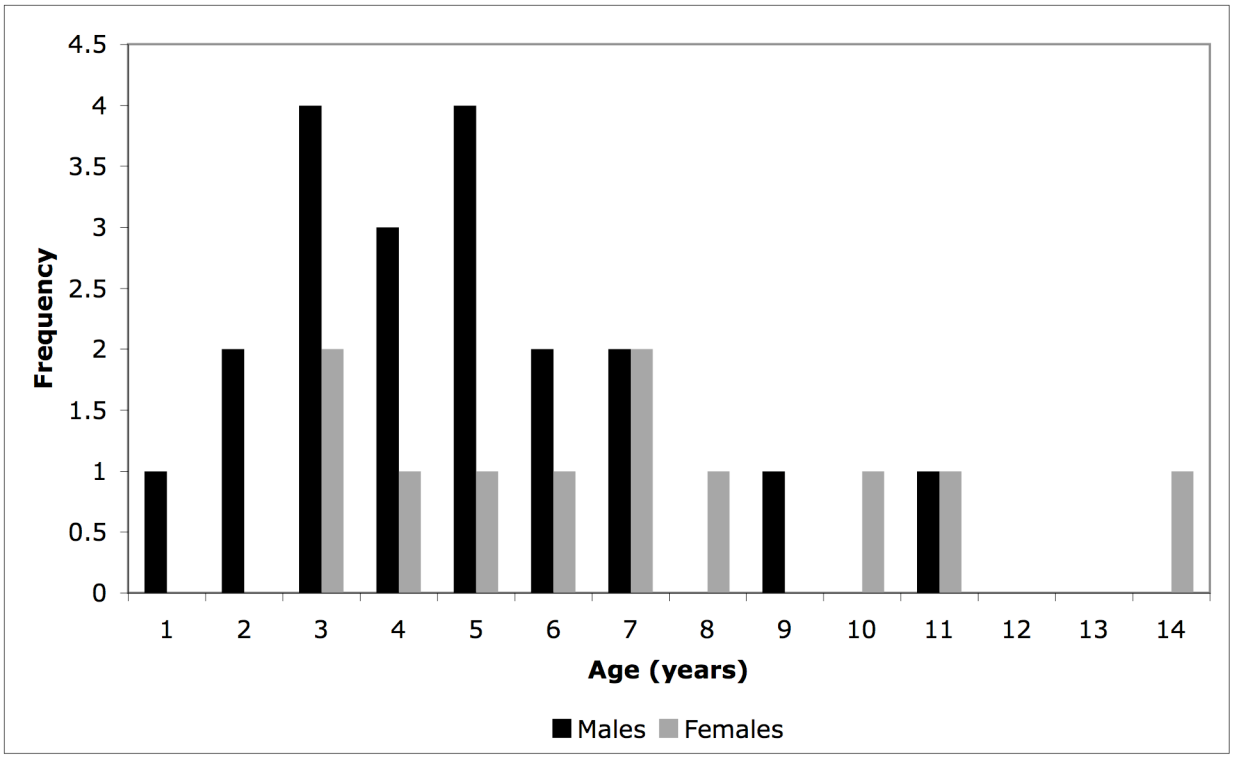


Figure 3.5. Age frequency of American black bears at initial capture in Middle Georgia in 2003.

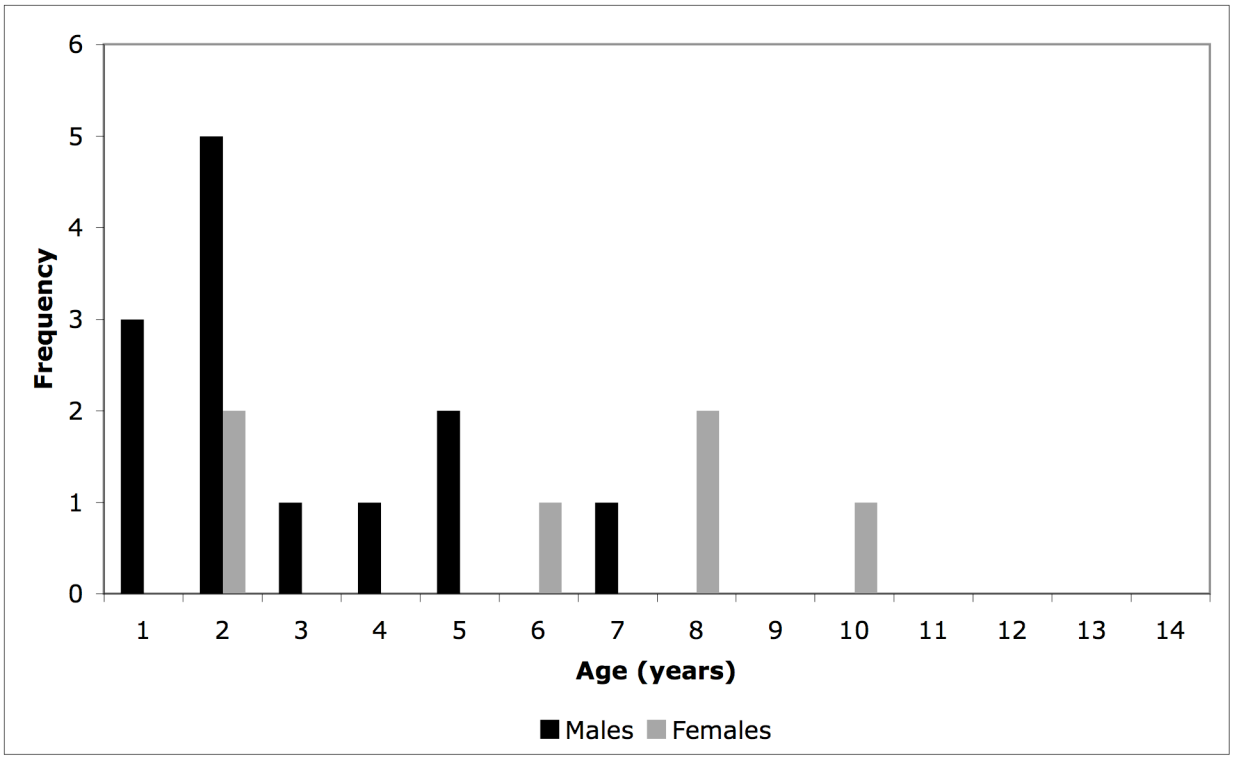


Figure 3.6. Age frequency of American black bears at initial capture in Middle Georgia in 2004.

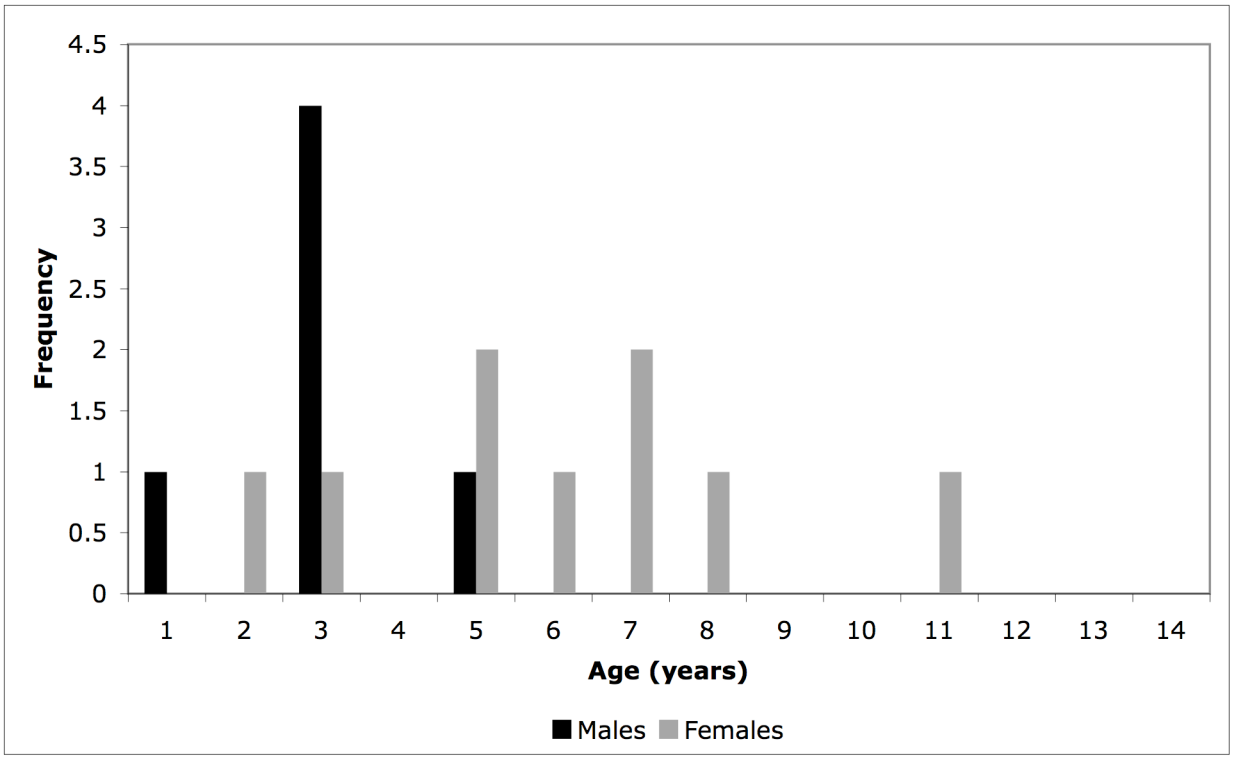


Figure 3.7. Age frequency of American black bears at initial capture in Middle Georgia in 2005.

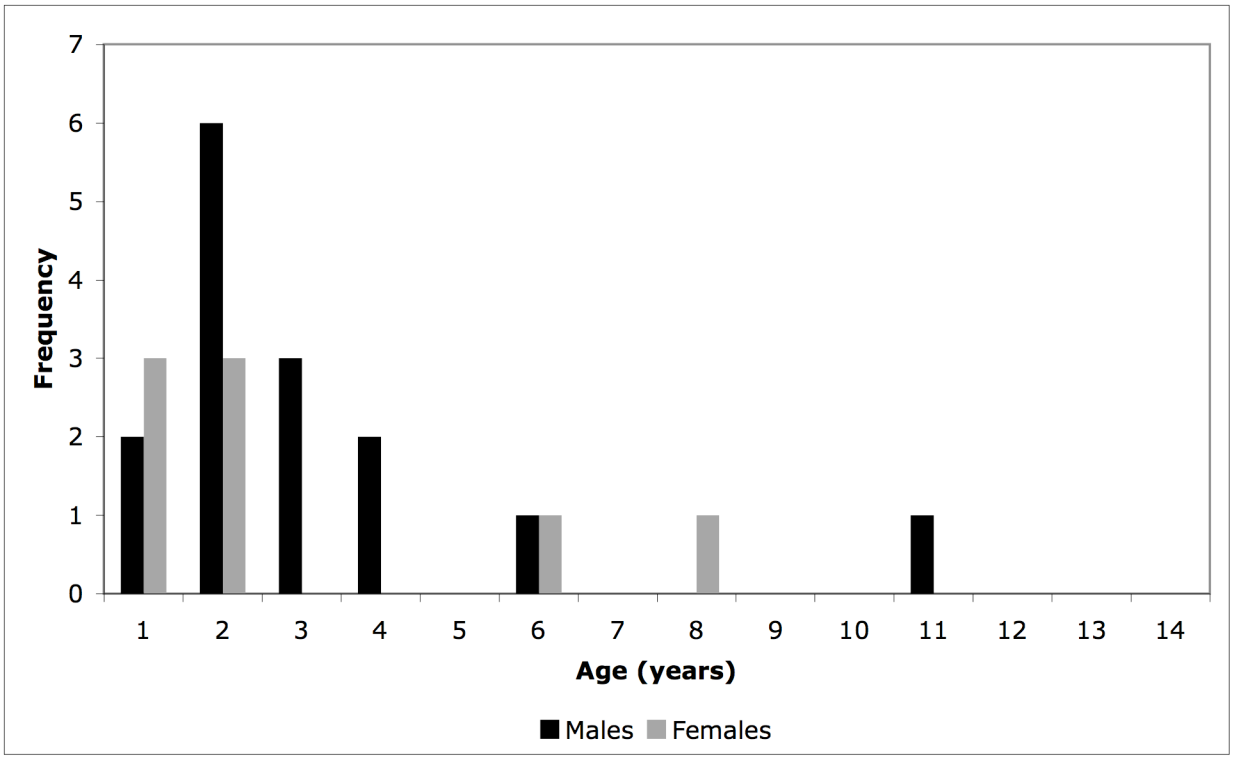
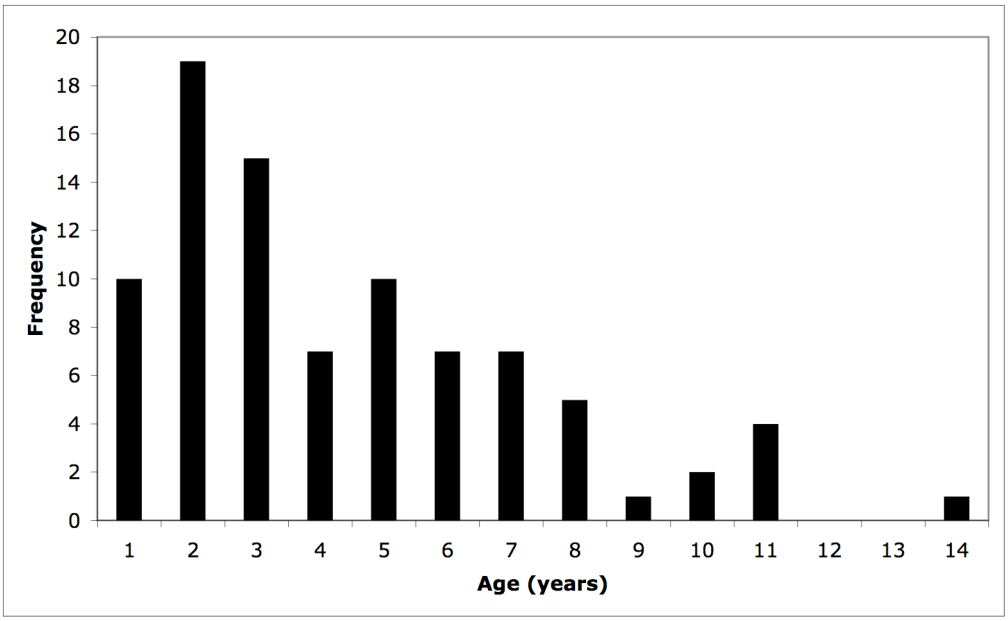


Figure 3.8. Age frequency of American black bears at initial capture in Middle Georgia in 2006.

a)



b)

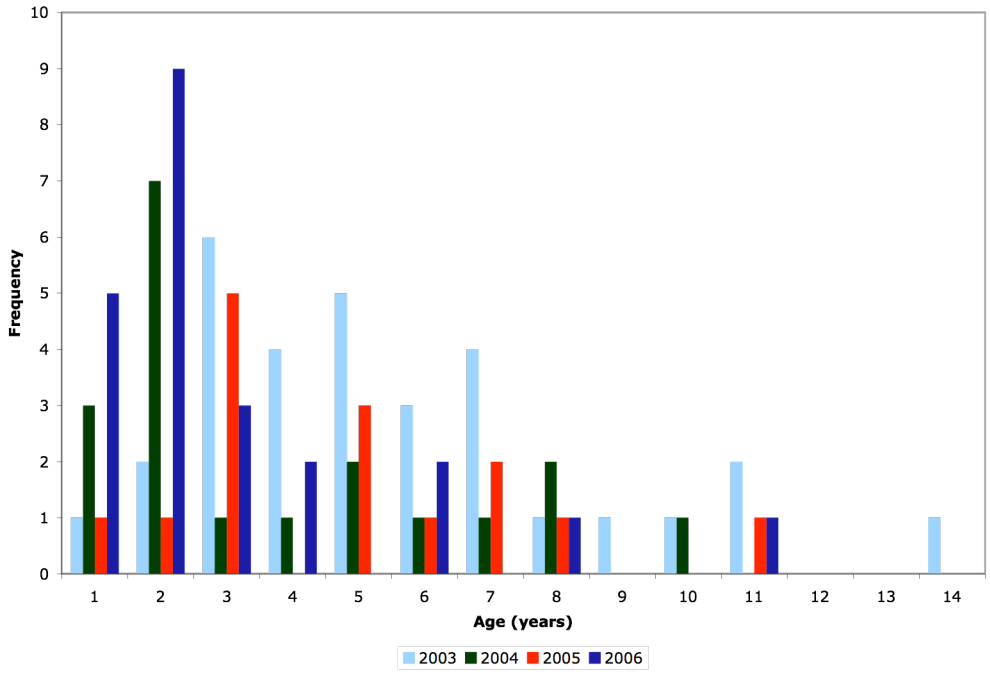


Figure 3.9. Age frequency of all American black bears at initial capture in Middle Georgia from 2003 to 2006 with a) all years combined, and b) separated by year.

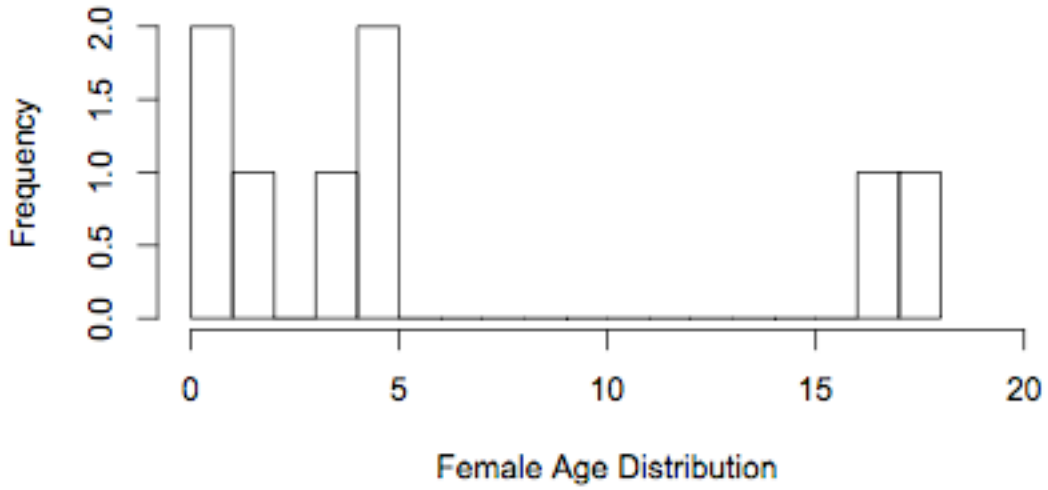


Figure 3.10. Age frequency of dead recovery female American black bears in Middle Georgia, 2003-2006.

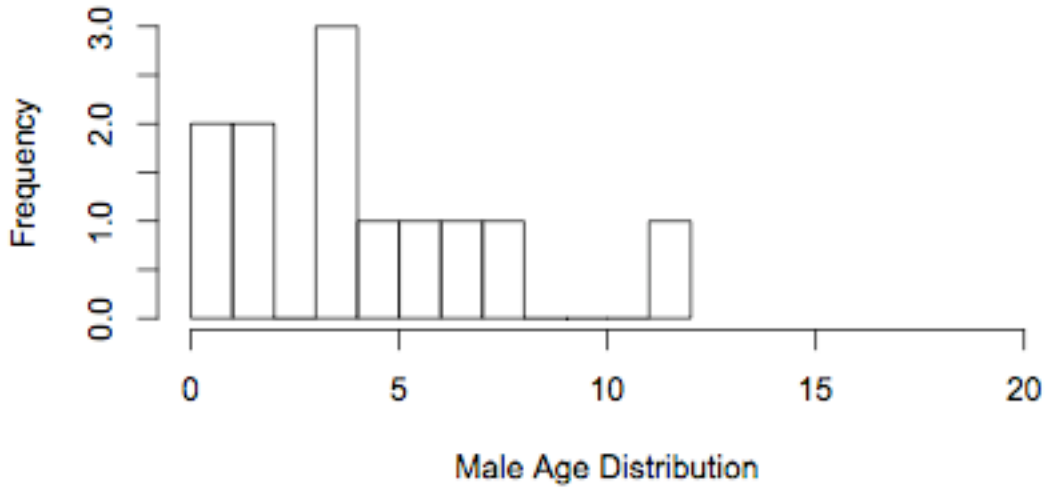


Figure 3.11 Age frequency of dead recovery male American black bears in Middle Georgia, 2001-2007.

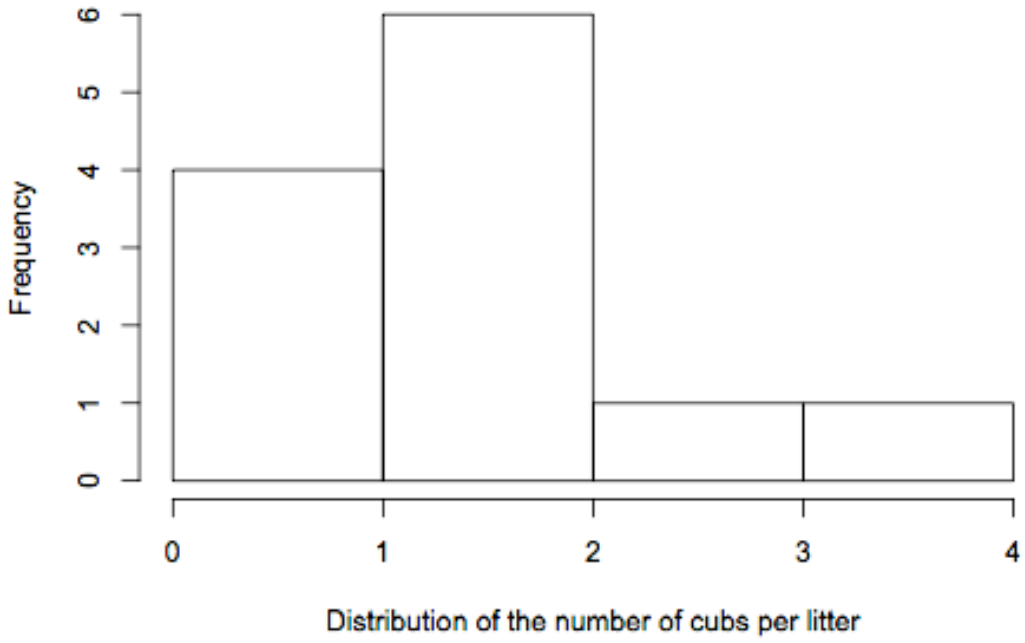


Figure 3.12. Number of cubs per litter from den observations of American black bears in Middle Georgia from 2003 to 2007 (*n*=12 bears).

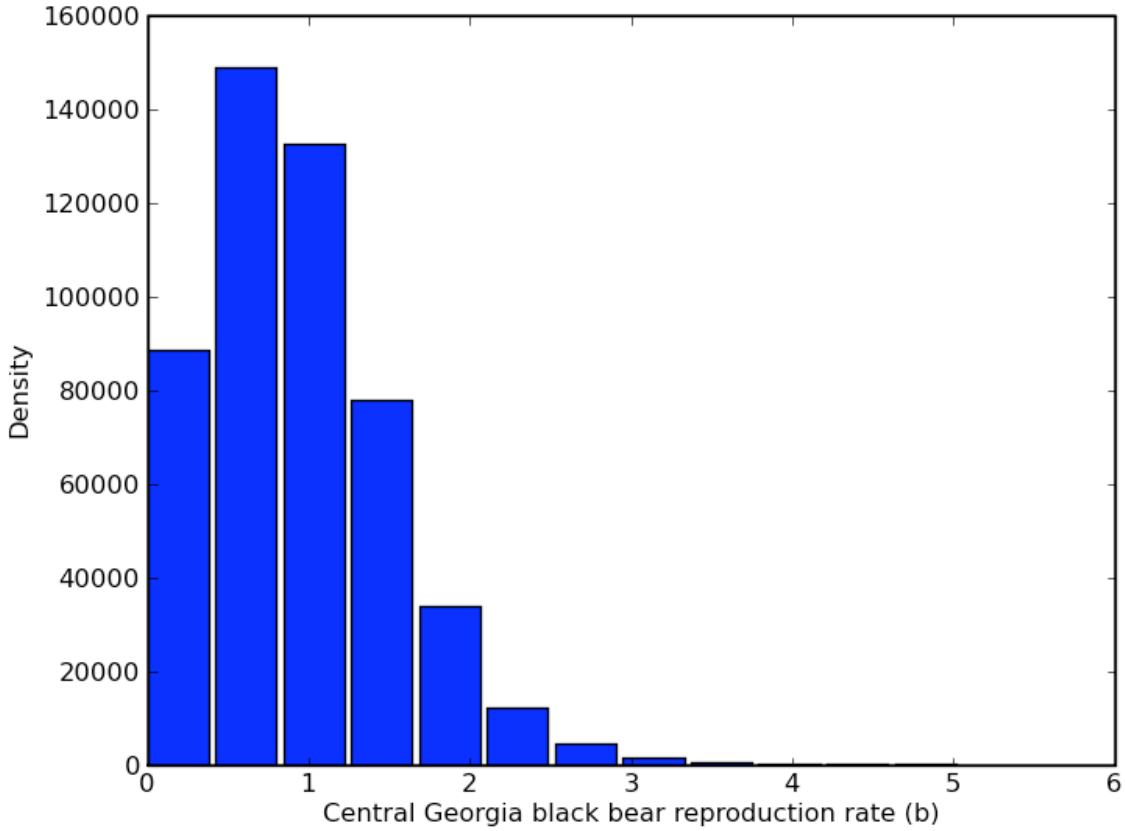


Figure 3.13. Simulated distribution of reproduction rate for the central Georgia American black bear population using data from 2003 to 2007.

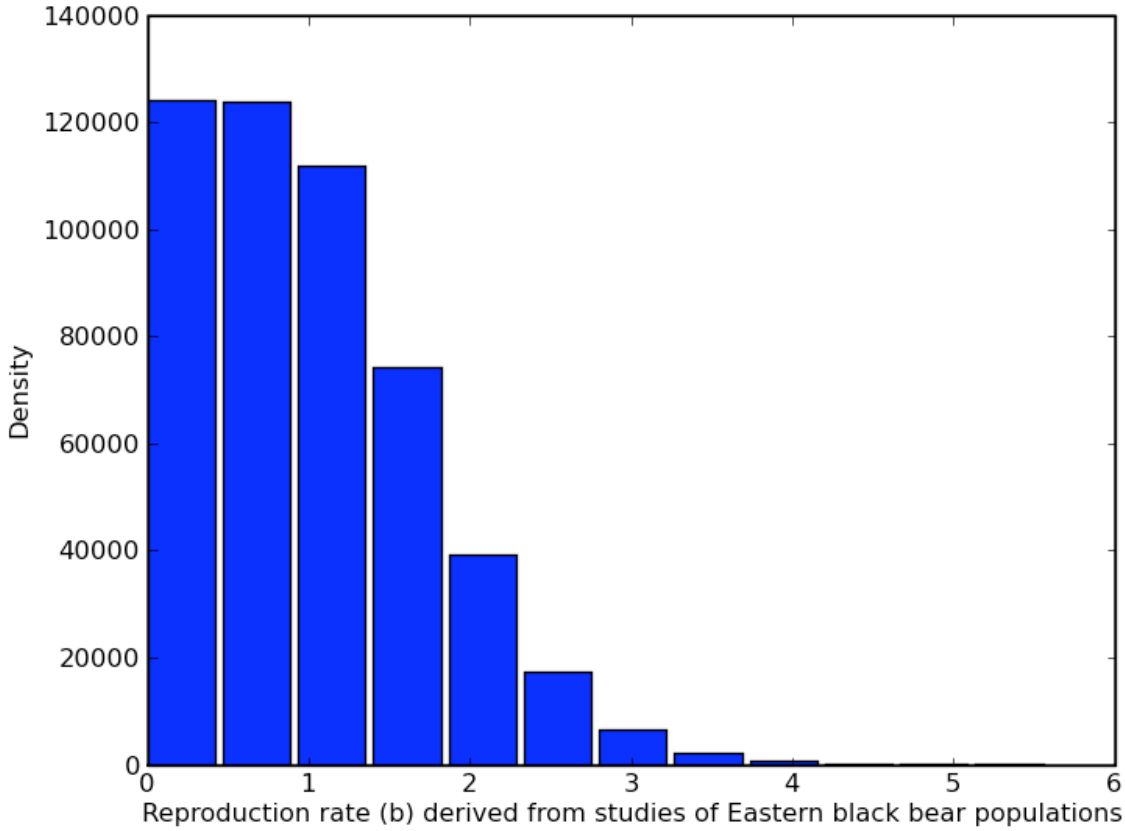


Figure 3.14. Simulated distribution of reproduction rate from eastern American black bear populations (*n*=22 studies).

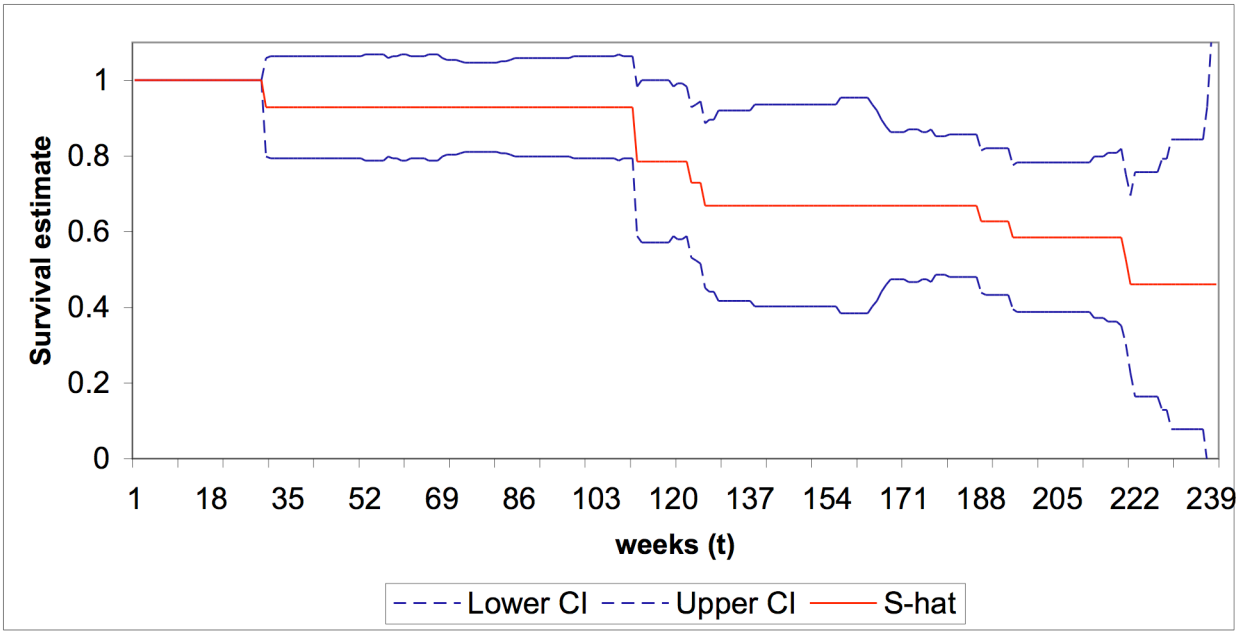


Figure 3.15. Kaplan-Meier survival estimates for male American black bears by week for the central Georgia population from 2003 to 2008. Lower and upper confidence intervals are also displayed.

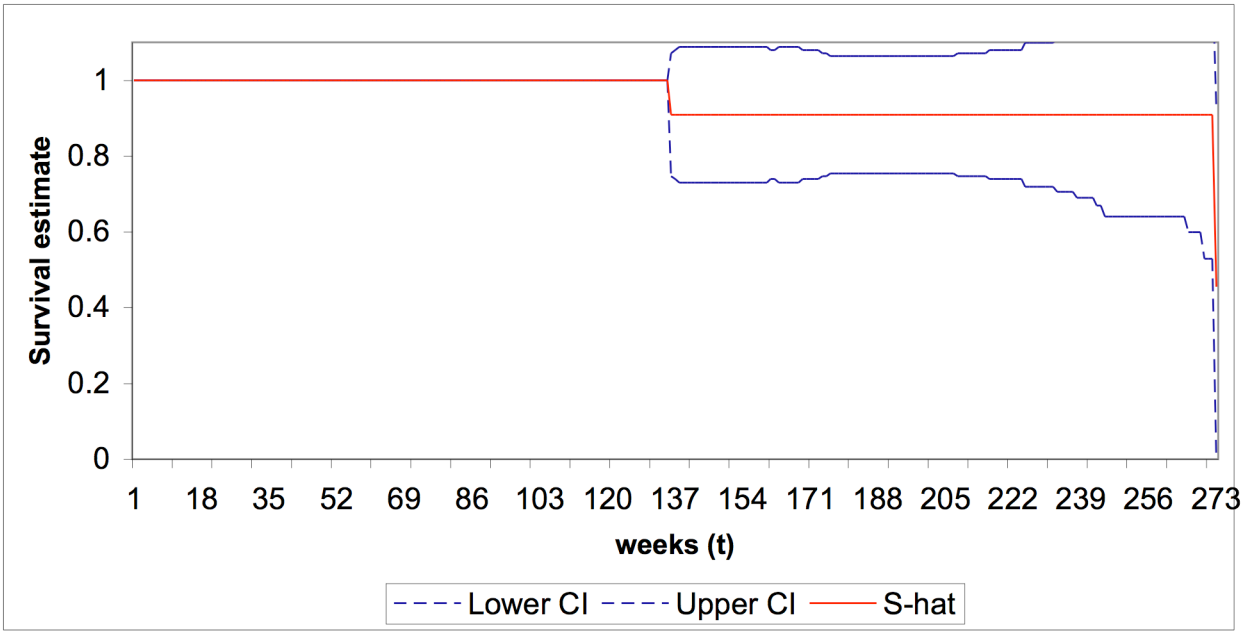


Figure 3.16. Kaplan-Meier survival estimates for female American black bears by week for the central Georgia population from 2003 to 2008. Lower and upper confidence intervals are also displayed.

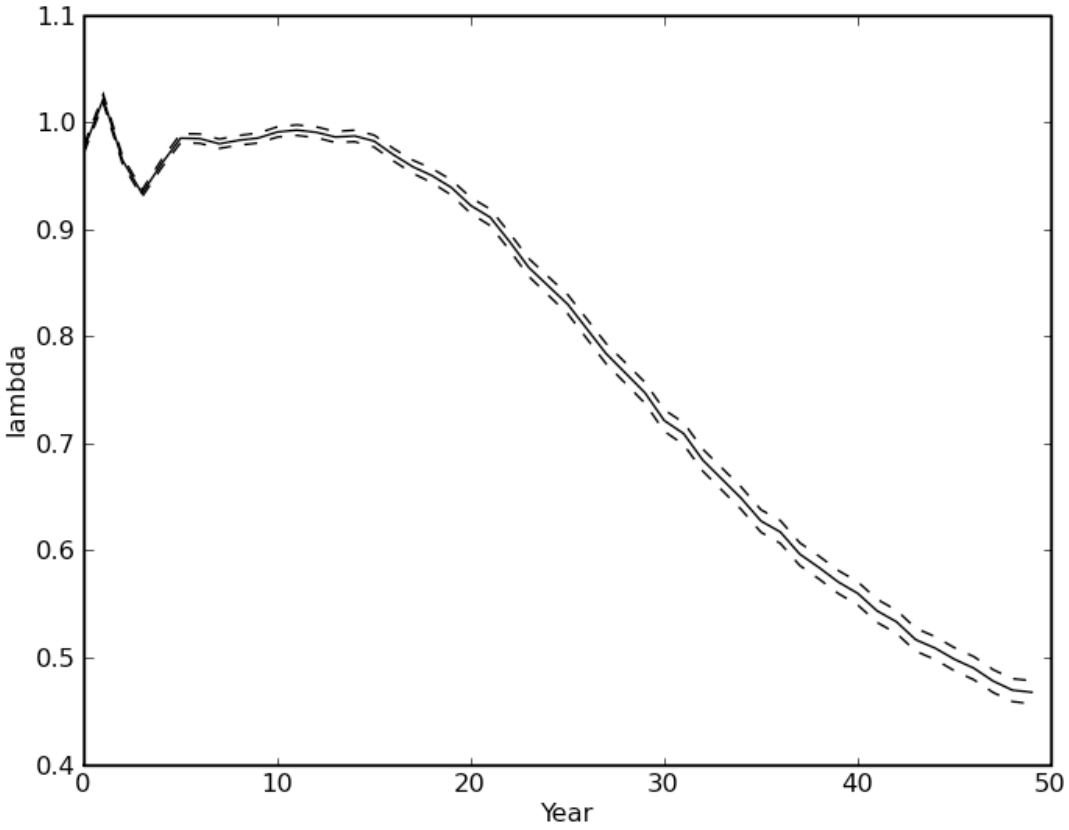


Figure 3.17. Stochastic simulations (n=10,000) of mean λ_s and 95 % CI lines over 50 years with reproduction and survival data from the central Georgia American black bear population and no harvest.

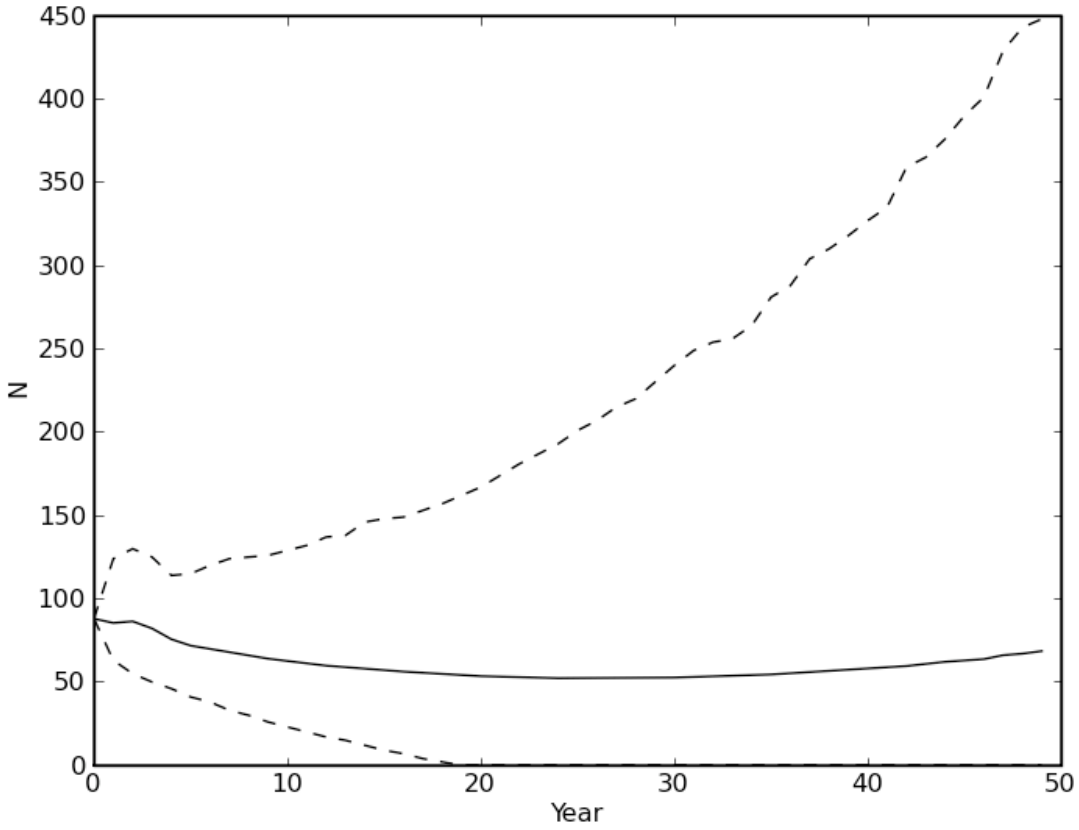


Figure 3.18. Stochastic simulations (n=10,000) of American black bear abundance (N) and 95 % CI lines over 50 years with reproduction and survival data from the central Georgia population and no harvest.

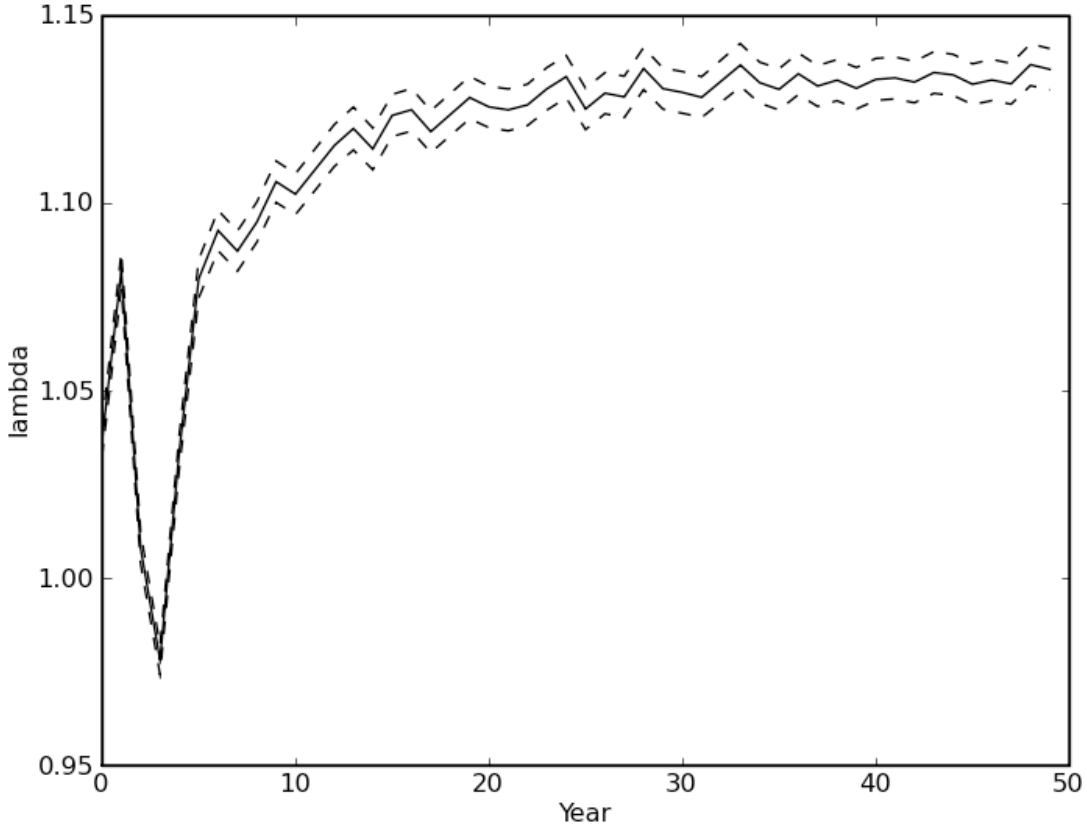


Figure 3.19. Stochastic simulations (n=10,000) of mean λ_s and 95 % CI lines over 50 years with reproduction and survival data from eastern American black bear populations and no harvest.

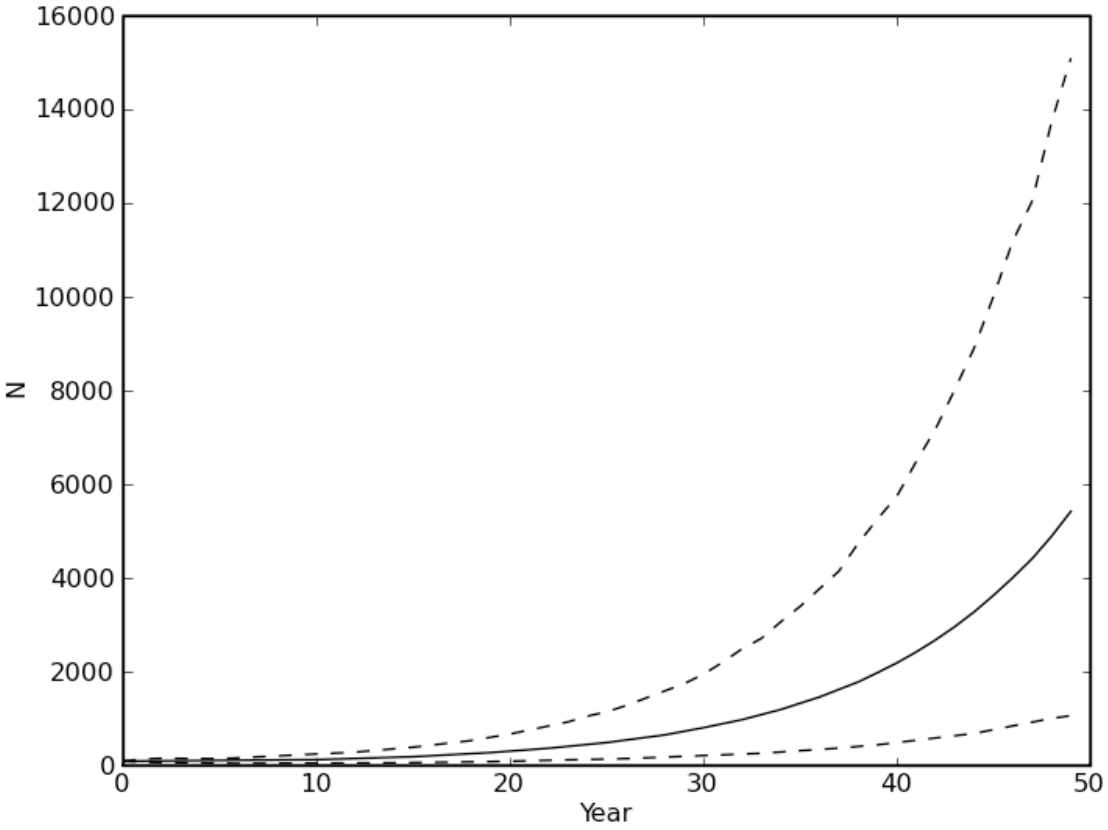


Figure 3.20. Stochastic simulations (n=10,000) of black bear abundance (N) and 95 % CI lines over 50 years with reproduction and survival data eastern American black bear populations and no harvest.

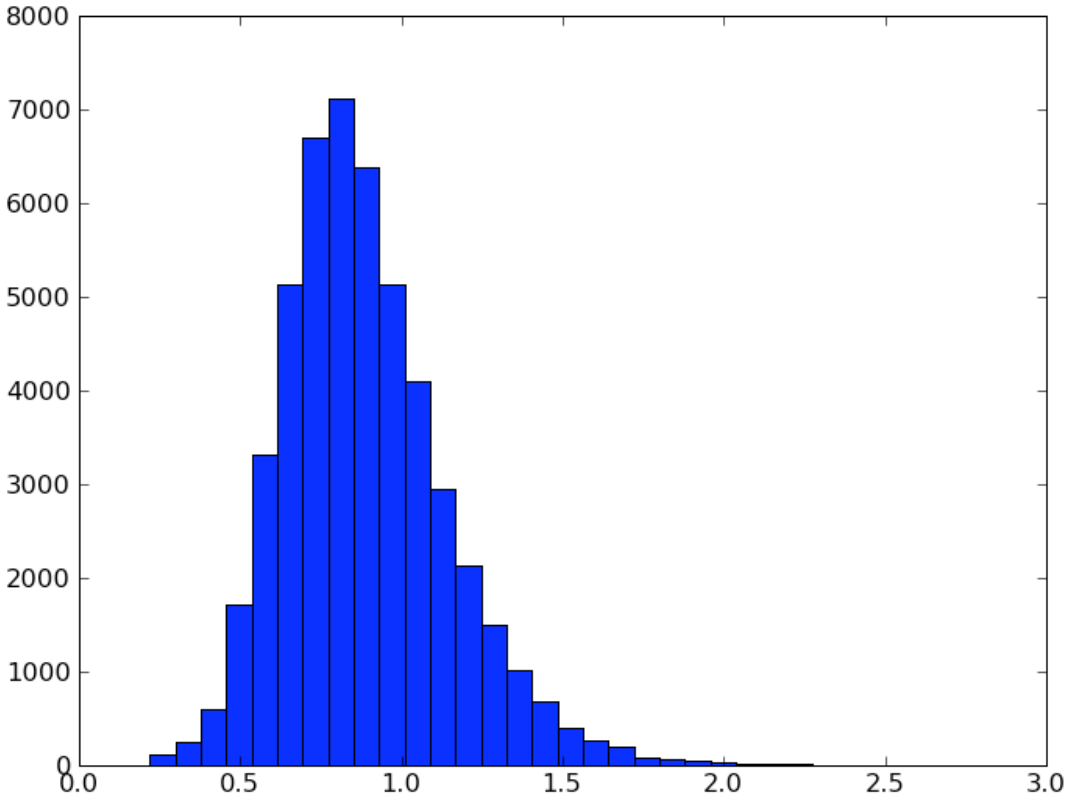


Figure 3.21. American black bear distribution of λ from 2 chains of 50,000 MCMC iterations (25,000 burn-in period) from the three data structure joint model for total abundance, for the time period from summer 2004 to summer of 2005 in central Georgia.

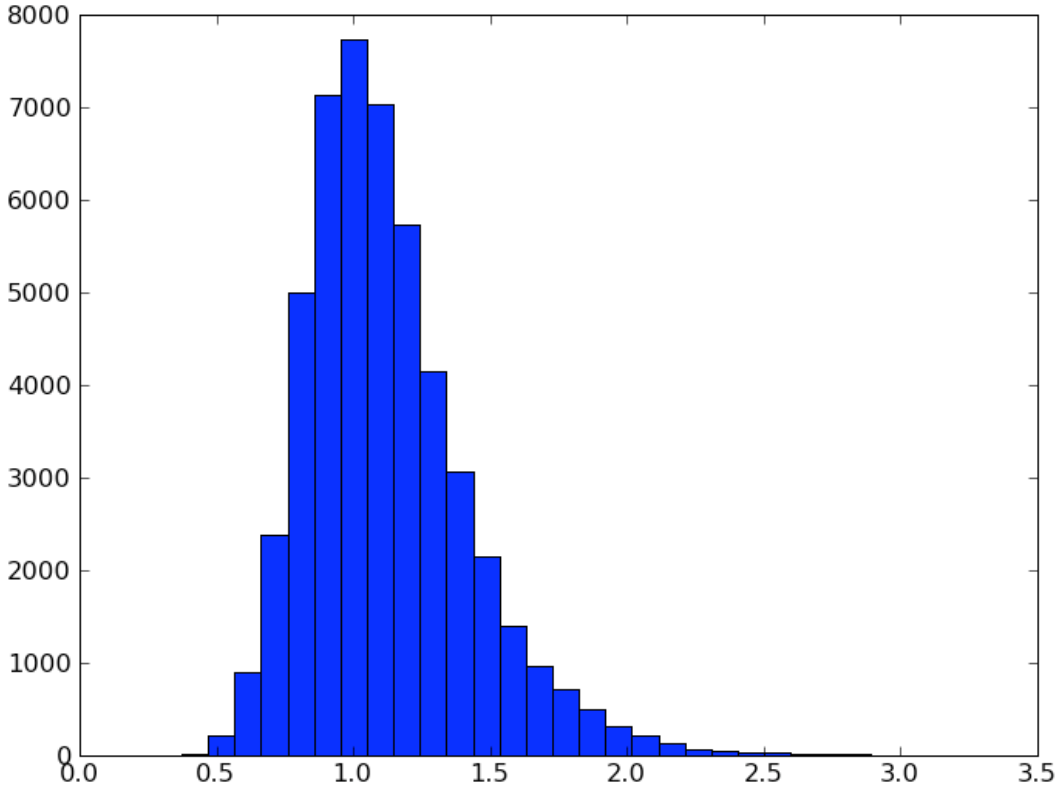


Figure 3.22. American black bear distribution of λ from 2 chains of 50,000 MCMC iterations (25,000 burn-in period) from the three data structure joint model for total abundance, for the time period from summer 2005 to summer 2006 in central Georgia.

CHAPTER 4

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Management implications

Bear management is often considered an exercise in 'people management'. Since bears are a wide-ranging species, they are more likely to have competing resources with humans. With the increase in human population growth in central Georgia and Georgia in general, the increase in human-bear conflicts is inevitable. Efforts to minimize human-bear conflicts include: public education and setting aside protected areas for bears. The highest source of mortality observed with marked bears from this study was from vehicle collisions. To reduce vehicle kills, least costly methods include reducing traffic speeds in areas prone to vehicle mortality. More costly strategies include building tunnels, building longer elevated road bridges over streams and rivers to allow continuity of a broad riparian vegetation, elevating highways in selected areas to create broad underpasses, and bridges over known locations where bears cross roads.

Our results indicate that there may be evidence of a low reproduction rate with the CGP and low female survival rate, according to the population viability analyses. These are important parameters in population viability models of the CGP. Future efforts should focus on obtaining more observations of litter size per female, and other methods of assessing reproduction in the CGP. Cub and sub-adult survival are also important aspects of a population viability model, and should be monitored for more accurate population viability analyses. Since we did not have data for cub and sub-adult survival estimates, we are relying on the assumption that the CGP has similar survival estimates in the eastern United States. The age-structure data analysis of

sub-adults indicated that the sub-adult survival rate from eastern black bear populations was similar, so this assumption may be warranted. Cub survival may not differ much from other populations in the Southeast. Adult females are exposed to similar habitats in the southeastern United States, which leads to similar diets and nutrition, a key component of cub survival (Wathen 1983).

Reproduction and survival estimates from mainly CGP data in the population viability analyses, indicated population growth estimates were decreasing. Therefore, increases in harvest rate, with these estimates of survival and reproduction, would not be sustainable. However, reproduction and survival estimates from eastern black bear populations in population viability analyses indicated the population was increasing, and could sustain an increase in harvest up to 7%. Since there is uncertainty in key values (e.g., cub and sub-adult survival, and reproduction), the most conservative and recommended course of action is not to increase harvest in the CGP.

Preliminary estimates presented in Chapter 2 should be used as initial estimates of the WMA property in central Georgia for population viability models and harvest decisions. Of particular interest is the population size for the central Georgia region, although our current efforts were focused on the WMA land. The spatial relationship of density with respect to habitat may be quite different not on WMA land, which is why future models should incorporate a spatial-abundance relationship with explicit formulation of habitat covariates. Currently, management decisions should only be focused on the WMA land, not the entire proposed expanse (~1200 km^2) of the black bear range in central Georgia.

Future work

The classification of the CGP regarding subspecies to either *Ursus americanus americanus or Ursus americanus floridanus* is not known. Miller (1995) classifies the population as *U. a. americanus*, but there has not been a study since then to explore this assumption. To investigate this assumption, multiple samples from other populations are needed to compare within and between population genetic variability. We had tissue samples from only one of the three populations of black bears in Georgia. The subspecies classification of the population may have management implications if the population is more closely related to the Florida black bear subspecies. Future studies in Georgia should be focused on a larger scale encompassing the whole state of Georgia, with respective genetic samples from the other two populations. Apparent rates of migration from the genetic studies would also be of interest. One could infer the degree of genetic exchange among the populations, if there is any. Similarly, there does not exist a statewide study exploring the black bear distribution. Occupancy samples on a county-by-county basis would be helpful for delineating populations or possible avenues of migration and genetic exchange.

One avenue for populations with reduced genetic variability and/or population numbers is reintroduction. Bear reintroductions have been successful in the southeastern U.S. (Smith and Clark 1994, Eastridge and Clark 2001). A preliminary study by Miller (1995) suggests that the Ocmulgee River population in central Georgia 'may warrant protection as a distinct population due to low population size and a high degree of within-population similarity'. We also found that the old Paetkau markers had low diversity, compared to other black bear populations in the Southeast. However the tetranucleotide markers used in this study were not consistent with this pattern, since allelic diversity was similar to other southeastern black bear populations.

Optimal sampling designs under the joint data structure model would have applications to other bear and wildlife populations with similar sampling protocols. An optimal sampling design for demographic parameter estimation, which we define as the design that maximizes the ratio of accuracy to cost, is important with limited resources. The sampling design is influenced by the spatial and behavioral ecology of the study species, the amount of resources available, and the desired accuracy for the parameter of interest. There is a trade-off between increasing effort to obtain increased sample observations, which likely increase accuracy of estimates, and costs (e.g., time and money) required to obtain the estimates. An optimal sampling design with noninvasive sampling techniques, such as DNA hair traps, includes a laboratory component with the field component. Study objectives should guide where resources are allocated in a sample design, especially with future Georgia DNR resources for management of the CGP.

One component of future abundance models of this population should explore ways of approximating the age class distribution from the abundance joint data structure model. All age classes have the opportunity of being sampled with DNA hair snares, and camera trapping, however, it is not possible to distinguish age with DNA samples, unless the bear is a known captured bear. The camera traps could be used as an approximation. Another source of heterogeneity not accounted for is the difference between sexes in capture rate with the DNA hair snares or cameras. The use of sex-ID markers in the genetic analysis should be considered in future efforts with this population to account for any sex biases, if they exist.

The current joint data structure model assumes a constant capture probability with respect to time, behavior, and heterogeneity. Future models should incorporate this flexibility in a model-selection framework. Also, a joint model of density and CMR samples with the trapping web design and Distance sampling methods would be of interest. The current model also

includes limited information about the spatial relationship of bear density and habitat, thus future models could incorporate this relationship more explicitly (e.g., CAR models) described previously in chapter 2.

Conclusions

Estimating demographic parameters of cryptic species, like the black bear, is difficult because of their elusive nature. Non-invasive sampling methods may be valuable for wildlife studies with consideration of incomplete detection, although there are biases associated with non-invasive methods that should be accounted for in statistical models. Bears tend to have low levels of genetic variation because of low population densities and low effective population sizes (Paetkau and Strobeck 1994). These conditions may increase the difficulty of identifying individuals in capture-recapture studies. The southeastern black bear populations tend to be more fragmented than other populations in the United States.

Grahl (1985) reported a population estimate of 64 (*sd*=18) bears using the Lincoln Index method for Ocmulgee River population in Georgia, which corresponded to a density of 0.323 bears per km^2. Our results suggest a population size that is three times the preliminary estimate for the WMA land only, not all of Middle Georgia. This could indicate population growth since 1985. However, comparisons between this preliminary estimate from 1985 and now may be weak, due to differences in population estimation techniques, scale of population inference, and the time that has elapsed since the first study in 1985.

Hierarchical state-space models provide a way of linking observations from data, such as capture-mark-recapture (CMR) or occupancy samples, to the underlying ecological or state processes (Royle and Dorazio 2008). Often, it is not possible to observe ecological processes

directly, and samples from a population or groups of populations are used to make inference on the processes. One of the main goals of this study was to estimate abundance of black bears in central Georgia using a combination of several sources of data. The common parameter of inference between the data sources was abundance, which could not be directly observed. This joint data structure model can be applied to other bear populations and other wildlife populations, especially those with noninvasive sampling techniques.

The main objectives for this study were to estimate bear abundance in an efficient and accurate manner, in addition to other demographic parameters, specifically survival and reproduction of the CGP. We used various sampling techniques for abundance, including noninvasive genetic sampling. Since statistical models incorporating the three data structures (DNA hair snares, camera traps, and radiotelemetry) used to estimate abundance did not exist, we formulated hierarchical Bayesian statistical models incorporating the three data structures. The use of DNA hair snares introduces an additional source of error from genetic laboratory error, thus a model incorporating the three data structures and genetic error was developed. This model has wide scale use for other bear populations and other wildlife species with multiple sampling techniques.

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APPENDIX A.

SIMULATION ANALYSIS OF JOINT DATA MODEL INCORPORATING THREE DATA STRUCTURES OF DNA HAIR SNARES, CAMERAS, AND TELEMETRY FOR AMERICAN BLACK BEAR CGP DATA

A simulation analysis was conducted to evaluate model performance using the Python, version 2.5.2 (Python Software Foundation, http://python.org) programming language. A few parameter levels (Table A.1) of simulated data from the three data structures were selected. Specifically, the percentage of webs sampled, the influence of different individual capture probabilities for camera data, and the presence of genetic error was evaluated. A smaller sample size of total abundance was selected to increase the processing time of the simulations. Since the simulated data was mainly from a small population size, a larger population size was selected for one simulation combination to evaluate an increase in sample size. To evaluate if camera data assists with estimation of total abundance, one simulation combination included no camera data.

Methods

Data were simulated for each scenario using the parameter values from each simulation combination. True abundance was simulated for 10 webs using the same Poisson distribution for each web. The true genotypes were simulated using an even distribution of allelic frequencies for each locus for each individual. True captures were simulated using a series of Bernoulli trials

for each individual in the population with the given capture probability for hair snares. Observed captures were modified from the true captures by permuting each individual and locus with the amount of genetic error given. If the individual at a specific locus was a true homozygote, the true genotype was not modified. If the individual at a specific locus was a true heterozygote, one of the alleles was modified using the probability of genetic error from equation 2.21 in Chapter 2 with equal probability of selection of another allele if it was chosen to have error. The observed capture histories were then modified based on the number of times the observed unique individuals were captured. All simulation combinations used 30% of the samples for genetic replication samples, also permuted through the genetic error process with equation 2.21 for true heterozygotes. All simulation combinations used 25 samples as calibration samples, also permuted through the genetic error process with equation 2.21 for true heterozygotes. Detection probability for cameras was calculated using the known r parameter and using equation 2.18 from Chapter 2. Camera detections were simulated on each sampled web using a binomial distribution with number of trials as the number of cameras and the detection probability calculated from equation 2.18. All combinations included 50% of the true bears with collars. The true probability of being on a web (p_w) was calculated as the true number of bears on the specific web divided by the total number of true bears in the population. The number of bears with collars on each sampled web was simulated from a binomial distribution with the number of trials as the total number of bears with collars in the population, and the probability of being on a web. The total number of bears with collars was modified with sampling without replacement for each successive web sampled.

For each scenario, 100 replications of the simulation-MCMC estimation algorithm were processed in Python, version 2.5.2 (Python Software Foundation, http://python.org). The

frequentist properties of Bayesian credible interval (BCI) percent coverage, BCI length, relative mean squared error (RMSE), and relative bias (RBIAS) were used to evaluate the following parameters: N_{tot}, r, θ, p, λ, and p_w. Each replication of the simulation-MCMC process included 10,000 iterations with a burn-in period of 5,000 iterations, a tuning period of 4,000 iterations and no thinning.

The 95% Bayesian credible interval (BCI) coverage is the sum of the number of replications where the true parameters were contained in the BCI, divided by the total number of replications. The BCI interval is the distance between the lower and upper 95% credible interval values. Relative root mean-squared error (RMSE) with r being the total number of replicates, i the individual replicate, $\hat{\theta}_i$, the estimated parameter at replicate i, θ_i the true value of parameter at replicate i, and $\bar{\theta}$ the mean of the true parameter values over all replicates, is:

$$RMSE = \frac{\sqrt{1/r\sum_{i}^{n}(\hat{\theta}_i - \theta_i)^2}}{\bar{\theta}}$$

Relative bias (RBIAS), following the same notation as above, is:

$$RBIAS = \frac{1/r\sum_{i}^{n}(\hat{\theta}_i - \theta_i)}{\bar{\theta}}$$

Results

BCI coverage

In general, an increase in the number of webs increased the BCI coverage for total abundance, individual capture probability for cameras and density (Table A.2). The BCI coverage did not change with increased number of webs for CMR capture probability, genetic error, and the probability of being in the web parameters (Table A.2). An increase in individual capture probability for cameras had an increase in coverage for individual capture probability for cameras and a slight increase in coverage with total abundance (Table A.2). The BCI coverage did not change with increased individual camera capture probability for CMR capture probability, genetic error, density, and the probability of being in the web parameters (Table A.2). The only consistent pattern with an increase in the true genetic error for all parameters was an increase in coverage for the genetic error probability (Table A.2).

The simulation combination with no cameras had lower BCI coverage for total abundance, CMR capture probability, and density (Table A.2). The simulation combination with larger population size had lower BCI coverage for total abundance, CMR capture probability, and density, but higher BCI coverage for camera individual capture probability and genetic error (Table A.2).

BCI length

An increase in the number of webs increased the BCI length for total abundance, CMR capture probability, and density (Table A.3). The BCI length did not change with increased number of webs for individual capture probability for cameras, genetic error, and the probability of being in the web parameters (Table A.3). An increase in individual capture probability for

cameras had an increase in interval length for individual capture probability for cameras (Table A.3). The BCI length did not change with increased individual camera capture probability for CMR capture probability, genetic error, density, total abundance and the probability of being in the web parameters (Table A.3). The only consistent pattern with an increase in the true genetic error for all parameters was an increase in BCI length for the genetic error probability (Table A.3).

The simulation combination with no cameras had the same BCI length for all parameters (Table A.3). The simulation combination with larger population size had lower BCI length for CMR capture probability, genetic error, density, and probability of being in a web, but higher BCI length for total abundance, camera and individual capture probability (Table A.3).

Relative bias

An increase in the number of webs decreased the positive relative bias for total abundance and density, and decreased the negative relative bias in capture probability (Table A.4). The RBIAS did not change the negative values of individual capture probability for cameras, CMR capture probability, genetic error, and the probability of being in the web parameters (Table A.4). An increase in individual capture probability for cameras had no consistent pattern for RBIAS over all parameters (Table A.4). The only consistent pattern with an increase in the true genetic error for all parameters was a decrease in RBIAS for the genetic error probability parameter (Table A.4).

The simulation combination with no cameras had increased RBIAS for total abundance and density, but decreased RBIAS for CMR capture probability and probability of being in a web parameters (Table A.4). The simulation combination with larger population size had lower

RBIAS for individual capture probability and genetic error probability, but higher RBIAS for total abundance and density (Table A.4).

Relative root mean square error

An increase in the number of webs increased accuracy (decreased RRMSE) for total abundance, CMR capture probability, individual capture probability for cameras, and density (Table A.5). The RRMSE did not change with increased number of webs for individual capture probability for cameras, genetic error and the probability of being in the web parameters (Table A.5). An increase in individual capture probability for cameras had an increase in accuracy (decrease in RRMSE) for individual capture probability for cameras (Table A.5). The RRMSE did not change with increased individual camera capture probability for CMR capture probability, genetic error, density, total abundance and the probability of being in the web parameters (Table A.5). The only consistent pattern with an increase in the true genetic error for all parameters was an increase in accuracy (decrease RRMSE) for the genetic error probability (Table A.5).

The simulation combination with no cameras had the same level of accuracy (RRMSE) for all parameters (Table A.5). The simulation combination with larger population size had increased accuracy with total abundance, individual capture probability with cameras, CMR capture probability, genetic error, and density, but lower accuracy for probability of being in a web (Table A.5).

Discussion

Number of webs sampled

With an increase in sample size, or an increase in the number of webs sampled, BCI coverage and accuracy increased, and bias decreased for total abundance and density. This should be expected with samples size differences. There are implications for study design, where an increase in samples may increase coverage and decrease bias with an associated cost for each additional web sampled.

Genetic error

An increase in genetic error increased BCI coverage and BCI length, decreased relative bias, and increased accuracy of the genetic error parameter. This could be a result of a low ability to detect genetic error with a small population size and small genetic error rate. Changes in genetic error did not influence the rest of the model parameters with BCI coverage, interval length, RBIAS and RRMSE.

Individual capture probability for cameras

An increase in individual capture probability for cameras increased BCI coverage for individual capture probability for cameras and a slightly increased coverage with total abundance. There was also an increase in interval length and increase in accuracy for individual capture probability for cameras. There was no consistent pattern for bias over all parameters. These results may also reflect a sample size difference where increases in individual capture probability for cameras increases the amount of camera data available to estimate that capture

probably in a model. Since there are a low number of replicates (12), this may have implications for estimating true individual capture probability for cameras.

Joint data model with no camera data

The simulation combination with no cameras compared to the simulation combination with camera data had lower BCI coverage for total abundance, CMR capture probability, and density. The simulation combination with no cameras also had increased RBIAS for total abundance and density, but decreased RBIAS for CMR capture probability and probability of being in a web parameters. These results provide evidence that the joint model with all three data structures leads to less bias and increased coverage for total abundance, the main parameter of interest in for the black bear CGP, compared to the joint model with just DNA hair snare data and telemetry.

Large true population size

The simulation combination with larger population size had lower BCI coverage for total abundance, CMR capture probability, and density, but higher BCI coverage for camera individual capture probability and genetic error. Higher coverage and lower bias would be expected with individual capture probability and genetic error since the sample size for genetic samples is higher (more individuals lead to more errors) and there are more individuals that can be detected with cameras. The reduced coverage in total abundance, and CMR capture probability may indicate some bias in the model (e.g., positive bias was also increased with higher population size). However, 0.87 and 0.90 coverage for abundance and CMR capture probability, respectively, is still relatively high. The simulation combination with larger

population size had lower BCI length for CMR capture probability, genetic error, density, and probability of being in a web, which is probably due to the difference in sample size. Finally, the simulation combination with larger population size had increased accuracy with total abundance, individual capture probability with cameras, CMR capture probability, genetic error, and density, but lower accuracy for probability of being in a web. This result for accuracy is expected with increases in sample size.

In conclusion, these simulation results indicate that the joint model for three data structures used in the abundance models for the black bear CGP is valid for small and large population sizes, and robust to differences in individual capture probability for cameras and genetic error. The inclusion of camera data with the joint model both increases parameter coverage and decreases bias with respect to total abundance, the most important parameter for black bear CGP abundance models. Finally, the simulation results of varied effort in sampling (3 versus 5 webs sampled) have implications for study design, where an increase in sampling effort increases coverage and decreases bias. However, there is an associated cost for each additional web sampled. This warrants future exploration for sampling effort with the different components (DNA hair snares, telemetry, camera replicates) versus cost for study designs under the joint data structure model for abundance.

Table A.1. Parameter values for simulation combinations of the joint data model incorporating DNA hair snares, cameras, and telemetry for American black bear CGP data.

Parameter	Simulation levels
Webs sampled	3, 5
Camera replicates	12
Individual capture probability, r	0.01, 0.005
Density, λ	5
CMR capture probability, θ	0.40
Collared bears (% of N_{tot})	0.50
Genetic error, p	0.01, 0.05
Total combinations	8

Table A.2. 95% Bayesian credible interval (BCI) percent coverage for parameters N_{tot}, r, θ, p, λ, and p_w, for all 10 webs for the joint data model incorporating DNA hair snares, cameras, and telemetry for American black bear CGP data. Each simulation combination included 100 replications of the combination. All combinations included 12 camera replicates, true λ of 5, CMR capture probability of 0.4, and 50% of the true bears with telemetry collars. 'NC' indicates no cameras and 'LP' indicates large population size.

		True			BCI Coverage													
Level	Webs	r	p	N_{tot}	r	θ	p	λ	p_{w1}	p_{w2}	p_{w3}	p_{w4}	p_{w5}	p_{w6}	p_{w7}	p_{w8}	p_{w9}	p_{w10}
1	5	0.01	0.01	0.95	0.91	0.94	0.94	0.95	0.97	0.97	0.96	0.98	1.00	0.97	0.98	0.99	0.98	1.00
2	3	0.01	0.01	0.92	0.84	0.93	0.96	0.93	0.99	0.99	1.00	0.99	0.99	0.98	0.96	0.97	0.96	0.98
3	5	0.01	0.05	0.95	0.94	0.95	1.00	0.95	0.99	0.99	0.97	0.99	0.97	0.98	0.98	0.98	0.98	0.95
4	3	0.01	0.05	0.94	0.82	0.95	0.97	0.93	1.00	0.99	0.98	0.96	0.99	0.95	0.94	0.98	0.98	0.99
5	5	0.005	0.01	0.93	0.79	0.93	0.94	0.95	0.99	0.98	0.98	1.00	1.00	0.99	1.00	0.98	0.96	0.98
6	3	0.005	0.01	0.93	0.61	0.96	0.94	0.91	0.97	0.99	1.00	0.97	0.97	0.95	0.97	0.94	0.97	0.98
7	5	0.005	0.05	0.92	0.80	0.95	0.97	0.92	0.99	0.98	0.99	0.99	0.97	0.98	0.94	0.95	0.96	0.98
8	3	0.005	0.05	0.90	0.61	0.94	0.95	0.96	0.99	0.98	0.99	0.98	0.98	0.95	0.97	0.98	0.97	0.99
NC	5	0.01	0.01	0.92	-	0.92	0.96	0.92	0.99	0.98	0.98	1.00	0.99	0.98	0.97	0.95	0.99	0.98
LP	10	0.01	0.01	0.87	0.99	0.9	0.96	0.85	0.98	0.98	0.98	0.98	0.94	0.97	0.95	0.98	0.98	0.96

Table A.3. Mean 95% Bayesian credible interval (BCI) length for parameters N_{tot}, r, θ, p, λ, and p_w, for all 10 webs for the joint data model incorporating DNA hair snares, cameras, and telemetry for American black bear CGP data. Each simulation combination included 100 replications of the combination. All combinations included 12 camera replicates, true λ of 5, CMR capture probability of 0.4, and 50% of the true bears with telemetry collars. 'NC' indicates no cameras and 'LP' indicates large population size.

		True		BCI length														
Level	Webs	r	p	N_{tot}	r	θ	p	λ	p_{w1}	p_{w2}	p_{w3}	p_{w4}	p_{w5}	p_{w6}	p_{w7}	p_{w8}	p_{w9}	p_{w10}
1	5	0.01	0.01	48.53	0.04	0.27	0.04	5.73	0.15	0.14	0.15	0.14	0.13	0.22	0.22	0.22	0.21	0.22
2	3	0.01	0.01	78.97	0.02	0.35	0.04	8.55	0.15	0.15	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
3	5	0.01	0.05	48.82	0.02	0.28	0.07	5.74	0.14	0.14	0.14	0.15	0.14	0.22	0.22	0.22	0.22	0.22
4	3	0.01	0.05	75.59	0.06	0.35	0.07	8.20	0.15	0.15	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
5	5	0.005	0.01	48.94	0.01	0.27	0.04	5.76	0.14	0.14	0.14	0.14	0.14	0.21	0.21	0.21	0.21	0.21
6	3	0.005	0.01	73.80	0.01	0.35	0.04	8.01	0.15	0.15	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
7	5	0.005	0.05	47.09	0.01	0.28	0.07	5.60	0.14	0.15	0.14	0.14	0.14	0.22	0.22	0.22	0.22	0.22
8	3	0.005	0.05	79.32	0.01	0.35	0.08	8.55	0.15	0.14	0.15	0.22	0.22	0.22	0.22	0.22	0.22	0.22
NC	5	0.01	0.01	48.22	-	0.27	0.04	5.73	0.14	0.14	0.14	0.14	0.14	0.21	0.21	0.21	0.21	0.21
LP	10	0.01	0.01	65.37	0.11	0.19	0.03	3.91	0.07	0.07	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11

Table A.4. Relative bias (RBIAS) for parameters N_{tot}, r, θ, p, λ, and p_w, for all 10 webs for the joint data model incorporating DNA hair snares, cameras, and telemetry for American black bear CGP data. Each simulation combination included 100 replications of the combination. All combinations included 12 camera replicates, true λ of 5, CMR capture probability of 0.4, and 50% of the true bears with telemetry collars. 'NC' indicates no cameras and 'LP' indicates large population size.

		True		RBIAS														
Level	Webs	r	p	N_{tot}	r	θ	p	λ	p_{w1}	p_{w2}	p_{w3}	p_{w4}	p_{w5}	p_{w6}	p_{w7}	p_{w8}	p_{w9}	p_{w10}
1	5	0.01	0.01	0.12	-0.21	-0.12	0.48	0.15	0.08	0.04	0.03	-0.04	-0.03	0.07	0.05	0.04	0.04	0.05
2	3	0.01	0.01	0.18	-0.20	-0.13	0.37	0.19	0.03	0.04	-0.02	0.09	0.05	-0.05	0.10	0.22	0.03	0.11
3	5	0.01	0.05	0.11	-0.11	-0.11	0.08	0.14	0.02	0.04	0.05	0.02	-0.05	0.05	0.01	0.05	0.12	0.05
4	3	0.01	0.05	0.16	-0.22	-0.08	0.07	0.19	0.05	0.00	-0.01	0.09	0.06	0.12	0.06	0.05	0.00	0.13
5	5	0.005	0.01	0.12	-0.10	-0.09	0.43	0.17	0.04	0.03	0.06	-0.02	-0.01	0.09	0.01	0.02	0.07	0.06
6	3	0.005	0.01	0.25	-0.21	-0.09	0.50	0.28	0.03	0.03	0.03	0.10	0.10	0.03	0.08	0.12	0.00	0.04
7	5	0.005	0.05	0.11	-0.17	-0.09	0.01	0.14	0.08	0.05	0.01	-0.03	-0.04	0.06	0.03	0.03	0.12	0.08
8	3	0.005	0.05	0.18	-0.32	-0.12	0.12	0.21	0.06	0.02	0.02	0.04	0.12	0.09	0.08	0.00	0.08	0.07
NC	5	0.01	0.01	0.15	-	-0.10	0.48	0.19	0.05	0.00	0.00	-0.03	-0.06	0.09	0.08	0.05	0.09	0.11
LP	10	0.01	0.01	0.15	0.03	-0.12	0.31	0.17	0.04	0.07	0.10	0.02	0.11	0.15	0.08	0.04	0.08	0.04

Table A.5. Relative root mean square error (RRMSE) for parameters N_{tot}, r, θ, p, λ, and p_w, for all 10 webs for the joint data model incorporating DNA hair snares, cameras, and telemetry for American black bear CGP data. Each simulation combination included 100 replications of the combination. All combinations included 12 camera replicates, true λ of 5, CMR capture probability of 0.4, and 50% of the true bears with telemetry collars. 'NC' indicates no cameras and 'LP' indicates large population size.

		True		RRMSE														
Level	Webs	r	p	N_{tot}	r	θ	p	λ	p_{w1}	p_{w2}	p_{w3}	p_{w4}	p_{w5}	p_{w6}	p_{w7}	p_{w8}	p_{w9}	p_{w10}
1	5	0.01	0.01	0.25	0.57	0.21	0.92	0.29	0.26	0.29	0.29	0.27	0.27	0.38	0.44	0.38	0.43	0.37
2	3	0.01	0.01	0.37	0.70	0.24	0.86	0.39	0.26	0.28	0.24	0.46	0.41	0.44	0.49	0.49	0.45	0.44
3	5	0.01	0.05	0.21	0.58	0.20	0.27	0.26	0.24	0.23	0.35	0.22	0.27	0.43	0.42	0.44	0.51	0.42
4	3	0.01	0.05	0.37	0.74	0.26	0.35	0.42	0.28	0.30	0.30	0.51	0.37	0.44	0.41	0.36	0.41	0.40
5	5	0.005	0.01	0.25	0.82	0.21	0.86	0.30	0.27	0.26	0.24	0.26	0.26	0.37	0.39	0.41	0.43	0.42
6	3	0.005	0.01	1.43	0.95	0.25	0.93	1.46	0.30	0.28	0.27	0.44	0.44	0.45	0.45	0.50	0.37	0.37
7	5	0.005	0.05	0.24	0.77	0.20	0.31	0.28	0.28	0.28	0.28	0.26	0.26	0.28	0.42	0.45	0.46	0.47	0.43
8	3	0.005	0.05	0.41	0.91	0.25	0.40	0.42	0.26	0.29	0.28	0.37	0.40	0.47	0.43	0.38	0.43	0.39
NC	5	0.01	0.01	0.25	-	0.20	0.91	0.32	0.27	0.25	0.27	0.23	0.26	0.38	0.45	0.45	0.44	0.41
LP	10	0.01	0.01	0.21	0.33	0.16	0.78	0.24	0.28	0.28	0.45	0.44	0.48	0.48	0.43	0.44	0.44	0.41

APPENDIX B

METROPOLIS ALGRORITHM FOR UPDATING ABUNDANCE AND INDIVIDUAL CAPTURE PROBABILITY FROM CAMERA PARAMETERS FROM THE JOINT MODEL INCORPORATING THE THREE DATA STRUCTURES OF DNA HAIR SNARES, TELEMETRY, AND CAMERA TRAPS FOR CGP AMERICAN BLACK BEAR DATA

Updating the camera parameter, *r*

The probability of detecting occupancy d_i with the camera samples is a transformation of the individual probability of camera detection, r, and N_i, the abundance of bears on web i:

$$[d_i] = 1 - (1 - r)^{N_i} \qquad \text{(Equation B.1)}$$

The probability of individual detection from cameras is assumed constant among bears and among webs. The conditional distribution of camera detections, Y_i, on web i, given the probability of detection, d_i, follows a binomial sampling model, where each camera is an independent Bernoulli trial of bear detection:

$$[Y_i \mid d_i] = \binom{j}{y_i} d_i^{Y_i} (1 - d_i)^{j - Y_i}, \qquad \text{(Equation B.2)}$$

where j is the total number of cameras or sites on web i. Additionally, we assume that detection does not vary by occasion k, so j is condensed data consisting of the number of camera by occasion replicates in web i, and y_i is the number of bear detections over all cameras*occasions in web i in one season.

A reasonable value of r was selected as the starting value with the Metropolis algorithm. The new proposed value of the parameter, r^*, was generated from a normal distribution with mean log(r), to keep the value positive, and tuning parameter τ_r. The tuning parameter was adapted based on whether the previous proposed r was accepted or rejected. Then, the ratio of binomial likelihoods (Equation B.1, B.2) of r given the camera data was calculated as follows,

$$r_r = \frac{p(r^* \mid y)}{p(r \mid y)} \qquad \text{(Equation B. 3)}$$

A uniform random variable was generated, and the proposed value, r^*, was accepted with probability min(r_r,1), and the previous value, r^{t-1}, otherwise.

Updating the abundance of sampled areas, N_i

The full conditional distribution of abundance on sampled areas (N_i) is the joint distribution of the three data structures and the spatial model of N. The full conditional likelihood is:

$$[\{N_i\} \mid \bullet] = \prod_{i=1}^{m} [\{Y_{ijk}\} \mid r, N_i][\{N_i\} \mid p_{w_i}][\{N_i\} \mid \lambda_i][\mathcal{G} \mid N_i, \gamma][X_{ik} \mid N_i, \theta_{ik}][\{N_i\}]$$

$$\propto \prod_{i=1}^{w} \left\{ \frac{\lambda_i^{N_i} e^{-\lambda_i}}{N_i!} \right\} \binom{j}{Y_i} (1-(1-r)^{N_i})^{Y_i} (1-r)^{N_i(j-Y_i)} \binom{N_{tot}}{N_i} (p_{w_i})^{N_i} (1-p_{w_i})^{N_{tot}-N_i} \frac{N_i!}{(N_i-u_{\cdot i})!} \theta^{n_{\cdot i}} (1-\theta)^{k(N_i)-n_{\cdot i}}$$

$$\propto \prod_{i=1}^{w} \left\{ \frac{\lambda_i^{N_i} e^{-\lambda_i}}{N_i!} \right\} \binom{j}{Y_i} (1-(1-r)^{N_i})^{Y_i} (1-r)^{N_i(j-Y_i)} \binom{N_{tot}}{N_i} (p_{w_i})^{N_i} (1-p_{w_i})^{N_{tot}-N_i} \frac{N_i!}{(N_i-u_{\cdot i})!} (\pi_0)^{N_i-u_{\cdot i}}$$

(Equation B.4)

where π_0 is the probability of not being captured at least once over the three occasions (i.e., $\pi_0 = (1-\theta)^3$). A sequential update of N_i was used, where N_{tot} of the current accepted N_i s were used in N_{tot} from the telemetry portion, or probability of a bear on a web.

For each N_i, a reasonable value of N_i was selected as the starting value with the Metropolis algorithm. The new proposed value of the parameter, N_i^*, was generated from a discrete uniform jumping distribution from the current value of N_i, and tuning parameter, τ_N, which controls how big the proposed jump will be. The tuning parameter was adapted based on whether the previous proposed N was accepted or rejected. Then, the ratio abundance likelihoods (Equation B.4) of N_i given the DNA hair snare, telemetry, and camera data was calculated as follows,

$$r_N = \frac{p(N_i^* \mid y)}{p(N_i \mid y)} \qquad \text{(Equation B. 3)}$$

A uniform random variable was generated, and the proposed value, N_i^*, was accepted with probability min(r_N,1), and the previous value, N_i^{t-1}, otherwise.

Based on the dimension of a proposed value of N^*, the genotype matrix G and the capture-history matrix are augmented (Tanner and Wong 1987) by N^*- N rows. Therefore, N could potentially change matrix dimensions if the proposed value, N^*, is greater than N and is accepted, which utilizes this reversible jump Metropolis step, as in Wright et al. (2009).

Literature cited

Tanner, M. A. and W. H. Wong. 1987. The calculation of posterior distributions by data augmentation. Journal of the American Statistical Association 82: 528-540.

Wright, J. A., R. J. Barker, M. R. Schofield, A. C. Frantz, A. E. Byrom and D. M. Gleeson. 2009. Incorporating genotype uncertainty into mark-recapture-type models for estimating abundance using DNA samples. Biometrics. DOI: 10.1111/j.1541-0420.2008.01167.

APPENDIX C.

METHODS OF UPDATING TRUE GENOTYPES, TRUE CAPTURE HISTORIES, AND GENOTYPE FREQUENCIES FROM WRIGHT ET AL. (2009) FOR THE JOINT MODEL INCORPORATING THE THREE DATA STRUCTURES OF DNA HAIR SNARES, TELEMETRY, AND CAMERA TRAPS FOR CGP AMERICAN BLACK BEAR DATA

The following description of updates of matrices and parameters follows directly from Wright et al. (2009), both with equations and notation.

Updating true genotype matrix, $\mathcal{G}$

The true genotypes for each individual *i* and locus *l* are updated through direct sampling. The first step involves updating individuals that appeared in the observed samples. For those individuals, we consider all values for $\mathcal{G}_{il}$ that are compatible with observed genotypes in all replicated samples where the individual appeared and do not result in an individual genotype, $\mathcal{G}_i$, that is the same for any other individual in the population. Consider k_i compatible genotypes with the *k*th one denoted as $\mathcal{G}_{il}^{(k)}$. The contribution $\lambda_{il}^{(k)}$ made by individual *i* at locus *l* to the joint probability is:

$$\lambda_{il}^{(k)} = \left\{ \prod_{j=1}^{S} X_{ij} \prod_{r=1}^{R} \Pr(G_{jlr}^{obs} \mid \mathcal{G}_{il}^{(k)}) \right\} x \Pr(\mathcal{G}_{il}^{(k)} \mid \gamma)$$

Where $\mathcal{G}^{(k)}$ is the matrix $\mathcal{G}$ with element $\mathcal{G}_{il}$ replaced by the proposed value of $\mathcal{G}_{il}^{(k)}$ and $\Pr(G_{jlr}^{obs} \mid \mathcal{G}_{il}^{(k)})$ is given here and in Chapter 2. For true heterozygotes ($A_{il1} \neq A_{il2}$), the probability of observing a true heterozygote is 1-*p*, while the probability of observing a homozygote is 0.5**p*, since there are 2 ways that an allele can drop out:

$$\Pr(G_{jlr}^{obs} \mid \mathcal{G}_{jl}) = \begin{cases} 1 - p_l & A_{il1r}^{obs} \neq A_{il2r}^{obs} \\ 0.5\,p_l & A_{il1r}^{obs} = A_{il2r}^{obs} \end{cases}$$

Since we are only considering allelic dropout, the probability of observing a homozygous individual at locus *l*, replicate *r*, given that the true individual at locus *l* is homozygous is 1. Most $\lambda_{il}^{(k)}$ are zero, except when a sample is observed. Finally, considering all candidate values of $\mathcal{G}_{ij}$ one is selected with probability for the *k*th one by:

$$\frac{\lambda_{il}^{(k)}}{\sum_{h=1}^{K_i} \lambda_{il}^{(h)}}$$

For animals not in the samples, a value for $\mathcal{G}_{il}$ is drawn directly from the multinomial distribution of genotype frequencies, so that the resulting genotype (across all loci) does not correspond to a genotype of any other animal in the population.

Updating the true capture history matrix, X

This step is also accomplished using direct sampling. It directly follows that a vector *G* (*S*x*L*) of true genotypes that appeared in the samples is the combination of *X* and *G*. The capture history for one out of the three sessions for each sample *i*, is updated by swapping the capture history of all other individuals in the population that have compatible genotypes over all loci and then computing the contribution made by this switch, similar to the updating of true genotypes. Let $X^{(j)}$ denote the *X*-matrix associated with the *j*th switch and

$$\lambda_{ij} = \Pr(X^{(j)} \mid N)\Pr(G_i^{obs} \mid \mathcal{G}_i^{(j)}, p)$$

From the set of candidate *G*-matrices one is selected with probability $\frac{\lambda_{ij}}{\sum_{h=1}^{N}\lambda_{ij}}$ and the new value of X in the matrix $X^{(j)}$ associated with this choice and replaces the old value.

Updating the genotype frequencies, γ

Consider a parameter array $\boldsymbol{\gamma}$ comprised of L vectors $\underline{\gamma}_j$, each of length $l_j=m_j(m_j+1)/2$; these are the number of distinct genotypes g_{kj}, at locus j. A Dirichlet prior on vector $\underline{\gamma}_j$ (j=1,…,L) results in:

$$[\underline{\gamma}_j] = \frac{\Gamma(\sum_{k=1}^{l_j}\alpha_{kj})}{\prod_j \Gamma(\alpha_{kj})}\prod_{k=1}^{l_j}\gamma_{kj}^{\alpha_{kj}-1}$$

and

$$[\mathcal{G} \mid \underline{\gamma}, N] = \prod_{i=1}^{N}\prod_{j=1}^{L}\prod_{k=1}^{l_j}\gamma_{kj}^{I(\mathcal{G}_{ij}=g_{kj})}$$
$$= \prod_{j=1}^{L}\prod_{k=1}^{l_j}\gamma_{kj}^{y_{kj}}$$

where y_{kj} is the number of the N individuals with genotype g_{kj} at locus j.

Therefore, we can obtain the full conditional distribution of the $\underline{\gamma}$ parameter:

$$[\underline{\gamma} \mid \bullet] = \prod_{j=1}^{L}\prod_{k=1}^{l_j}\gamma_{kj}^{y_{kj}+\alpha_{kj}-1}$$

This is the kernel of the joint distribution of L independent Dirichlet random variables, where the jth component has parameter vector $\{y_{kj}+\alpha_{kj}\}$ (k=1,….,l_j) of dimension l_j. To simulate a draw from a Dirichlet distribution with parameters α_1,…, α_{lj}, we sample l_j values from gamma

$Ga(\alpha_k,1)$ distributions, where $k=1,\ldots,n_j$. Using the notation of y_k for these gamma random variables, then a vector $(x_1,\ldots,x_{lj})$ is a vector of Dirichlet random variables, where $x_k = \frac{y_k}{\sum_h y_h}$.

Literature Cited

Wright, J. A., R. J. Barker, M. R. Schofield, A. C. Frantz, A. E. Byrom and D. M. Gleeson. 2009. Incorporating genotype uncertainty into mark-recapture-type models for estimating abundance using DNA samples. Biometrics. DOI: 10.1111/j.1541-0420.2008.01167.

APPENDIX D

CENTRAL GEORGIA AMERICAN BLACK BEAR POPULATION CLOSED POPULATION MODEL RESULTS WITH PROGRAM MARK USING DNA HAIR SNARES FROM 2004 TO 2006

Closed population models from Program MARK (White and Burnham 1999) were used to assess capture heterogeneity with DNA hair snare data from the bear CGP. The option 'full closed captures with heterogeneity' was selected in Program MARK (White and Burnham 1999). Each season was analyzed separately. Behavior effects (M_b), time (M_t), individual heterogeneity (M_h) and web group effects (M_g), and combinations of the above were used to assess capture heterogeneity.

Comparisons of competing models can be done in a model selection framework using the corrected version of Akaike's Information Criterion (*AICc*) (Sugiura 1978), a modification of *AIC* (Akaike 1973) for small sample size, described below:

$$AICc = -2\log(\mathcal{L}(\hat{\theta})) + 2K\left(\frac{n}{n-K-1}\right),$$

where $\mathcal{L}(\hat{\theta})$ is the likelihood of the estimated model parameters given the data, K is the number of parameters, and n is the effective sampling size. The low *AICc* model is classified as the most likely model in a candidate model set.

All seasons had the M_{bt} model as the low *AICc* model, indicating that there is evidence of behavior and time heterogeneity in the DNA hair snare data, when genetic error is ignored (Tables D.1, D.2, D.3, D.4, D.5). The group 'web' effect models, or the models where capture probability is different for each web, had no model weight for all seasons. Therefore, this model was not selected as a potential model in Chapter 2. The null model (M_0) had some model weight, albeit a small amount, for most seasons. This is the simplest model to implement in the joint model of DNA hair snares, cameras, and telemetry, and was selected for models in Chapter 2. Future work will incorporate behavior and time effects. There also is some evidence of individual heterogeneity, according to the models presented here.

Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov, and F. Csaki, (eds.) Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory and Methods A7: 13-26.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Table D. 1. Closed population MARK models from CMR hair snare data collected in Summer 2004 for the American black bear CGP. The model, *AICc*, Δ *AICc, AICc* model weight, model likelihood, number of parameters (*np*), and model deviance are included.

Model	*AICc*	Δ *AICc*	*AICc* Weights	Model Likelihood	*np*	Deviance
M_{bt}	18.48	0.00	0.94	1.00	10	29.16
M_{bth}	26.07	7.59	0.02	0.02	16	21.92
M_0	27.00	8.51	0.01	0.01	6	46.79
M_b	28.96	10.48	0.01	0.01	7	46.53
M_h	29.22	10.74	0.00	0.00	7	46.79
M_g	29.29	10.81	0.00	0.00	10	39.97
M_t	30.59	12.11	0.00	0.00	8	45.90
M_{bg}	30.91	12.43	0.00	0.00	15	29.33
M_{bh}	31.22	12.74	0.00	0.00	8	46.53
M_{gh}	31.66	13.18	0.00	0.00	11	39.97
M_{bgh}	33.49	15.01	0.00	0.00	16	29.34
M_{ht}	36.88	18.40	0.00	0.00	12	42.78
M_{gt}	38.67	20.19	0.00	0.00	20	23.76
M_{bgt}	51.72	33.24	0.00	0.00	30	6.29
M_{tgh}	84.27	65.79	0.00	0.00	36	17.54
M_{tbgh}	161.39	142.91	0.00	0.00	56	0.00

Table D. 2. Closed population MARK models from CMR hair snare data collected in Fall 2004 for the American black bear CGP. The model, *AICc*, Δ *AICc, AICc* model weight, model likelihood, number of parameters (*np*), and model deviance are included.

Model	*AICc*	Δ *AICc*	*AICc* Weights	Model Likelihood	*np*	Deviance
M_{bt}	52.98	0.00	0.83	1.00	11	24.58
M_{th}	57.68	4.70	0.08	0.10	13	23.50
M_0	59.34	6.35	0.03	0.04	7	41.45
M_t	59.86	6.88	0.03	0.03	9	36.88
M_b	61.62	8.64	0.01	0.01	8	41.22
M_h	61.85	8.86	0.01	0.01	8	41.45
M_{bh}	64.21	11.22	0.00	0.00	9	41.22
M_{bth}	67.48	14.50	0.00	0.00	17	20.53
M_g	70.02	17.03	0.00	0.00	12	38.77
M_{gh}	72.95	19.97	0.00	0.00	13	38.77
M_{bg}	83.80	30.82	0.00	0.00	18	33.37
M_{bgh}	87.40	34.42	0.00	0.00	19	33.37
M_{gt}	96.94	43.95	0.00	0.00	24	22.72
M_{bgt}	151.42	98.43	0.00	0.00	36	7.10
M_{ght}	210.87	157.89	0.00	0.00	43	0.59
M_{bght}	1437.93	1384.95	0.00	0.00	67	0.00

Table D. 3. Closed population MARK models from CMR hair snare data collected in Summer 2005 for the American black bear CGP. The model, *AICc*, Δ *AICc, AICc* model weight, model likelihood, number of parameters (*np*), and model deviance are included.

Model	*AICc*	Δ *AICc*	*AICc* Weights	Model Likelihood	*np*	Deviance
M_{bt}	34.75	0.00	0.97	1.00	13	42.58
M_{bht}	41.92	7.17	0.03	0.03	19	35.46
M_{t}	55.45	20.70	0.00	0.00	11	67.84
M_{th}	61.15	26.40	0.00	0.00	15	64.32
M_{0}	69.21	34.47	0.00	0.00	9	86.07
M_{b}	69.53	34.78	0.00	0.00	10	84.16
M_{h}	71.43	36.69	0.00	0.00	10	86.07
M_{bh}	71.77	37.03	0.00	0.00	11	84.16
M_{gt}	71.99	37.24	0.00	0.00	32	31.00
M_{g}	77.28	42.53	0.00	0.00	16	78.08
M_{gh}	79.68	44.93	0.00	0.00	17	78.09
M_{bg}	89.16	54.41	0.00	0.00	24	70.03
M_{bgh}	91.78	57.03	0.00	0.00	25	70.03
M_{bgt}	97.87	63.12	0.00	0.00	48	6.10
M_{ght}	139.79	105.04	0.00	0.00	57	14.37
M_{bght}	290.52	255.78	0.00	0.00	89	0.00

Table D. 4. Closed population MARK models from CMR hair snare data collected in Fall 2005 for the American black bear CGP. The model, *AICc*, Δ *AICc, AICc* model weight, model likelihood, number of parameters (*np*), and model deviance are included.

Model	*AICc*	Δ *AICc*	*AICc* Weights	Model Likelihood	*np*	Deviance
M_{bt}	49.86	0.00	0.99	1.00	11	34.85
M_0	60.31	10.45	0.01	0.01	7	54.74
M_t	62.30	12.44	0.00	0.00	9	52.10
M_b	62.32	12.46	0.00	0.00	8	54.46
M_h	62.61	12.75	0.00	0.00	8	54.74
M_{hbt}	63.76	13.90	0.00	0.00	17	33.19
M_{bh}	64.66	14.80	0.00	0.00	9	54.46
M_{ht}	67.38	17.51	0.00	0.00	13	47.38
M_g	67.62	17.76	0.00	0.00	12	50.14
M_{hg}	70.14	20.28	0.00	0.00	13	50.14
M_{bg}	71.49	21.63	0.00	0.00	18	38.15
M_{hbg}	74.32	24.46	0.00	0.00	19	38.15
M_{gt}	82.85	32.99	0.00	0.00	24	31.65
M_{bgt}	103.16	53.29	0.00	0.00	36	8.49
M_{hgt}	142.21	92.35	0.00	0.00	43	15.85
M_{hbgt}	299.80	249.93	0.00	0.00	67	0.00

Table D. 5. Closed population MARK models from CMR hair snare data collected in Summer 2006 for the American black bear CGP. The model, *AICc*, Δ *AICc, AICc* model weight, model likelihood, number of parameters (*np*), and model deviance are included.

Model	*AICc*	Δ *AICc*	*AICc* Weights	Model Likelihood	*np*	Deviance
M_{bt}	19.97	0.00	0.94	1.00	11	28.05
M_{b}	26.60	6.63	0.03	0.04	8	41.36
M_{bh}	28.79	8.82	0.01	0.01	9	41.35
M_{0}	30.39	10.43	0.01	0.01	7	47.33
M_{hbt}	30.79	10.82	0.00	0.00	17	24.82
M_{t}	32.57	12.60	0.00	0.00	9	45.13
M_{h}	32.57	12.60	0.00	0.00	8	47.33
M_{g}	34.20	14.23	0.00	0.00	12	40.00
M_{bg}	34.94	14.97	0.00	0.00	18	26.53
M_{hg}	36.50	16.53	0.00	0.00	13	40.00
M_{hbg}	37.41	17.44	0.00	0.00	19	26.53
M_{ht}	37.53	17.56	0.00	0.00	13	41.03
M_{gt}	49.52	29.55	0.00	0.00	24	25.88
M_{bgt}	66.79	46.82	0.00	0.00	36	9.15
M_{hgt}	100.01	80.04	0.00	0.00	43	19.99
M_{hbgt}	175.94	155.97	0.00	0.00	67	0.00

APPENDIX E

PYTHON CODE FOR THE JOINT MODEL INCORPORATING THE THREE DATA STRUCTURES OF DNA HAIR SNARES, TELEMETRY, AND CAMERA TRAPS FOR CGP AMERICAN BLACK BEAR DATA

The Python code is a collection of posterior parameter updates using Gibbs, Metropolis and reversible jump Metropolis-Hastings algorithms from the joint model for data from Fall 2005 season. There are also with references to equations from Chapter 2 presented with the code. The Python modules are separated by the sections from the MCMC steps (Figure E.1).

1) Input data, and 16) output parameter traces

```
def
run(nwebs=14,alleles=[8,4,8,4,4,7,4,4],occasions=3,collars=22.,rinit=0.04,Ninit=10,tune_r=0.5,t
une_N=30,iterations=50000,burn=25000,tuner=15000,reps=1,if_print=10,if_output=1000,estima
te=True,plotting=True):
    #data
    #total cameras
    kcam=[18,16,15,12,'NA',12,'NA','NA',31,'NA','NA','NA','NA','NA']
    #notes: k is number of cameras at each site
    #camera detections
    camera=[15,12,1,7,'NA',10,'NA','NA',20,'NA','NA','NA','NA','NA']
    #telemetry detections
    telem=[10,4,1,3,'NA',5,'NA','NA',3,'NA','NA','NA','NA','NA']
```

```
    loci=len(alleles)
    it=[x for x in range(iterations+1)]

    #import observed genetic samples and create dictionary
    data=csv.reader(open('gobs_5Fweb.csv','U'),dialect='excel')
    obssamp={}
    for line in data:
        temp=string.join((line[1],line[2],line[3],line[4],line[5],line[6],line[7],line[8]),",")
        obssamp[int(line[0])]=[eval(temp),int(line[9]),int(line[10])]

    #obs capture ids and capture history
    obsCap=sum_samples_webs(obssamp,occasions)

    #import replicate samples and create dictionary
    data2=csv.reader(open('rep_5F.csv','U'),dialect='excel')
    repsamp2={}
    for line in data2:
        temp=string.join((line[1],line[2],line[3],line[4],line[5],line[6],line[7],line[8]),",")
        repsamp2[int(line[0])]=[eval(temp)]

    #obs summary stats
    udot_obs,ndot_obs=sum_stats_web(obssamp,occasions,nwebs)
    print 'obs u,n dot',udot_obs,ndot_obs

    if estimate:

captrace,N_trace,errortrace,Ntottrace,denstrace,acceptancer,rtrace,dtrace,pwebtrace,acceptanceN
=MCMC_sampler(nwebs,udot_obs,ndot_obs,obsCap,obssamp,repsamp2,alleles,occasions,iterati
ons,tuner,if_print,if_output,Ninit,rinit,camera,kcam,collars,telem,tune_r,tune_N)

        if plotting:
```

```
        varnames=['Ntot','p_error','r','density','pcapt']
        vartraces=[Ntottrace,errortrace,rtrace,denstrace,captrace]
        plotnum=1
        for i in range(len(varnames)):
            plotnum=plot_tracepost(varnames[i],vartraces[i],plotnum)

        print 'r acceptance rate',acceptancer
        print 'N acceptance rate',acceptanceN
        print ''

        for i in range(len(varnames)):
            output_stats(varnames[i],vartraces[i])

if __name__ == '__main__':
    run()
```

2) Initialize parameters modules

```
def initial_parms(nwebs,alleles,sampobsinit,oc,initialN,perrinit):
    """generate initial matrices, parameters"""

    #genetic error init
    proberr_init=perrinit

    #prior alphas for gamma, genotype frequency, priors are all 1's
    alpha_init=[]
    for i in alleles:
        cat=i*(i+1)/2
        alpha_init.append([1]*cat)

    #create initial genotype frequencies (all equal)
    gam_init=geno_freq(alleles)
```

```
    gen_cat=gen_categories(alleles)

    #permute initial true sample ids
    sampletrue=copy.deepcopy(sampobsinit)
    #expected samples with at least one error
    experr=np.ceil(len(sampobsinit)*((1.-(1.-proberr_init)**len(alleles))))
    generr=random_sample(experr,len(sampobsinit))

    for samp in sampletrue:
        if generr[samp]:
            newgenid=[]
            for j in range(len(alleles)):
                compat=compat_gen(sampletrue[samp][0][j],gen_cat[j],proberr_init)
                probcompat=[1./(len(compat)) for i in range(len(compat))]
                newG=compat[mult(probcompat)]
                newgenid.append(newG)
            sampletrue[samp][0]=tuple(newgenid)

    #generate initial true script G matrix of true IDs and capture history
    Nmatrixinittemp,truewebdict=sum_samples_webs(sampletrue,oc)

    webNinit=sum_web(truewebdict,nwebs)

    #initial N is greater than the current value of N, add new rows
    for i in range(nwebs):
        if i==0:
            if initialN>webNinit[i]:
                webNinit[i]=initialN

Nmatrixinit1,truewebdictinit1=gen_rows(initialN,webNinit[i],Nmatrixinittemp,gam_init,alleles,i
,truewebdict)
```

```
            else:
                Nmatrixinit1=copy.copy(Nmatrixinittemp)
                truewebdictinit1=copy.copy(truewebdict)

        else:
            if initialN>webNinit[i]:
                webNinit[i]=initialN

Nmatrixinit,truewebdictinit=gen_rows(initialN,webNinit[i],Nmatrixinit1,gam_init,alleles,i,truew
ebdictinit1)
                Nmatrixinit1=copy.copy(Nmatrixinit)
                truewebdictinit1=copy.copy(truewebdictinit)

    return alpha_init,gam_init,sampletrue,Nmatrixinit1,truewebdictinit1,webNinit

def random_sample(m,M):
    """take a random sample m out of M possible items"""

    #first element of each tuple is sample label
    #second element is indicator for sampled (1) or not (0)
    x=np.arange(M)
    random.shuffle(x)
    y=[(x[i],(i<m)*1) for i in range(M)]
    y.sort()
    z=[w[1] for w in y]

    return z
```

3), 14), 15) Main MCMC sampler

```
def
MCMC_sampler(nwebs,udot_init,ndot_init,Gobsmatrix,obssamples,repsamples,alleles,occasions
,iterations,tuner,if_print,if_output,Ninit,rinit,xdetect,ncameras,totcollars,collars,tune_r,tuneN):
    """main program for MCMC sampler of genetic CMR data, camera data, telemetry data,
spatial process"""

    #static observation matrix
    G_obs=copy.copy(Gobsmatrix)
    #static obs samples,reps,calibration true and calibration obs samples
    sample_obs=obssamples.copy()
    sample_rep=repsamples.copy()

    samples=0
    accept_r=0
    accept_N=0

    d_=[]
    r_=[rinit]
    pweb_=[]
    dens_=[]

    sd_r=tune_r
    sd_N=tuneN

    #priors and initial parameter values
    #initial value of capture probability
    cap_p=[0.3]
    #initial value of genetic error probability
    error_p=[0.05]
    #prior alpha, initial gamma, initial true samples, initial Nmatrix, initial true web dictionary
```

```
prioralpha,gamma_init,sample_true_init,Nmatrix_init,true_webinit,webinit=initial_parms(nwebs
,alleles,sample_obs,occasions,Ninit,error_p[0])
    #initial values of abundance
    N_=[webinit]
    #Ntot
    Ntot=[sum(N_[0])]

    while samples<iterations:
        #--------------------------------
        #update genetic error probability
        #--------------------------------
        whet,whom=sum_dropout(sample_obs,sample_rep,alleles)
        #whet_c,whom_c=sum_dropout(calsamp_true,calsamp_obs,alleles)
        whet_c=[35,36,51,42,46,46,42,37]
        whom_c=[1,0,1,0,1,2,1,0]
        error_p.append(dropouterr_update(whet,whom,whet_c,whom_c))

        if samples==0:
            #-------------------------
            #update spatial parameter
            #-------------------------

            #density
            currentdens=density_update(N_[0],current_alpha=0.001,current_beta=0.001)

            #-----------------------
            #update camera r parameter
            #-----------------------
            d_.append([1.-(1.-rinit)**N_[0][i] for i in range(len(N_[0]))])
            dnew,rnew,acceptmhr=camera_mh_update(rinit,N_[0],xdetect,ncameras,sd_r)
```

```
        accept_r=accept_r+acceptmhr
        #----------------------------
        #update telemetry p_w parameter
        #----------------------------
        pwnew=pw_update(collars,N_[0],totcollars)

        #--------------------
        #update true genotypes
        #--------------------

Nmatrix_new,samp_truenew,trueweb_new=truegen_update(nwebs,true_webinit,Nmatrix_init,ga
mma_init,alleles,error_p[0],sample_obs,sample_rep,sample_true_init,occasions)
        #-----------------------------------------------
        #update true capture histories,and Gtrue of size(S)
        #-----------------------------------------------

Nmatrix_new2,Gtrue_new,Gtrue_web=truehist_update(nwebs,trueweb_new,Nmatrix_new,gam
ma_init,alleles,error_p[0],cap_p[0],occasions,samp_truenew,sample_obs,ncameras)

        #-------------
        #update gamma
        #-------------
        gamma_new=genfreq_update(Nmatrix_new2,prioralpha,alleles)

        #-----------------------
        #update pcapture (theta)
        #-----------------------
        #obtain new udot and ndot
        udot_new,ndot_new=sum_stats_web(Gtrue_new,occasions,nwebs)

currentpcapture=pcapture_update(udot_new,ndot_new,N_[0],occasions,cap_p[0],ncameras)
```

```
            #----------------------------
            #update N
            #----------------------------

currentN,acceptN=spatN_update(currentdens,N_[0],currentpcapture,udot_new,ndot_new,sd_N,x
detect,ncameras,occasions,pwnew,rnew,collars)
            accept_N=accept_N+acceptN
        else:
            #------------------------
            #update spatial parameter
            #------------------------

            #density
            currentdens=density_update(Nold,current_alpha=0.001,current_beta=0.001)
            #----------------------
            #update camera r parameter
            #----------------------
            dnew,rnew,acceptmhr=camera_mh_update(rold,Nold,xdetect,ncameras,sd_r)
            accept_r=accept_r+acceptmhr
            #----------------------------
            #update telemetry p_w parameter
            #----------------------------
            pwnew=pw_update(collars,Nold,totcollars)

            #--------------------
            #update true genotypes
            #--------------------

Nmatrix_new,samp_truenew,trueweb_new=truegen_update(nwebs,web_finalnew,Nmatrix_final
new,gamma_new,alleles,error_p[samples],sample_obs,sample_rep,Gtrue_new,occasions)
            #-----------------------------------------------
```

```
        #update true capture histories,and Gtrue of size(S)
        #-------------------------------------------------

Nmatrix_new2,Gtrue_new,Gtrue_web=truehist_update(nwebs,trueweb_new,Nmatrix_new,gam
ma_new,alleles,error_p[samples],cap_p[samples],occasions,samp_truenew,sample_obs,ncamera
s)
        #-------------
        #update gamma
        #-------------
        gamma_new=genfreq_update(Nmatrix_new2,prioralpha,alleles)

        #-----------------------
        #update pcapture (theta)
        #-----------------------
        #obtain new udot and ndot
        udot_new,ndot_new=sum_stats_web(Gtrue_new,occasions,nwebs)

currentpcapture=pcapture_update(udot_new,ndot_new,Nold,occasions,pcaptureold,ncameras)

        #----------------------------
        #update N
        #----------------------------

currentN,acceptN=spatN_update(currentdens,Nold,currentpcapture,udot_new,ndot_new,sd_N,xd
etect,ncameras,occasions,pwnew,rnew,collars)
        accept_N=accept_N+acceptN

      #augment N (add or delete rows) Reversible-jump M-H

Nmatrix_finalnew,web_finalnew=n_update(nwebs,Nmatrix_new2,currentN,gamma_new,alleles,
Gtrue_web,Gtrue_new)
```

```
densold=copy.copy(currentdens)
dens_.append(currentdens)
rold=copy.copy(rnew)
r_.append(rnew)
d_.append(dnew)
Nold=copy.copy(currentN)
N_.append(currentN)
Ntot.append(sum(currentN))
pcaptureold=copy.copy(currentpcapture)
cap_p.append(currentpcapture)
pweb_.append(pwnew)

samples+=1

acceptance_r=float(accept_r)/float(samples)
acceptance_N=float(accept_N)/float(samples*6)

if samples<tuner:
    if acceptN==1:
        sd_N=np.min(sd_N+1,5)
    else:
        sd_N=np.max(1,sd_N-1)
    if acceptmhr==1:
        sd_r=sd_r*0.999
    else:
        sd_r=sd_r*1.001

if (np.mod(samples,if_print)==0):
    print 'iter, N',samples,sum(currentN)
    print 'N accept',acceptance_N
```

```
        print 'r accept',acceptance_r

    if (np.mod(samples,if_output)==0):

MCMC_output(samples,nwebs,ncameras,cap_p,error_p,Ntot,r_,N_,dens_,d_,pweb_,Nmatrix_fin
alnew,gamma_new,Gtrue_new,web_finalnew)

  return cap_p,N_,error_p,Ntot,dens_,acceptance_r,r_,d_,pweb_,acceptance_N
def
MCMC_output(iteration,nwebs,kcam,captrace,errortrace,Ntottrace,rtrace,N_trace,denstrace,dtrac
e,pwebtrace,currentNmatrix,currentgamma,currentGtrue,currentwebdict):
  coda_out=[]
  coda_out.extend(errortrace)
  coda_out.extend(Ntottrace)
  coda_out.extend(rtrace)
  coda_out.extend(captrace)
  coda_out.extend(denstrace)

  Nall_trace=[]
  for j in range(nwebs):
    tempN=[]
    for k in range((len(N_trace))):
      tempN.append(N_trace[k][j])
    Nall_trace.append(tempN)
    coda_out.extend(tempN)

  dall_trace=[]
  for j in range(nwebs):
    tempd=[]
    if kcam[j]!='NA':
      for k in range((len(dtrace))):
```

```
            tempd.append(dtrace[k][j])
        dall_trace.append(tempd)
        coda_out.extend(tempd)

pweball_trace=[]
for j in range(nwebs):
    temppweb=[]
    for k in range((len(pwebtrace))):
        temppweb.append(pwebtrace[k][j])
    pweball_trace.append(temppweb)
    coda_out.extend(temppweb)

sumfile=open('iter'+str(iteration)+'_fall5.txt','w')
for i in range(len(coda_out)):
    alldat=[]
    dat=str(coda_out[i])
    alldat.append(dat)
    alldat.append("\n")
    sumfile.writelines(alldat)
sumfile.close()

sumfile2=open('iter'+str(iteration)+'_nmatrix_fall5.txt','w')
for i in currentNmatrix:
    alldat=[]
    dat=str(i)+str(':')+str(currentNmatrix[i])
    alldat.append(dat)
    alldat.append("\n")
    sumfile2.writelines(alldat)
sumfile2.close()

sumfile3=open('iter'+str(iteration)+'_gamma_fall5.txt','w')
```

```
    for i in range(len(currentgamma)):
        alldat=[]
        dat=str(currentgamma[i])
        alldat.append(dat)
        alldat.append("\n")
        sumfile3.writelines(alldat)
    sumfile3.close()

    sumfile4=open('iter'+str(iteration)+'_Gtrue_fall5.txt','w')
    for i in currentGtrue:
        alldat=[]
        dat=str(i)+str(":")+str(currentGtrue[i])
        alldat.append(dat)
        alldat.append("\n")
        sumfile4.writelines(alldat)
    sumfile4.close()

    sumfile5=open('iter'+str(iteration)+'_webdict_fall5.txt','w')
    for i in currentwebdict:
        alldat=[]
        dat=str(i)+str(":")+str(currentwebdict[i])
        alldat.append(dat)
        alldat.append("\n")
        sumfile5.writelines(alldat)
    sumfile5.close()

    return
```

4) Genetic error update modules

Equation 2.22

```
def dropouterr_update(whet,whom,whet_c,whom_c ):
```

```
    """update genetic error probability using Gibbs step"""

    #for now assume ado is constant across all loci
    tot_whet=sum(whet)
    tot_whom=sum(whom)
    tot_whetc=sum(whet_c)
    tot_whomc=sum(whom_c)

    #assume alpha=1 and beta=1 for priors
    a=1.
    b=1.
    newerr=pm.rbeta(2*a+tot_whom+tot_whomc-1, 2*b+tot_whet+tot_whetc-1)

    return newerr

def sum_dropout(obssamp,repsamp,alleles):
    """summarize dropout from observed and replicated genetic samples"""

    loci=len(alleles)
    w_het=[0]*loci
    w_hom=[0]*loci
    for obs in obssamp:
        for rep in repsamp:
            if obs==rep:
                for j in range(loci):
                    if isHom(obssamp[obs][0][j])==False:
                        if repsamp[rep][0][j]!='nn':
                            w_het[j]+=1
                            if isHom(str(repsamp[rep][0][j]))==True:
                                w_hom[j]+=1
```

```
    return w_het,w_hom
```

5) Spatial parameter update module

Equation 2.15

```
def density_update(current_N,current_alpha,current_beta):
    """update lambda using Gibbs sampling"""


nextlambda=pm.rgamma(np.mean(current_N)*len(current_N)+current_alpha,len(current_N)+cu
rrent_beta)


    return nextlambda
```

6) Camera parameter update module

Equations 2.18, 2.19, 2.20

```
def camera_mh_update(current_r,current_N,x_detect,n_cam,tune_r):
    """Metropolis-Hastings step of updating detection probability at camera under Royle-Nichols
model"""
    taur=tune_r
    #single animal detection probability r
    #detection probability
    d_current=[1.-(1.-current_r)**current_N[i] for i in range(len(current_N))]

    #proposal distribution
    x_prop=pm.rnormal(logit(current_r),taur)
    r_prop=expit(x_prop)
    d_prop=[1.-(1.-r_prop)**current_N[i] for i in range(len(current_N))]

    f=0.
    f_prop=0.
    for i in range(len(x_detect)):
        if x_detect[i]!='NA':
```

```
            #likelihood of current value
            f+=pm.binomial_like(x_detect[i],n_cam[i],d_current[i])
            #likelihood of proposed value
            f_prop+=pm.binomial_like(x_detect[i],n_cam[i],d_prop[i])

    #acceptance ratio
    r= np.exp(f_prop-f)

    if random.rand()<r:
        nextd=d_prop
        nextr=r_prop
        accept=1
    else:
        nextd=d_current
        nextr=current_r
        accept=0

    return nextd,nextr,accept
```

7) Telemetry parameter update module

Equation 2.17

```
def pw_update(ncollared,currentN,totcollars):
    """update probability of bear on web detected with collar using Gibbs sampling"""
    Ntot=sum(currentN)
    pwnew=[]
    for i in range(len(currentN)):
        if ncollared[i]!='NA':
            pwnew.append(pm.rbeta(ncollared[i]+currentN[i]+1.,totcollars-ncollared[i]+Ntot-
currentN[i]+1.))

        else:
            #posterior prediction onto webs not sampled
```

```
        pwnew.append(pm.rbeta(currentN[i]+1,Ntot-currentN[i]+1))

    return pwnew
```

8) Modules associated with genetic CMR parameters and matrices

```
def n_update(nwebs,Nmatrix,Nstar_,gammanew,alleles,truewebdict,truesampgen):

    Nmatrix_copy=Nmatrix.copy()
    N_=sum_web(truewebdict,nwebs)

    for i in range(len(N_)):
        if i==0:
            #proposed N is greater than the current value of N, add new rows
            if Nstar_[i]>N_[i]:

Nmatrixnew,truewebdictnew=gen_rows(Nstar_[i],N_[i],Nmatrix_copy,gammanew,alleles,i,true
webdict)
            #proposed N is less than the current value of N, delete rows
            else:
                Nmatrixnew=Nmatrix_copy.copy()
                truewebdictnew=truewebdict.copy()

                del_row=N_[i]-Nstar_[i]
                k=0
                for j in Nmatrix_copy:
                    if tuple(j) not in truesampgen:
                        if k<del_row:
                            #can only delete individuals not observed
                            if Nmatrix_copy[tuple(j)]=='000':
                                if truewebdict[tuple(j)]==i:
                                    del Nmatrixnew[tuple(j)]
                                    del truewebdictnew[tuple(j)]
```

```
                        k+=1
        else:
            #proposed N is greater than the current value of N, add new rows
            if Nstar_[i]>N_[i]:

Nmatrixnew1,truewebdictnew1=gen_rows(Nstar_[i],N_[i],Nmatrixnew,gammanew,alleles,i,true
webdictnew)

            #proposed N is less than the current value of N, delete rows
            else:
                Nmatrixnew1=copy.copy(Nmatrixnew)
                truewebdictnew1=copy.copy(truewebdictnew)
                del_row=N_[i]-Nstar_[i]
                k=0
                for j in Nmatrix_copy:
                    if tuple(j) not in truesampgen:
                        if k<del_row:
                            #can only delete individuals not observed
                            if Nmatrix_copy[tuple(j)]=='000':
                                if truewebdict[tuple(j)]==i:
                                    del Nmatrixnew1[tuple(j)]
                                    del truewebdictnew1[tuple(j)]
                                    k+=1

    return Nmatrixnew1,truewebdictnew1
def gen_rows(Nstar_,webmatrix,Nmatrix,gammanew,alleles,web,webdict):
    """simulates the true genotypes given number of alleles
    per locus and adds rows to genotypes. This does NOT require Hardy-Weinberg
Equilibrium"""

    Nmatrix_copy=Nmatrix.copy()
```

```
    nloc=len(alleles)
    gamman=gammanew
    webdictnew=webdict.copy()
    webm=copy.copy(webmatrix)

    while webm<Nstar_:

        g=[mult(gamman[i]) for i in range(nloc)]
        x=[gen_diction(y,z) for y,z in zip(g,alleles)]

        #check for identical genoptypes, if proposed value identical, redraw for new individual
        if tuple(x) not in Nmatrix_copy:
            Nmatrix_copy[tuple(x)]='000'
            webdictnew[tuple(x)]=web
            webm+=1

    return Nmatrix_copy,webdictnew
def geno_freq(loc):
    """returns the constant genotype frequency for each locus"""
    freq=[]
    for i in loc:
        cat=i*(i+1)/2
        freq.append([float(1./cat)]*cat)
    return freq

def mult(genprobs):
    """returns index value for multinomial rv"""
    gg=pm.rmultinomial(1,genprobs)
    for i in range(len(gg)):
        if gg[i]:
            return i
```

```
def gen_diction(genIndex,nallele):
    """creates genotype dictionary based on genotype index"""

    categories=(nallele*(nallele+1))/2
    allgen=list()
    m=0
    for i in range(nallele):
        for j in range(m,nallele):
            allgen.append(str(i)+str(j))
        m+=1

    genId={}
    for k in range(categories):
        genId[k]=allgen[k]

    gen=genId[genIndex]

    return gen

def prob_het(pgenerr):
    """computes prob of observing a genotype given the true heterozygous genotype
    with p the probability of one allele dropping out"""

    prob=[0.0]*3
    #obs het=true het
    prob[0]=1.-pgenerr
    #obs hom, dropout of first allele occured
    prob[1]=0.5*pgenerr
    #obs hom, dropout of second allele occured
    prob[2]=1.-sum(prob[0:2])
```

```
    return prob

def obs_trueHet(trueGen,obsIndex):
    """this function creates actual observed genotype, not index of observed genotype"""

    if obsIndex==0:
    #observed heterozygote (no ADO)
        actual=trueGen

    if obsIndex==1:
    #observed homozygote (first allele drops out)
        actual=string.replace(trueGen,trueGen[0],trueGen[1])

    if obsIndex==2:
    #observed homozygote (second allele drops out)
        actual=string.replace(trueGen,trueGen[1],trueGen[0])

    return actual

def isHom(string):
    """function returns true if genotype is homozygous, false otherwise"""
    intString=[int(ch) for ch in string]
    if intString[0]==intString[1]:
        return True
    else:
        return False
def gen_categories(alleles):
    """returns all genotype categories, given the number of
    alleles for each locus"""
```

```
    allgen=[]
    for k in range(len(alleles)):
        hold=[]
        m=0
        for i in range(alleles[k]):
            for j in range(m,alleles[k]):
                hold.append(str(i)+str(j))
            m+=1
        allgen.append(hold)

    return allgen

def sum_web(webdict,nwebs):
    """number of individuals in each web"""
    webN=[0]*nwebs
    for id in webdict:
        for j in range(len(webN)):
            if webdict[id]==j:
                webN[j]+=1
    return webN
def init_gen(initialN,gammapriors,alleles):
    """creates an initial true N matrix of genotypes given number of alleles
    per locus. This does NOT require Hardy-Weinberg Equilibrium"""

    initialNmatrix=[]
    nloc=len(alleles)
    gamman=copy.copy(gammapriors)

    while len(initialNmatrix)<initialN:

        g=[mult(gamman[i]) for i in range(nloc)]
```

```
        x=[gen_diction(y,z) for y,z in zip(g,alleles)]

        #check for identical genoptypes, if proposed value identical, redraw for new individual
        if tuple(x) not in initialNmatrix:
            initialNmatrix.append(tuple(x))

    return initialNmatrix

#factorial function
def fact(x): return (1 if x==0 else x * fact(x-1))

def x_like(Ntot,udot_,ndot_,pcapt,occasions,webcameras):
    """returns likelihood of X matrix, given N and p capture"""
    like=0.
    for i in range(len(Ntot)):
        if webcameras[i]!='NA':
            first=pm.gammaln(float(Ntot[i]+1.))-pm.gammaln(float(Ntot[i]-udot_[i]+1.))
            like+=(first+ndot_[i]*np.log(pcapt)+(occasions*Ntot[i]-ndot_[i])*np.log(1.-pcapt))

    return like

def geno_like(genlist,gammaprob):
    """returns likelihood of individual genotype at a locus, given allele freqencies at that given
locus"""

    cat=len(genlist)

    liketemp=0.
    for j in range(cat):
        liketemp+=pm.gammaln(float(genlist[j]))
```

```
    liketemp2=pm.gammaln(float(sum(genlist)+1.))-liketemp

    for i in range(cat):
        liketemp2+=genlist[i]*np.log(gammaprob[i])

    like=np.exp(liketemp2)

    return like

def genloc_compat(nmatrixkeys,loc):
    """compatible genotypes at locus"""
    loc_compat=[]
    for i in range(len(nmatrixkeys)):
        if nmatrixkeys[i][loc] not in loc_compat:
            loc_compat.append(nmatrixkeys[i][loc])

    return loc_compat

def listloop(list1,list2):
    """appends list in a loop"""
    all=[]
    for i in range(len(list2)):
        newlist=copy.copy(list1)
        newlist.append(list2[i])
        all.append(newlist)

    return all

def gen_diction_reverse(genIndex,allgen):
    """creates genotype dictionary based on genotype identity and
    returns genotype index"""
```

```
    categories=len(allgen)

    genId={}
    for k in range(categories):

        genId[allgen[k]]=k

    gen=genId[genIndex]

    return gen
def sum_genfreq(alleles,truepop):
    """this function computes the genotype frequencies over all loci"""

    gen_cat=gen_categories(alleles)

    true_freq=[]

    for k in range(len(alleles)):
        allgen=gen_cat[k]   #genotypes in each category

        sumid=[]
        #sum up all individuals with genotypes in each category at locus
        for cat in allgen:
            count=0
            for id in range(len(truepop)):
                if truepop[id][k]==cat:
                    count+=1
            sumid.append(count)
        hold=[float(sumid[i])/sum(sumid) for i in range(len(sumid))]
        true_freq.append(hold)
```

```
    return true_freq

def sum_genotypes(alleles,genlist):
    """this funciton computes the number of genotypes over all loci"""

    gen_cat=gen_categories(alleles)
    genlist_keys=genlist.keys()
    true_sums=[]

    for k in range(len(alleles)):
        allgen=gen_cat[k]       #genotypes in each category
        sumid=[]
        #sum up all individuals with genotypes in each category at locus
        for cat in allgen:
            count=0
            for id in range(len(genlist_keys)):
                if genlist_keys[id][k]==cat:
                    count+=1
            sumid.append(count)

        true_sums.append(sumid)

    return true_sums

def sum_stats_true(captures,nwebs,capturewebs):
    """calculates summary statistics for captured individuals and
    outputs udot,ndot"""

    captures_copy=captures.copy()
    udot_=[0]*nwebs
```

```
    ndot_=[0]*nwebs

    for id in captures:
        for idweb in capturewebs:
            if id==idweb:

                hist=list(captures[id])
                hist=[int(hist[x]) for x in range(len(hist))]
                ndot_[capturewebs[idweb]]+=sum(hist)
                if sum(hist)>0:
                    udot_[capturewebs[idweb]]+=1

    return udot_,ndot_

def sum_samples_webs(samplelist,occasions):
    """this function summarizes the capture histories for each web, and outputs the web
dictionary"""

    samples=samplelist.copy()
    captures={}
    samplewebs={}

    for samp in samples:
        id=samples[samp][0]

        if samples[samp][1]=='NA':
            captures[tuple(id)]='0'*occasions
            samplewebs[tuple(id)]=samples[samp][2]
        else:
            capt=int(samples[samp][1])
            if tuple(id) in captures:
```

```
            hold=list(captures[tuple(id)])
            hold[capt]='1'
            captures[tuple(id)]=''.join(hold)
        else:
            hist=['0']*occasions
            hist[capt]='1'
            captures[tuple(id)]=''.join(hist)
            samplewebs[tuple(id)]=samples[samp][2]

    return captures,samplewebs

def sum_stats_web(samplelist,occasions,nwebs):
    """calculates summary statistics for captured individuals and
    outputs udot,ndot"""

    captures,capturewebs=sum_samples_webs(samplelist,occasions)
    udot_=[0]*nwebs
    ndot_=[0]*nwebs

    for id in captures:
        for idweb in capturewebs:
            if id==idweb:

                hist=list(captures[id])
                hist=[int(hist[x]) for x in range(len(hist))]
                ndot_[capturewebs[idweb]]+=sum(hist)
                if sum(hist)>0:
                    udot_[capturewebs[idweb]]+=1

    return udot_,ndot_
```

```
def c_sum(samplelist,ident):
    """computes number of times an individual was observed in the genetic CMR data set"""

    samples=samplelist.copy()

    c_=0
    for samp in samplelist:
        if samplelist[samp][0]==tuple(ident):
            c_+=1

    return c_

def compat_gen(obsgen,gencat,perr):
    """creates a list of all compatible genotypes, given the observed genotype
    and number of alleles at a given locus"""

    compatible=[]
    if perr==0.0:
        compatible.append(obsgen)
        return compatible
    if isHom(str(obsgen))==False:
        compatible.append(obsgen)
        return compatible
    else:
        for id in gencat:
            if string.find(str(id),str(obsgen[0]))>-1:
                compatible.append(id)

        return compatible

def prob_obs(obsgen,truegen,perr):
```

```
    """returns the probability of an observed genotype, given the true genotype"""

    if perr==0:
        prob_=1.0
    else:
        if isHom(truegen)==True:
            if truegen==obsgen:
                prob_=1.0
            else:
                prob_=0.0
        else:

            prob=prob_het(perr)

            if isHom(obsgen)==True:
                prob_=prob[1]
            else:
                prob_=prob[0]

    return prob_
```

9) True genotype matrix update module

Appendix C

```
def
truegen_update(nwebs,true_webdict,Nmatrix,gamma_new,alleles,p_err,obssamples,repsamples,t
ruesamples,occasions):
    """returns the updated true genotpes given the observed genotypes,
    the number of times each genotype was observed (both in the samples S
    and the replicates R), , and the current genotypes in the true N matrix"""

    true_webcopy=true_webdict.copy()
```

```
Nmatrix_copy=Nmatrix.copy()
Nmatrix_keys=Nmatrix_copy.keys()
gen_cat=gen_categories(alleles)
loci=len(alleles)
samples_obs=obssamples.copy() #initial samples
obs_keys=samples_obs.keys()
samples_rep=repsamples.copy()
rep_keys=samples_rep.keys()
samples_true=truesamples.copy() #true samples
samples_truenew=copy.copy(truesamples)

gtrue,gtruewebs=sum_samples_webs(samples_true,occasions)
#compatible genotypes for each locus
loc_compat=[]
for i in range(loci):
   loc_compat.append(genloc_compat(Nmatrix_keys,i))

Nmatrix_new={}
true_webnew={}

#true genotypes not in samples
addgen={}
for genid in Nmatrix_copy:
   if genid not in gtrue:
      addgen[genid]=Nmatrix_copy[genid]



for genid in Nmatrix_copy:

   if genid in gtrue:
```

```
#number of times that individual was in true samples
c=c_sum(samples_true,genid)

for samp in range(len(samples_true)):
   newgenid=[]
   if samples_true[samp][0]==genid:

      for j in range(loci):

         #generate compatible genotypes for each inidividual by locus and replicate
         compatible=[]

         if c==1:
            if samp in rep_keys:
               compattemp=compat_gen(samples_obs[samp][0][j],gen_cat[j],p_err)
               if samples_rep[samp][0][j]!='nn':
                  morecompat=compat_gen(samples_rep[samp][0][j],gen_cat[j],p_err)
                  for m in morecompat:
                     if m in compattemp:
                        compatible.append(m)
            else:
               compatible=compat_gen(samples_obs[samp][0][j],gen_cat[j],p_err)

         else:
            #these are all the compatible genotypes from all c_i rep samples
            sampid=[]

            for s in samples_true:
               if samples_true[s][0]==samples_true[samp][0]:
                  sampid.append(s)
```

```
    compatible=[]
    compattemp=compat_gen(samples_obs[samp][0][j],gen_cat[j],p_err)

    for sid in sampid:
        if sid in rep_keys:
            if samples_rep[sid][0][j]!='nn':
                morecompat=compat_gen(samples_rep[sid][0][j],gen_cat[j],p_err)
                for m in morecompat:
                    if m in compattemp:
                        compatible.append(m)
        else:
            compatible=compattemp

#check that the compatible genotype at il does not result in any individual
#in population, if it does, eliminate it from compatible list
Gtrue_compat=[]
m=0
for i in compatible:

    test=copy.copy(samples_true[samp][0])
    test=list(test)
    test[j]=i
    if c==1:
        if tuple(test)==samples_true[samp][0]:
            Gtrue_compat.append(i)
        else:
            if tuple(test) not in Nmatrix_copy:
                Gtrue_compat.append(i)
    else:
        for sid in sampid:
            if tuple(test)==samples_true[sid][0]:
```

```
                if i not in Gtrue_compat:
                    Gtrue_compat.append(i)
            else:
                if tuple(test) not in Nmatrix_copy:
                    if i not in Gtrue_compat:
                        Gtrue_compat.append(i)


if len(Gtrue_compat)>0:

    prob=[]
    prob_gen=[]
    for i in Gtrue_compat:
        #prob(g_obs|G proposed)**(c_i**replicates)
        if c==1:
            probtemp=prob_obs(samples_obs[samp][0][j],i,p_err)
            if samp in rep_keys:
                if samples_rep[samp][0][j]!='nn':
                    probtemp2=prob_obs(samples_rep[samp][0][j],i,p_err)
                else:
                    probtemp2=1.
            else:
                probtemp2=1.

            prob.append(probtemp*probtemp2)

            #replace genotype matrix with proposed genotype at specific locus
            genmatrix=copy.copy(samples_truenew)
            temp=list(genmatrix[samp][0])
            temp[j]=i
            genmatrix[samp][0]=tuple(temp)
```

```
            totalgenmatrix,matrixwebs=sum_samples_webs(genmatrix,occasions)
            totalgenmatrix.update(addgen)
            genout=sum_genotypes(alleles,totalgenmatrix)
            #calculate likelihood with this replacement
            prob_gen.append(geno_like(genout[j],gamma_new[j]))

        else:
            probhold=1.
            for s in sampid:
                probhold*=prob_obs(samples_obs[s][0][j],i,p_err)
                if s in rep_keys:
                    if samples_rep[s][0][j]!='nn':
                        probhold*=prob_obs(samples_rep[s][0][j],i,p_err)

            prob.append(probhold)

            #replace genotype matrix with proposed genotype at specific locus
            genmatrix=copy.copy(samples_truenew)

            for s in sampid:
                temp=list(genmatrix[s][0])
                temp[j]=i
                genmatrix[s][0]=tuple(temp)

            totalgenmatrix,matrixweb=sum_samples_webs(genmatrix,occasions)
            totalgenmatrix.update(addgen)
            genout=sum_genotypes(alleles,totalgenmatrix)
            #calculate likelihood of replacement
            prob_gen.append(geno_like(genout[j],gamma_new[j]))

    #calculate lambda contributions for all compatible genotypes
```

```
                    lambda_k=[prob[i]*prob_gen[i] for i in range(len(Gtrue_compat))]
                    #calculate probability of lambda
                    prob_lambda=[lambda_k[i]/sum(lambda_k) for i in range(len(lambda_k))]
                    #selecte one of the lambdas (i.e. replaced genotypes) based on the probability
                    newG=Gtrue_compat[mult(prob_lambda)]
                    newgenid.append(newG)

                else:
                    newgenid.append(samples_true[samp][0][j])

            if c==1:
                samples_truenew[samp][0]=tuple(newgenid)
            else:
                for sid in sampid:
                    samples_truenew[sid][0]=tuple(newgenid)

            Nmatrix_new,true_webnew=sum_samples_webs(samples_truenew,occasions)

    udot_temp,ndot_temp=sum_stats_web(samples_truenew,occasions,nwebs)

    #for all individuals not sampled, select new genotypes conditioned on current gamma
probabilities
    for genid in Nmatrix_copy:
        if genid not in gtrue:
            g=[mult(gamma_new[i]) for i in range(loci)]
            x=[gen_diction(y,z) for y,z in zip(g,alleles)]

            #check for identical genoptypes, if proposed value identical, redraw for new individual
            if tuple(x) not in Nmatrix_new:
                Nmatrix_new[tuple(x)]='0'*occasions
                true_webnew[tuple(x)]=true_webdict[genid]
```

```
    return Nmatrix_new,samples_truenew,true_webnew
```

10) True capture history matrix update module

Appendix C

```
def
truehist_update(nwebs,trueweb,Nmatrix,gamma_new,alleles,p_err,captureprob,occasions,samptr
ue,sampobs,wcams):
    """update true capture history matrix of genetic CMR samples, given capture probability, and
true genotypes"""

    Nmatrix_copy=Nmatrix.copy()
    currentNweb=sum_web(trueweb,nwebs)
    gen_cat=gen_categories(alleles)
    loci=len(alleles)
    pcapt=copy.copy(captureprob)
    true_samp=copy.copy(samptrue)
    true_keys=samptrue.keys()
    true_sampnew=copy.copy(samptrue) #true genotypes in samples
    gobs_samp=sampobs.copy()
    gobs_keys=sampobs.keys()
    gtrue,gtruewebs=sum_samples_webs(true_samp,occasions)

    addgen={}
    addgenwebs={}
    for genid in Nmatrix_copy:
        if genid not in gtrue:
            addgen[genid]=Nmatrix_copy[genid]
            addgenwebs[genid]=trueweb[genid]

    for ident in gobs_keys:
```

```
#create list of all compatible individual genotypes with observed genotype
for j in range(loci):
    compat=compat_gen(gobs_samp[ident][0][j],gen_cat[j],p_err)

    if j>0:
        new=[]
        for i in range(len(compatible)):
            new.extend((listloop(compatible[i],compat)))
        del compatible
        compatible=copy.copy(new)

    else:
        compatible=[]
        for k in compat:
            compatible.append([k])

#find all compatible genotypes in Gtrue matrix, and eliminate all not in matrix
Gtrue_compat=[]
compat_hist=[]
for i in compatible:
    if tuple(i) in Nmatrix_copy:
        if tuple(i) not in gtrue:
            Gtrue_compat.append(tuple(i))
            compat_hist.append('NA')

        else:
            place=copy.copy(gobs_samp[ident][1])
            compat_hist.append(place)
            Gtrue_compat.append(tuple(i))
```

```
    if len(Gtrue_compat)>0:
        #update true sample histories

        probgobs=[]
        for i in Gtrue_compat:
            prob=1.
            #prob(g_obs individual|G proposed individual) over all loci
            for j in range(loci):
                prob*=(prob_obs(gobs_samp[ident][0][j],i,p_err))

            probgobs.append(prob)

        #likelihood of X(j) matrix given N and p
        probX=[]
        for i in range(len(Gtrue_compat)):
            xmatrix=copy.copy(true_sampnew)
            xmatrix[ident][1]=compat_hist[i]
            udottemp,ndottemp=sum_stats_web(xmatrix,occasions,nwebs)
            probX.append(x_like(currentNweb,udottemp,ndottemp,pcapt,occasions,wcams))

        lambda_X=[probgobs[i]*probX[i] for i in range(len(probgobs))]
        prob_lambdaX=[lambda_X[i]/sum(lambda_X) for i in range(len(lambda_X))]

        #new X matrix associated with new G matrix
        newX=copy.copy(compat_hist[mult(prob_lambdaX)])

        true_sampnew[ident][1]=newX

Gtrue_new,Gtruewebs=sum_samples_webs(true_sampnew,occasions)
obsu,obsn=sum_stats_web(true_sampnew,occasions,nwebs)
Gtrue_new.update(addgen)
```

```
    Gtruewebs.update(addgenwebs)

    return Gtrue_new,true_sampnew,Gtruewebs
```

11) True genotype frequency update module

Equation 2.23

```
def genfreq_update(genotypes,priorgenfreq,alleles):
    """returns the new genotype frequencies, or gamma, given the number of
    alleles at all loci, current number of individuals with each genotype and
    priors for alphas with Gibbs sampling step"""

    gen1=genotypes.copy()
    gen=gen1.keys()

    gen_cat=gen_categories(alleles)

    gamma_new=[]

    for k in range(len(alleles)):
        allgen=gen_cat[k] #genotype categories
        sumid=[]

        #sum up all individuals with genotypes in each category at locus
        for cat in allgen:
            count=0
            for id in gen:
                if id[k]==cat:
                    count+=1
            sumid.append(count)

        prior=priorgenfreq[k]
```

```
        #this simulates a draw from Dirichlet distribution
        alphagammas=[pm.rgamma(i+j,1) for i,j in zip(sumid,prior)]
gammanew=[float(alphagammas[i])/(sum(alphagammas)) for i in range(len(alphagammas))]
        gamma_new.append(gammanew)

    return  gamma_new
```

12) Capture probability update module

Equation 2.24

```
def pcapture_update(udotnew,ndotnew,N_current,occasions,prevpcapt,numbcameras):
    """update capture probability parameters for genetic CMR data using Gibbs"""

    #constant time and web (but not estimate webs not sampled)
    ncurrent=0
    ndotnew_=0
    for i in range(len(numbcameras)):
        if numbcameras[i]!='NA':
            ncurrent+=N_current[i]
            ndotnew_+=ndotnew[i]

    b=ncurrent*occasions-ndotnew_+1.
    a=ndotnew_+1.
    try:
        temp=pm.rbeta(a,b)
    except:
        temp=prevpcapt

    return temp
```

13) True abundance update modules

Equation 2.25

```
def
N_like(currentdensity,allN,currentpcapt,currentudot,currentndot,occasions,x_detect,n_cam,curre
ntr,currentpw):
    """joint 3 data and spatial likelihood of N using Metropolis step"""

    like1=0.
    like2=0.
    like3=0.
    like4=0.
    like=0.
    badvalue=False

    for i in range(len(x_detect)):
        if x_detect[i]!='NA':

            like1+=pm.poisson_like(allN[i],currentdensity)                    #spatial like
            like2+=pm.binomial_like(x_detect[i],n_cam[i],(1.-(1.-currentr)**allN[i]))          #camera
like
            like3+=pm.binomial_like(allN[i],sum(allN),currentpw[i])                  #telemetry
like
            #calculate pi0, probability of capture at least once
            pi0=1.-(1.-currentpcapt)**occasions
            genalpha=currentudot[i]+1.
            genmu=genalpha*(1.-pi0)/pi0
            like4+=pm.negative_binomial_like(allN[i]-currentudot[i],genmu,genalpha)
#genetic CMR like


    like=like1+like2+like3+like4

    return like
```

```
def
spatN_update(currentdensity,curN,currentpcapt,currentudot,currentndot,tune_n,xdetect,ncameras
,occasions,currentpw,current_r,brcollars):
    """update N using M-H with joint 3 data model"""

    currentN_=copy.copy(curN)
    tempN=copy.copy(curN)
    nextN=copy.copy(curN)
    taun=tune_n
    accept=0

    for i in range(len(curN)):
        if xdetect[i]!='NA':
            fpropbadvalue=True
            while fpropbadvalue==True:

                Njump=int(np.ceil(randu()*taun))
                u=bern(0.50)
                Ni_prop=u*(currentN_[i]+Njump)+(1-u)*(currentN_[i]-Njump)

                #constrain to nonnegative values
                if Ni_prop<0:
                    fpropbadvalue=True
                else:
                    #constraint based on genetic CMR data
                    if Ni_prop<currentudot[i]:
                        fpropbadvalue=True
                    else:
                        #constraint based on telemetry data
                        if Ni_prop<brcollars[i]:
```

```
                fpropbadvalue=True
            else:
                #constraint based on camera data
                if xdetect[i]>0:
                    if Ni_prop==0:
                        fpropbadvalue=True
                    else:
                        fpropbadvalue=False
                else:
                    fpropbadvalue=False

        nextN[i]=copy.copy(Ni_prop)
        #likelihood of proposed value

f_prop=N_like(currentdensity,nextN,currentpcapt,currentudot,currentndot,occasions,xdetect,nca
meras,current_r,currentpw)
        #likelihood of current value

f=N_like(currentdensity,currentN_,currentpcapt,currentudot,currentndot,occasions,xdetect,ncam
eras,current_r,currentpw)
        #ratio of likelihoods
        ratio_N= np.exp(f_prop-f)

        #generate r.v. and accept or reject based on if less than r
        if random.rand()<ratio_N:
            nextN[i]=copy.copy(Ni_prop)
            accept+=1
        else:
            nextN[i]=copy.copy(currentN_[i])

    else:
```

```
        #posterior prediction onto webs not sampled using marginal negative binomial
distribution
        nextN[i]=pm.rpoisson(currentdensity)

    return nextN,accept
```

Additional modules

```
def bern(x):
    u=randu()
    if u<x:
        out=0
    else:
        out=1
    return out

def plot_tracepost(var,vartrace,plotnum):
    """plot the posterior traces and histograms"""

    it=np.arange(0,len(vartrace))
    figure(plotnum)
    plot(it,vartrace)
    savefig(var+'trace')
    close()

    figure(plotnum+1)
    hist(vartrace,bins=50)
    savefig(var+'posterior')
    close()

    nextplotnum=plotnum+2

    return nextplotnum
```

```
def output_stats(varname,vartrace):
    """print to screen all output statistics"""
    samples=len(vartrace)
    vartrace.sort()
    lower=int(samples*.025)
    upper=int(samples*.975)
    print varname
    print 'lower',vartrace[lower]
    print 'upper',vartrace[upper]
    print 'median',np.median(vartrace)
    print 'mean',np.mean(vartrace)
    print ''

    return

def logit(p):
    """compute logit of a value"""
    x=np.log(p/(1.-p))
    return x

def expit(x):
    """compute expit of a value"""
    p=1./(1.+np.exp(-x))
    return p
```

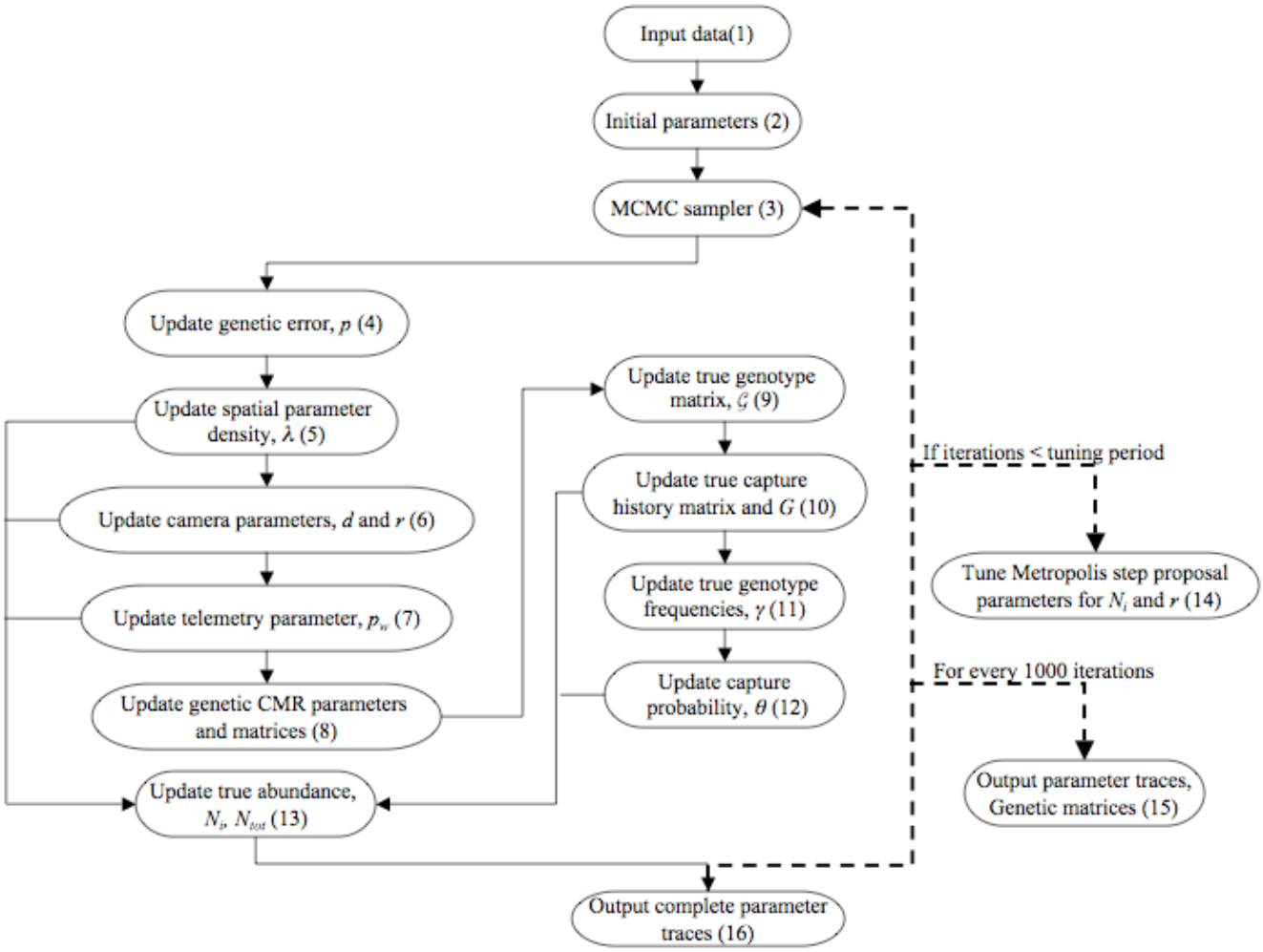

Figure E.1. Flowchart of the MCMC steps from the joint model incorporating the three data structures of DNA hair snares, telemetry, and camera traps for CGP black bear data.