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POPULATION DYNAMICS OF BLACK BEARS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Alex Blandon Coley

May 1995

DEDICATION

This thesis is dedicated to the memory of those souls misfortunate enough to foresee the destruction and degradation of our wild and natural places for the sake of progress and were helpless to prevent it.

> "This we know: the earth does not belong to man; man belongs to the earth. This we know.
>
> All things are connected like blood that unites a family. All things are connected.
>
> Whatever befalls the earth befalls the sons of the earth. Man did not weave the web of life; he is merely a strand in it. Whatever he does to the web, he does to himself."
>
> "What will happen when the buffalo are all slaughtered and the horses are all tamed, when the secret corners of the forest are heavy with the scent of many men, and the view of ripe hills is blotted by talking wires?
>
> Where is the thicket? Gone.
>
> Where is the eagle? Gone.
>
> The end of living and the beginning of survival."
>
> *Chief Noah Seattle*

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A special thanks goes to technicians and fellow graduate students who made school and trapping wonderful experiences. Especially helpful were: Bill Stiver and Steve Seibert, for teaching me how to trap; Keith Weaver, for his encouragement and his infinitely-upbeat attitude; Greg Schildwachter, for a nickname I'll never shake; and Frank van Manen, for his ability to know and do all things when it comes to computers. I thank Wendy Crawford of the National Park Service for her assistance with the hard mast survey data and Drs. Joe Clark and Stephen Nodvin of the National Biological Service for allowing me to use their computer system. I am deeply indebted to the numerous graduate students and technicians who sustained this project over the last 20+ years, without whom this project would not be possible.

Lastly, and most importantly, I would like to thank my family. The support (emotional, financial, and any other way possible) of my parents, Jim and Judy Coley, and my 2nd parents, Jim and Patricia Riddle, has been nothing short of

incredible. Finally, to Tracy and Brennan, the loves of my life, without whom all is meaningless.

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ABSTRACT

Previous estimates of black bear (*Ursus americanus*) population density from Great Smoky Mountains National Park (GSMNP or Park) were low to intermediate when compared to other populations throughout the range of the species. These estimates conflicted with other research on GSMNP bears that indicated a high-density population with consistent growth from the early 1970's to the late 1980's. Thus, the focus of my research was to calculate appropriate estimates of population size and density and evaluate them with respect to trapping regime, demographic data, and hard mast production.

I determined effective study area sizes by calculating the average distance between summer centers of activity and capture locations. The average distance for females approximated the average summer home range radius (1.3 km), while the average distance for males was roughly half the average summer home range radius (1.9 km). The mean distance for males was misleading because the distribution was bimodal with one node located near the maximum distance (2.5 km). I used these distances (1.3 and 2.5 km, respectively) as radii for circles circumscribed around each trap site to determine the effective study area sizes. Size of the current study area for males and females is 254.7 km^2 and 112.6 km^2, respectively.

I used summer capture data of black bears from GSMNP to estimate population size and demographic parameters. Summer trapping between 1972 and 1991 resulted in 887 (501♂;386♀) captures of 558 (335♂;223♀) individual bears. For females, average time interval between first and second captures ($\bar{x}$ = 2.38

years, SD = 1.85, n = 78) was longer (t' = 3.01, df = 127, P = 0.0031) than the average time interval between subsequent captures ($\bar{x}$ = 1.61 years, SD = 1.09, n = 54). Females were older ($\bar{x}$ = 6.80, SD = 3.46, n = 211) than males ($\bar{x}$ = 4.85, SD = 2.51, n = 321) (t' = 7.04, df = 351, $P < 0.001$).

Using den records from 1978-1991, I calculated litter size, sex ratio, and cub survival. The average size of 74 litters was 2.24 with a sex ratio of 102♂:100♀. Overall cub survival was 61.3% with females and cubs from intermediate-size litters exhibiting slightly higher survival rates.

I estimated population size using Calendar of captures (or backdating), Lincoln-Petersen, nonparametric, and Jolly-Seber (computer program JOLLY) population estimators. With the exception of the nonparametric estimator, all were highly correlated. JOLLY estimates appear to be most appropriate for long-term studies with low capture probabilities. JOLLY produced an average annual estimate of 185 animals from 1973 to 1990; this equated to a mean density of 1.36 bears/km^2. Lincoln-Petersen estimates and trends were surprisingly consistent with those from JOLLY. Backdating provided a reasonable baseline population estimate but the nonparametric estimator was inappropriate for our data set. My data indicated that population estimates generated with <5 years of data may be biased because of long inter-capture intervals for individual bears. This is especially relevant if capture probabilities are low. Using backdating data, the proportion of females in the population was negatively correlated with population size (P = 0.00228).

I estimated population size on groups of trap lines that were consistently sampled over a given time interval because of inconsistencies in trapping from year to year. This partitioning of the data provided an opportunity to examine the effects of study duration and altered trapping regimes on population estimates. Longer time intervals provided more reliable population estimates, but our data indicate inconsistent trapping does not necessarily invalidate the usage of such data to estimate population size. Average population densities for groups of trap lines ranged between 0.81 and 2.47 bears/km^2.

Model selection in JOLLY seemed to indicate males and females exhibit different population dynamics. Female models indicated stability with internal recruitment (model A' - death but no immigration) while male models demonstrated more external population forces (model A - death and immigration).

I incorporated estimates of demographic parameters from den work (litter production rate, litter size, and cub survival), computer program JOLLY (adult survival), and backdating (subadult survival and beginning population size) into computer program ANURSUS in an attempt to rectify population estimates with demography. ANURSUS simulations predicted severe population declines from 1991-1996 using both stochastic (44% - density independent) and deterministic models (33% - density independent; 59% - density dependent). Population estimates for 1992 and 1993, however, contradict the simulation results. Estimates of subadult and adult survival were suspect and likely caused the predicted declines.

I calculated 4 indices of trap activity to determine whether or not capture success is a reflection of population size. All indices were correlated with population estimates, with the percentage of nights with no activity and the percentage of nights with bear activity exhibiting the strongest relationships. I also calculated 4 indices of female reproductive status to examine potential density-dependant impacts on reproduction. None of the indices were correlated with population estimates.

Using National Park Service (NPS) hard mast index data, I investigated relationships between population size and hard mast production. No distinctive pattern was evident. The most prominent correlations were between population estimates and hard mast production of the same year; this may indicate that both mast production and the bear population respond to the same environmental and climatic conditions.

I constructed models to predict black bear ages from morphological measurements. Because of sexual dimorphism and differential growth rates, I created separate models, by sex, for wild and panhandler Park bears. Total length, height at shoulder, chest circumference, neck circumference, weight, and distance between ears were important ($P < 0.0001$) predictors of age. However, bears ≥ 5.5 years were indistinguishable with these models. Although models were not applicable beyond the population they were developed for, the method is potentially suitable for most black bear populations. This predictive relationship between morphometrics and age should aid nuisance relocations, telemetry studies, and researchers with bears of unknown age.

Future research on black bear density estimation should utilize home range data to establish trapping grids or routes that effectively cover the desired area. Emphasis should be placed on effectively sampling females because of the primary importance of females to population dynamics and the relative unreliability of male home range estimates. Distance between traps should equal the average female summer home range diameter to provide maximum coverage without gaps in the trapping grid.

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PART 1

Population Dynamics

CHAPTER 1

INTRODUCTION

The American black bear ranged over the entire forested regions of North America during pre-Columbian times (Hall 1981). Currently, the status of the species ranges from abundant in the western United States and Canada to extirpated in many midwestern states (Pelton 1982). In the Southeast, the present black bear distribution is less than 10% of the historic range and the remaining habitat is becoming increasingly fragmented (Maehr 1984). Currently, the black bear is designation as a featured management species by the NPS in GSMNP (Herrmann and Bratton 1977). Human demands on private and public land adjacent to the Park continue to grow. Development of private land in the area has recently accelerated and demands for timber and recreation on public and private land continue to increase. Furthermore, the likely infestation of the gypsy moth (*Porthetria dispar*) has the potential to devastate oak mast production. This combination of biological and social pressures makes it imperative that we have a thorough understanding of population size and dynamics, in addition to the interactions among genetic population stability, habitat quantity, and habitat quality.

Previous investigations of the density of black bear populations combined data for males and females and ignored the potential impact that differences between the sexes (home range size, behavior, mortality rates) could have on estimation of population size and density and understanding the dynamics of the population. Inconsistent sampling and arbitrary definitions of study area boundaries further

complicated attempts to identify interactions among bears and between bears and their environment.

In recent years, researchers have attempted to estimate densities with methods that would allow comparisons among areas. Miller et al. (1987) estimated black and brown bear (*Ursus arctos*) density in Alaska using fixed-wing aircraft and defining study area boundaries based on telemetry locations. Dean (1987) used fixed-wing aircraft in combination with multi-observer ground coverage to estimate brown bear density. Dean also utilized digitized topographic and vegetation data to calibrate sighting efficiency. Other researchers have used only radiocollared bears as marks (McLellan 1989) or determined the proportion of home ranges encompassed by the study area and weighted densities according to the amount of time spent in the study area (Garshelis 1991). Aerial sighting was not feasible in the thick vegetation of GSMNP and the available telemetry data was inappropriate for this study. Clark (1991) used GIS buffer capabilities to add a strip equal to the average home range radius to the trapping grid.

This research was an attempt to incorporate 20 years of field research into a coherent view of black bear population dynamics including the influence of hard mast production on population parameters. Specific objectives of this study were:

(1) To identify and delineate meaningful study area boundaries for male and female bears,

(2) To compare 4 estimators of population size relative to the validity of their use on black bear populations,

(3) To estimate population size, density, survival rates, and capture probabilities for adult male and female bears during consistent periods of sampling,

(4) To summarize size, sex ratios, and survival rates of black bear litters,

(5) To determine the effective genetic population size for bears within the defined study area boundaries,

(6) To simulate black bear population dynamics using computer program ANURSUS and determine if our data are sufficient for this model,

(7) To investigate relationships between population estimates and indices of trap success and female reproductive status,

(8) To investigate relationships between hard mast production and population size.

CHAPTER 2

STUDY AREA

Location

GSMNP lies in eastern Tennessee and North Carolina between 35° 26' and 35° 47' N latitude and 83° 2' and 84° 0' W longitude and encompasses approximately 2100 km^2. The Park is bordered by federally-protected land on 3 sides; Cherokee Indian Reservation and Nantahala National Forest, North Carolina, to the south, Cherokee National Forest, Tennessee, to the southwest, and Pisgah National Forest, North Carolina, to the northeast. This represents approximately 17,000 km^2 of contiguous habitat occupied by black bears, 8000 km^2 of which is administered by the USDA Forest Service but owned by other parties (USDA 1993). The remainder of the northern boundary is formed by private lands (Figure 2.1). The study area encompassed approximately 500 km^2 and was located in the northwest quadrant of GSMNP (Figure 2.2).

Geology and Physiography

The Great Smoky Mountains lie in the southern Appalachian Highlands and are part of the Unaka Mountain Range of the Blue Ridge Province (Fenneman 1938). The ridge crest extends from northeast to southwest and forms the boundary between Tennessee and North Carolina. The Park is typified by distinct ridges and steep, stream-cut valleys with more than 90% of the Park having a slope greater than 10%

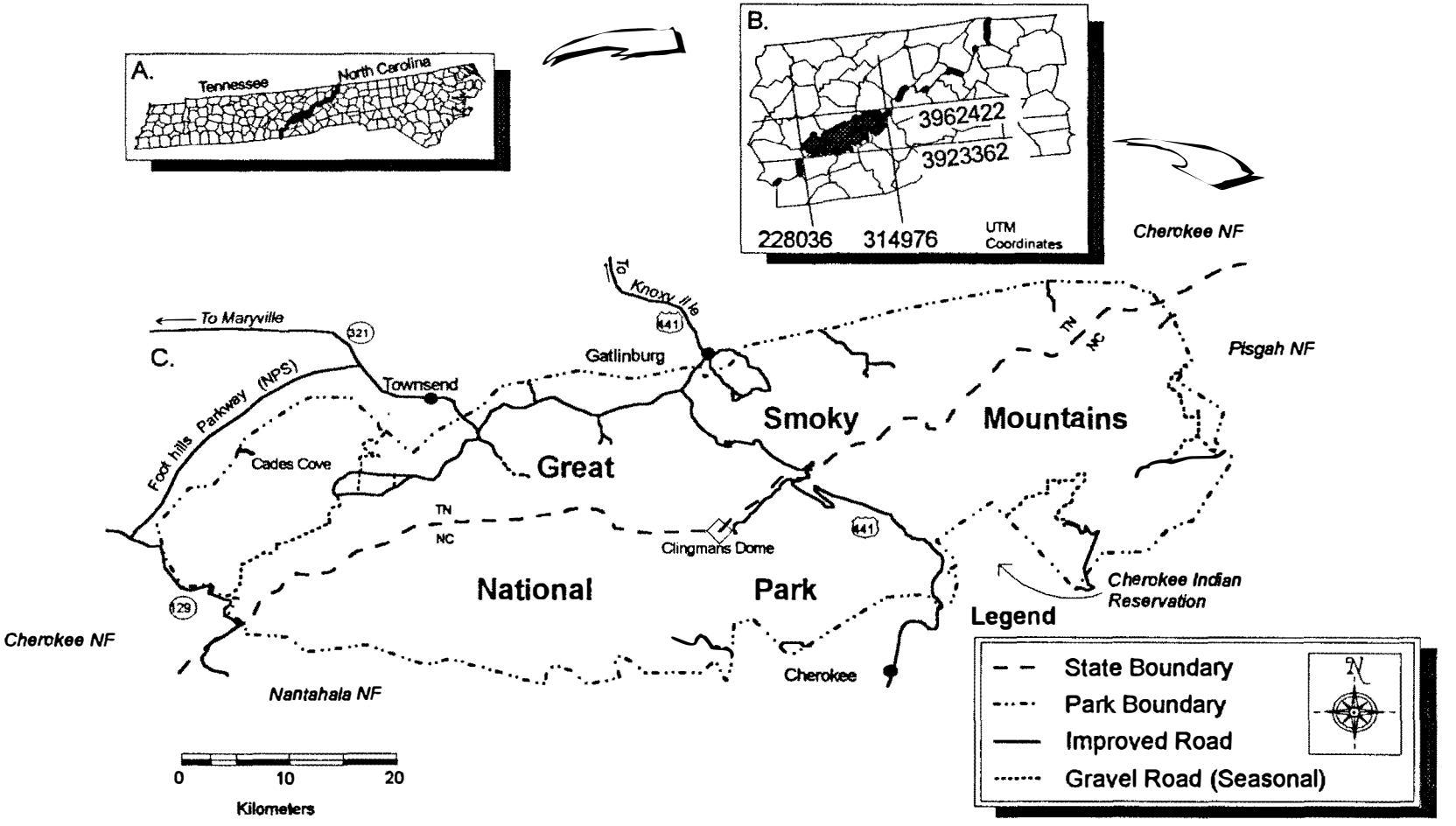


Figure 2.1. Location of Great Smoky Mountains National Park in East Tennessee and western North Carolina (Figure courtesy of Frank van Manen).

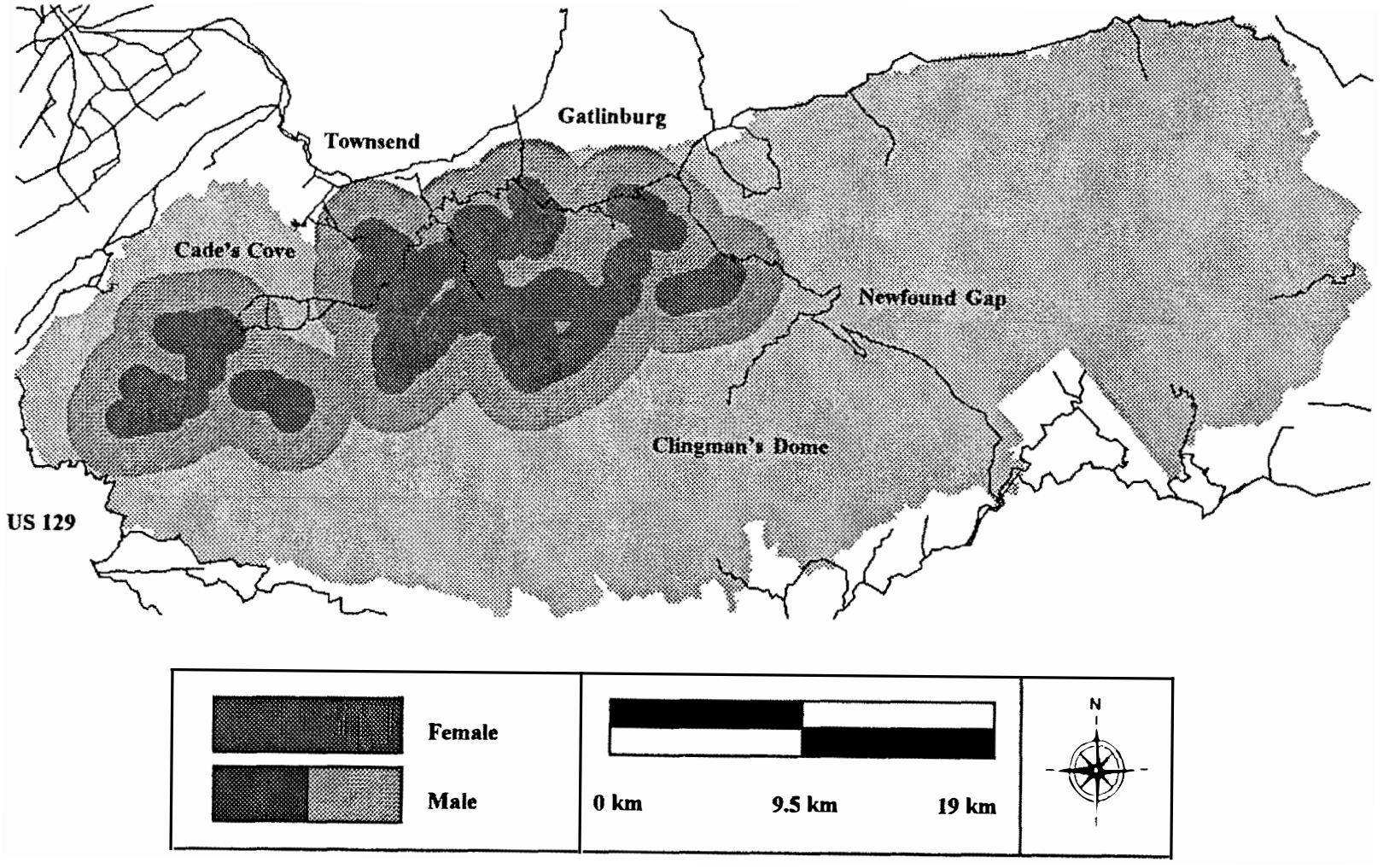


Figure 2.2. Location of cumulative effective study area in Great Smoky Mountains National Park. Male study area encompasses dark inner bands (female study area) as well as the lighter, outer band.

(Anonymous 1902). Elevations range from 266.4 m at Chilhowee Lake to 2024.8 m at Clingman's Dome. Bedrock within the Park is feldspathic sandstone, siltstone, and conglomerate from the Ocoee series formed during the late Precambrian period (King et al. 1968). Soils formed from these parent materials are primarily of the Ramsey association, with most mountain slopes in the Ramsey series and the lower slopes in the Jefferson series. These soils are characterized by low water storage capacity, medium to high acidity levels, and moderate fertility (Soil Survey 1945, 1953).

Climate

Thornthwaite (1948) categorized the Great Smoky Mountains as a warm-temperate rain forest (mesothermal perhumid). Average annual temperature ranges from 8°C at higher elevations to 14°C at lower elevations. Coldest temperatures are usually recorded in January or February ($\overline{x}$ = 3.3°C) and highest temperatures in July or August ($\overline{x}$ = 23.9°C) (U. S. Dept. Commerce 1972; Stephens 1969). Precipitation varies with elevation and ranges from 140 cm per year to more than 200 cm per year. Maximum precipitation usually occurs during July with minimum levels normally in September or October (Stephens 1969). Cloud cover increases with elevation and during the colder part of the year (Stephens 1969).

Biota

Extreme variation in elevation, precipitation and temperature combined with some remnants of the last glacial period have produced a tremendous diversity of

plant species within the Park. Stupka (1960) reported more than 1300 species of vascular plants within the Park, including 131 native tree species. White (1982) listed an additional 288 species of exotic flowering plants. Stupka (1960) also identified more than 2000 species of fungi, 230 lichens, and approximately 350 mosses and liverworts. Approximately 95% of the Park is forested (Stupka 1960); the predominant cover types are: spruce-fir, northern hardwoods, open oak-pine, closed oak, hemlock, and cove hardwoods (Shanks 1954). The remaining 5% of the Park consists primarily of the open fields of Cades Cove and several grass and heath balds. Understory species common throughout the Park include blueberry (*Vaccinium* spp.), huckleberry (*Gaylussacia* spp.), rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*).

Linzey and Linzey (1971) reported 59 mammal species in the Park, with an additional 6 species being listed as extirpated. Of these 6 species, beaver (*Castor canadensis*) have recolonized the lower elevations of watersheds on Fontana Lake (Van Gelder 1982), the river otter (*Lutra canadensis*) has been reintroduced (Greiss 1987; Miller 1992), and a study is currently underway to determine the feasibility of reintroducing elk (*Cervus elaphus*) to GSMNP. In addition, a pilot reintroduction of red wolves (*Canis rufus*) was begun in 1991. GSMNP is also home to more than 200 bird species, 130 species of reptiles, 72 species of fish and 39 amphibian species. Peregrine falcons (*Falco peregrines*) were reintroduced into the Park during the mid-1980's and efforts are currently being made to expand the range of the brook trout

(*Salvelinus fontinalis*) which was greatly reduced by habitat alteration during the late 1800's and early 1900's.

CHAPTER 3

MATERIALS AND METHODS

Effective Study Area Validation

Caughley (1977) stated the effective sampling area of a trap was defined by a circle with a radius of one-half the average home range diameter of the target animal circumscribed around the location of the trap. However, he gave no evidence to support his statement. Caughley's assertion implies that animals are effectively sampled whose center of activity lay within one home range radius of a trap. I tested this assertion by determining the distances between known centers of activity for males and females and capture locations with known UTM coordinates. All captures tested occurred during the interval bears were monitored by telemetry and for periods in which centers of activity of those individuals were known. I then compared distances between capture locations and centers of activity to the home range radius for each bear. I conducted tests for summer, annual, and overall 95% home range estimates (van Manen 1994) obtained from the adaptive kernel method (Worton 1989) using the paired-difference t-test in proc univariate (SAS 1989).

Study Area Definition

I delineated study area peripheries with a boundary strip equal to the average summer home range radius (1.3 km) around each trap site for females and two-thirds the average summer home range radius for males (2.5 km) using GIS buffer

capabilities (Clark 1991). Significantly larger male home ranges necessitated separate effective study areas for females and males (Figure 2.2). I drew boundaries with the proximity analysis function in ERDAS (ERDAS 1991) using 95% summer home range estimates of bears radiotracked between 1976 and 1982 (van Manen 1994) obtained from the adaptive kernel method.

Capture and Handling

A variety of capture and immobilization techniques were employed during the 20 years encompassed by this study. Prior to the closing of many unimproved roads to motor vehicle traffic, barrel or trailer-mounted culvert traps were transported by truck and positioned at pre-determined intervals. These barrel traps consisted of 2, 50-gallon barrels welded together with an angle iron door frame and a plywood door (Cook 1982). Immobilization darts fired from a CO_2 pistol were used to capture free-ranging bears. Aldrich (Clallam Bay, Wa.) and Fremont (Candle Lake, Saskatchewan) spring-activated snares were used exclusively after 1982 with traditional cubby sets, trail sets, and trick sets as per the procedures of Johnson and Pelton (1980). Snares were modified with automobile hood springs and swivels to reduce trap injuries. Construction of cubbies with burlap began in 1984 (Pozzanghera 1990), but was abandoned in 1990 because of concern over the potential for leg injuries due to entanglement.

Free-ranging bears were immobilized with Cap-chur darts (Palmer Chemical and Supply Co., Inc., Douglasville, Ga.) fired from a CO_2 pistol. Bears captured in

culvert traps were immobilized with a jabstick consisting of a syringe mounted on the end of a rod. In recent years, commercially manufactured jabsticks were used in addition to 2-piece aluminum jabsticks machined by The University of Tennessee Department of Agricultural Engineering to accept barrels from CO_2 pistols.

Immobilization was achieved using a mixture of Ketaset (Ketamine hydrochloride, Bristol Laboratories, Syracuse, NY), Rompun (Xylazine, Haver-Lockhart, Inc., Shawnee, Ks.), and Carbocaine (Mepivicaine hydrochloride, Winthrop Laboratories, New York, NY) (KRC) at the ratio of 200 mg Ketaset: 100 mg Rompun: 20 mg Carbocaine. KRC was administered intramuscularly at a dosage level of 1 ml per 22.7 kg of estimated body weight. Cubs captured during their first summer were tranquilized with pure Ketaset at a dosage of 0.1 ml per 4.5 kg body weight. Other immobilization drugs utilized in the past include M99 (Etorphine hydrochloride, D-M Pharmaceuticals, Rockville, Md.) at a dosage of 1 ml per 45.5 kg body weight and Sernylan (Phencyclidine hydrochloride, Parke Davis and Co., Morris Plains, NJ) at a dosage level of 1 ml per 1 kg body weight (Cook 1982).

Mycitracin was applied to cable cuts and other minor wounds and bears with more serious injuries were intramuscularly injected with Liquamycin at a dosage level of 1 ml per 50 kg body weight. Lactating females were given a 1 ml intramuscular injection of oxytocin (Burns Veterinary Supply, Oakland, Ca.) to stimulate milk production. Beginning in 1990, Yohimbine hydrochloride (Sigma Chemical Co., St. Louis, Mo.) was administered intravenously at a dosage of 1 ml per 45.5 kg body weight as an antagonist to Rompun (Garshelis et al. 1987).

Data Collection

Immobilized bears were marked with metal ear tags; one round, one rectangular. Males received the round tag in the left ear and females in the right ear for sex identification of free-ranging, marked bears. Ear tag numbers were tattooed into the upper lip of bears and the loose skin of the inner thigh. Marks of recaptured bears were inspected and replaced if needed. A premolar was extracted for age determination; teeth were sectioned, stained and aged according to the protocol of Eagle and Pelton (1978). Greater accuracy in age determination occurs in the lower age classes (Matson *et al.* 1993); therefore, ages determined at the time of initial capture were extrapolated to the time of recapture. A premolar was extracted during each capture, however, to confirm proper aging at the time of the initial capture. Ages obtained from premolars of recaptured bears have sometimes revealed errors in the initial aging procedure (F. Van Manen, pers. comm., pers. obs., this study). Morphological, reproductive, conditional, and locational data were collected and recorded on field data sheets which were, in turn, transcribed to computer data sheets and entered into the data set.

Population Estimation

I calculated population density from 4 different mark-recapture estimation methods: (1) calendar of captures, (2) Lincoln-Petersen, (3) nonparametric estimator, and (4) Jolly-Seber. Density estimates were derived for the cumulative effective study area for the entire 20-year period and for effective study areas that

corresponded with trap lines that were consistently trapped over a given interval of time. Program JOLLY was used to estimate population size with the Jolly-Seber technique for consistent trapping intervals. Captures were required to meet 3 criteria to be used in the interval analyses: (1) capture must have occurred during the defined time interval; (2) capture must have occurred on a route that was trapped every year of the interval; and (3) capture must have occurred prior to the fall period as defined by van Manen (1994) whose home range estimates were used to determine effective study areas. Summer was defined as 16 June - 15 September, but captures occurring between mid-May and 15 June were included because spring home ranges were smaller than summer home ranges (Carr 1983; van Manen 1994).

I calculated the calendar of captures estimate by backdating each individual of known age from the last capture to the birth, adding 1 to the appropriate sex/age category for each year the animal was alive. Backdating provided a baseline for comparison because it is the minimum number of individuals alive at a given time. The estimator provides a minimum because it does not estimate the number of animals that are not captured. This estimator does not provide for immigration and could therefore be biased upward. This model also does not account for animals that return to the study area after having been gone longer than one year.

The Lincoln-Petersen estimator was developed for closed populations, that is, populations with no births, deaths, immigration, or emigration between 2 sampling periods (Pollock et al. 1990). I compared this estimate to the JOLLY and nonparametric estimates to provide some indication of the magnitude of immigration,

emigration, natality, and mortality. Chapman (1951) modified the estimator to reduce bias as follows:

$$N=\frac{(M+1)(n+1)}{(m+1)}-1$$

An approximately unbiased estimate of the Lincoln-Petersen model's variance is:

$$\sigma_N^2=\frac{(M+1)(n+1)(M-m)(n-m)}{(m+1)^2(m+2)}$$

where

N = the population estimate,

M = the number of bears marked during the initial sampling period,

m = the number captured during the second sampling period that have been previously captured and marked, and

n = the total number captured during the second sampling period (Pollock et al. 1990).

The assumptions associated with this and other closed models are equal catchability, no loss of marks between sampling periods, and negligible births, deaths, immigration, and emigration. The assumptions of no emigration and mortality can be relaxed if the probability is equal for marked and unmarked animals, with the estimate in that case being unbiased at the time of first sampling. Yearlings captured during the second sampling period and bears known to have died between the 2 sampling periods were not included in the analysis to lessen the effects of births and mortalities. Cubs counted during denning investigations and untagged yearlings

captured during the second sampling period were added to the estimate (Clark 1991). Analyses included only the initial capture of an individual during one given sampling period; subsequent captures within the same sampling period were ignored.

I utilized the nonparametric estimator developed by Overton (1969), based on the frequencies of capture, because of its tendency to be less affected by learned trap response. It is defined as (from Zarnoch 1979):

$$\hat{N}=\sum_{l=1}^{s}\frac{f_l}{\theta_l}$$

where

N = number of individuals in the population,

S = number of samples taken,

l = number of times an individual is caught,

f_l = number of individuals caught l times, and

$$\theta_l=1-(1-\frac{l}{S})^{s}.$$

Zarnoch (1979) evaluated the nonparametric estimator, Chapman's (1952) modification of the Schnabel method, and the geometric estimator (Eberhardt 1969) in relation to the magnitude of bias and variability introduced into the estimate by learned trap response. He concluded that the nonparametric estimator was the most robust when either trap happy or trap shy learning processes were present in the population. There was evidence of trap response from both the data set and personal experience:

(1) there was a relatively large number of single captures

(2) there were often several years between captures of an individual

(3) direct observation (confirmed by telemetry) of a radio-collared female that stole bait from the same trap site 6 consecutive days, 10-20 minutes after the trap was set (time acquired by use of trail timers (Trail Timer Inc., St. Paul, MN)) without being captured (pers. obs., this study).

Trap response by black bears appears to be trap intelligence instead of happiness or shyness; they are able to avoid capture while still obtaining the bait (Pedersen 1995). Pedersen (1995) concluded that trap heterogeneity bias in this population likely has little effect on demographic parameter estimates. He also found evidence of trap response bias due to learning, but concluded there was no differential learning by sex. Although the nonparametric method has not given accurate estimates on populations of known size (Tanner 1978), the length of the GSMNP study and the cumulative number of captures may allow us to more accurately estimate the size of the unsampled portion of the population.

I also used the Jolly-Seber open population mark-recapture model to estimate population size (Jolly 1965, Seber 1965). The Jolly-Seber model requires data from at least 3 sampling periods but it allows estimation of survival rates, recruitment, and capture probabilities in addition to population size. Model assumptions are equal probability of survival among individuals, equal probability of capture, marks are not lost, and samples are instantaneous with each release occurring immediately after the

sample is taken (Pollock et al. 1990). I entered data in the capture history format (Figure 3.1) and performed analyses using computer program JOLLY developed by Pollock et al. (1990), which included chi-square tests to determine which of a variety of different models was most appropriate for the data set. Coefficients of variation of the estimates and evidence for heterogeneity of capture were compared for population estimates provided by the basic Jolly-Seber model with survival and capture probabilities allowed to vary over sampling periods (Model A), death but no immigration (Model A'), constant survival rates (Model B), constant survival rates and capture probabilities (Model D), and with survival rates different for animals which are captured for the first time than unmarked or previously marked animals (Model 2) (Pollock et al. 1990). When 2 or more models were not rejected by the chi-squared tests, I reported results from the model with the most precise estimates. I reported survival rates and capture probabilities from model 2 when there was evidence of differential survival between newly-captured and previously-captured animals. However, this did not affect model choice for population estimates.

Interval Population Estimates

I estimated population size for groups of trap lines that were sampled consistently during a given time interval. By partitioning the data, I was able to eliminate assumption violations because of annual changes in trap lines. This also allowed me to calculate multiple estimates for each year and to investigate the effects

```
TITLE=FEMALE BLACK BEARS 1977-1991
PERIODS=15
FIRST=1977
INTERVALS=1,1,1,1,1,1,1,1,1,1,1,1,1,1
FORMAT=(15I1,I3)
100000000000000  6
010000000000000  3
001000000000000  6
000100000000000  5
000010000000000  4
000000100000000 12
000000010000000  3
000000001000000  7
000000000100000  5
000000000010000  6
000000000001000  4
000000000000100  5
000000000000010  1
000000000000001  3
000000000000011  1
000000000001001  1
000000000001010  1
000000010001010  1
000000000101000  1
000000000011000  2
000100000001000  1
000000010010000  1
000101000000000  1
000110000000000  1
010110000000000  1
100110000000000  1
101010000000000  1
011000000000000  1
110000000000000  3
000000000000101  2
000000000100001  1
000000000100100  1
000110100001000  1
000010110000000  1
000010100000000  1
001100100000000  2
000011000000000  1
010010000000000  1
100010000000000  1
011100000000000  1
001100000000000  1
010100000000000  2
000000100000100  1
000000001110000  1
000001100100000  1
011111001000000  1
000000000010001  1
000001101000100  1
000011100000000  1
111110100000000  1
000000000000110  2
000001011010000  1
000001110000000  1
110101000000000  1
```

Figure 3.1. Capture history data for analysis of female population size in Great Smoky Mountains National Park using computer program JOLLY for the time interval 1977-1991.

of study duration on population estimates. I defined 7 time intervals for which consistent trapping data were available (Table 3.1).

Effective Population Size

I estimated the effective genetic population size using the program JOLLY population estimates and the model for calculating effective population size for species with overlapping generations developed by Hill (1972:equation 18) and modified by Reed et al. (1986). Their model allows for males and females breeding in unequal numbers and have different generation lengths. The equation is defined as:

$$\frac{1}{N_e} = \frac{1}{4 \times L_M \times M_{br} \times \bar{n}_M \times \bar{u}_M} + \frac{1}{4 \times L_F \times F_{br} \times \bar{n}_F \times \bar{u}_F}$$

where

N_e = the effective population size,

M_{br} = the number of breeding males,

F_{br} = the number of breeding females,

$\bar{n}_M$ = the number of young born to males per year,

$\bar{n}_F$ = the number of young born to females per year,

$\bar{u}_M$ = the probability that a newborn male survives to the mean age of reproduction and breeds (not all individuals of breeding age breed),

$\bar{u}_F$ = the probability that a newborn female survives to the mean age of reproduction and breeds (not all individuals of breeding age breed),

Table 3.1. Trap lines sampled annually within a given time interval in Great Smoky Mountains National Park. Population estimates for a given interval were derived using only data from these trap lines.

Interval	Trap lines used for population analysis
1973-1977	Bent Arm, Bote Mountain, Defeat Ridge, Rabbit Creek, Sugarland Mountain
1977-1991	Bote Mountain, Bunker Hill, Parson's Branch, Sugarland Mountain
1980-1983	Bote Mountain, Bunker Hill, Hannah Mountain, Parson's Branch, Sugarland Mountain
1984-1991	Bote Mountain, Bunker Hill, Parson's Branch, Sugarland Mountain, Turkey Pen
1987-1991	Bote Mountain, Bunker Hill, Green Camp Gap, Parson's Branch, Rabbit Creek, Sugarland Mountain, Turkey Pen
1988-1991	Bote Mountain, Bunker Hill, Green Camp Gap, Lumber Ridge, Parson's Branch, Rabbit Creek, Sugarland Mountain, Turkey Pen
1989-1991	Bote Mountain, Bunker Hill, Curry Mountain, Green Camp Gap, Lumber Ridge, Parson's Branch, Rabbit Creek, Sugarland Mountain, Turkey Pen

L_M = the generation length, (the mean age of all males that reproduce in a population with a stable age distribution),

L_F = the generation length, (the mean age of all females that reproduce in a population with a stable age distribution) (Caughley 1977:123-124).

I estimated model parameters from age structures obtained from the calendar of captures population estimate. The assumptions of this model are (1) random mating, (2) no difference in fertility between individuals, (3) a stable age distribution, (4) no covariance between the numbers of male and female progeny, (5) no year-to-year variation in the number of males and females, and (6) a Poisson distribution of family sizes. Violation of assumptions results in an underestimate of the number of breeders required to maintain a particular N_e (Reed et al. 1986). Although the number of males and females varied from year to year, I saw no compelling evidence of assumption violation that would invalidate the model. I used both means and minima of population estimates to calculate effective population size because effective population size is influenced most by the year with the smallest breeding population (Franklin 1980).

Survival

I estimated annual survival rates from the mark-recapture data using program JOLLY (Model A, Pollock et al. 1990); however, mortality cannot be separated from emigration using this estimator. This model provides estimates for male and female

bears ≥ 1 year of age. I calculated cub survival from recent cub-yearling observations and compared it to Wathen's (1983) results.

Population Dynamics

I used a population model developed for polar bears (*Ursus maritimus*) (Taylor et al. 1987a, 1987b) and adapted for use on black bears to simulate population dynamics on the study area. This model is a mathematical simulation of black bear life history, incorporating age-specific survival and recruitment rates, population size, standing or stable age distributions, harvest rates and hunter selectivity values, and can function either stochastically or deterministically. The model assumes a closed population and that some proportion of 2-year-old females breed. The proportion of 2-year-old breeders is estimated by the user.

The reproductive cycle and survival rates of bears present problems in modeling because multi-year reproduction cannot be summarized with mean annual rates (Taylor et al. 1987c). The loss of partial litters compared to whole litters can result in significant differences in overall rates of population growth, even though the mortality rates of individual cubs may be the same, because bears that lose entire litters may be able to reproduce again the following year. Therefore, reproductive parameters were chosen to mimic rather than summarize the reproductive cycle of black bears. The following is a description of model parameters (from Taylor et al. 1987b):

Age-specific recruitment rate m_x, is:

$$m_x = \frac{(N_{x-1,t-1} \cdot A_{x-1} \cdot B_{x-1} \cdot p_{x-1} \cdot L_x)}{N_{x,t}}$$

where

x = discrete age class (0 = initial age class),

w = final age class,

t = discrete time interval (1 year),

$N_{x,t}$ = number of females of age x at time t,

p_{x-1} = fraction of $N_{x-1,t-1}$ that survive to be $N_{x,t}$ (annual survival rate, animals that emigrate are treated as mortalities),

m_x = age-specific recruitment rate of $N_{x,t}$ (the number of $N_{0,t}/N_{x,t}$ at the time of census),

A_{x-1} = proportion of $N_{x-1,t-1}$ available for breeding,

B_{x-1} = proportion of $A_{x-1,t-1}$ available for reproduction at time t-1 that would produce recruits at time t if all $N_{x-1,t-1}$ survived to be $N_{x,t}$ (litter production rates),

L_x = litter size of female recruits produced by those $N_{x,t}$ that produced recruits.

The number of cubs of the year (COYs) (Clark 1991) at time t, produced by x-year-old females is then:

$$coy_t = m_x \cdot N_x$$

and the total number of COYs produced over the entire interval is:

$$\sum_{x=1}^{w} m_x \cdot N_x$$

The model divides cub survival rates into 3 types:

1. survival rate of mother (death of adult female results in loss of COYs or yearling litters),
2. loss of whole litters as units given that the mother survived (litter survival rate (p_{litter})), and
3. survival rate of individual cubs given that the mother survived and the litter was not lost as a unit ($p_{individual}$).

Population Indices

I evaluated potential indices to population size or relative changes in population size (trap success, lactation rates, estrus rates, and age structure (both capture and projected)) with respect to their relationships to program JOLLY population estimates. An index or indices that accurately reflects either population size or relative changes in population size could be used as a management alternative to long-term mark-recapture experiments. I evaluated all indices among years, and within effective study areas between years. I performed correlation analysis with indicators of population size, structure, and dynamics as dependant variables and program JOLLY population estimates as the independent variable.

Mast Surveys

Hard mast surveys were conducted by NPS personnel in GSMNP. Pozzanghera (1990) reported non-standardization of mast data collection in GSMNP and subsequently used only TWRA mast data in his analysis. However, mast production can vary greatly with elevation and between apparently similar areas. Therefore, I included only Park data in the analysis. GSMNP utilized the Whitehead survey method where eight hardy mast producing trees (30.5 cm $\leq$ DBH $\leq$ 80 cm) were sampled along established survey routes (one tree every 0.8 km). Percentage of the crown bearing acorns was estimated and the number of twigs, number of twigs with acorns, and total number of acorns were recorded for each of 5 randomly-selected limbs $\geq$91.4 cm (3 feet) long. Limb observations were then summed, creating category totals for each tree (Whitehead 1969). The Whitehead index was calculated as:

$$I=((D+\frac{B}{A})\times 0.0124)+(\frac{C}{B}\times 0.4178)+2.4281$$

where,

A = Total number of twigs,

B = Total number of twigs with acorns or nuts,

C = Total number of acorns or nuts,

D = Estimated percentage of crown producing acorns or nuts,

I = Mast index.

Nicholas and White (1984) contend that Whitehead's calculation of the percentage of the crown that is productive has no "biological rationale". Pozzanghera (1990:24-32) developed the Maximum Production Potential Index (MPPI) which incorporated the formula of Nicholas and White (1984) into the format of Whitehead's data collection, allowing both indices to be calculated from the same data. MPPI was defined as:

$$Ni = \frac{(Ci \times Ti \times Fi)}{10^4}$$

where,

Ni = the percentage of maximum possible mast crop for each sample tree,

Ci = the percentage of the crown in fruit for each sample tree,

Ti = the percentage of twigs within the productive crown which bear fruit for each sample tree,

Fi = the percentage of the maximum number of fruits per twig for each sample tree.

Pozzanghera (1990) incorporated the suggestion by Nicholas and White (1984) of calculating separate scalars for white oak and red oak groups using data from Sharp (1958) and Sharp and Sprague (1967). Scalars for white oaks were:

$$Fi = (\frac{TA}{93.8}) \times 100$$

$$Ci = (\frac{PCPY}{85.8}) \times 100$$

and red oak scalars were:

$$Ti = \frac{(\frac{NWTA}{NTW})}{0.78} \times 100$$

$$Fi = (\frac{TA}{120.5}) \times 100$$

$$Ci = (\frac{PCPY}{91.5}) \times 100$$

$$Ti = \frac{(\frac{NWTA}{NTW})}{0.78} \times 100$$

where,

TA = Total number of acorns recorded on 5 limbs,

PCPY = Estimated percentage of the crown in fruit,

NTWA = Five limb total for the number of twigs with acorns,

NTW = Five limb total for the number of twigs.

Trees producing 0 acorns on the 5 counted limbs were deleted from the sample (Pozzanghera 1990) to avoid biased results created by inherently unfruitful individual trees (Sharp 1958).

I used both Whitehead's method and the MPPI in the analysis. I performed correlation analyses between mast indices and indicators of population size, structure, and dynamics. McLean (1991) found a correlation between lactation rates and mast production, and the primary purpose of these additional indices was to attempt to identify the indices that are most sensitive to changes in mast production. I

investigated time lags of up to 5 years between population responses and variation in mast production. I conducted analyses on the study area as a unit, and using only data from mast survey routes that were located within effective study area boundaries to lessen the effects of geographic variation on mast production. Hard mast survey routes located within effective study area boundaries were determined by circumscribing a circle of radius 4.8 km around each trap site. A radius of 4.8 km corresponded to a home range size of 73.8 km^2, the largest annual home range of a male black bear in GSMNP (van Manen 1994). A smaller radius for females (3.1 km) created an insufficient sample size of routes within the effective study area to conduct analyses separately by sex. Survey routes were included in the analyses if any portion fell within the effective study area boundaries (Table 3.2). I did not perform correlation analysis on sampling intervals 1980-1983, 1987-1991, 1988-1991, and 1989-1991 because of insufficient data.

Table 3.2. Hard mast index routes in Great Smoky Mountains National Park that were within effective study areas of consistent sampling periods.

Sampling Period	Hard Mast Index Routes
1973-1977	No mast data before 1977.
1977-1991	Anthony Creek, Bote Mountain, Bullhead, Bunker Hill, Cove Mountain, Curry/Meigs Mountain, Hannah Mountain, Lead Cove, Lumber Ridge, Old Sugarlands, Rabbit Creek, Sam's Gap, Schoolhouse Gap, Sugarland Mountain, and US 129.
1980-1983	Bote Mountain, Bullhead, Bunker Hill, Cove Mountain, Curry/Meigs Mountain, Lead Cove, Old Sugarlands, Sam's Gap, and US 129.
1984-1991	Anthony Creek, Bote Mountain, Bullhead, Bunker Hill, Cades Cove, Cove Mountain, Curry/Meigs Mountain, Hannah Mountain, Lead Cove, Old Sugarlands, Rabbit Creek, Rich Mountain Road, Sam's Gap, Schoolhouse Gap, Sugarland Mountain, and US 129.
1987-1991	Bote Mountain, Bullhead, Bunker Hill, Cades Cove, Cove Mountain, Curry/Meigs Mountain, Old Sugarlands, Rabbit Creek, Rich Mountain Road, Sam's Gap, Schoolhouse Gap, Sugarland Mountain, and US 129.
1988-1991	Same routes as 1987-1991.
1989-1991	Same routes as 1987-1991.

CHAPTER 4

RESULTS

Effective Study Area Validation

Distances between 19 capture locations and the center of summer activity of the females averaged 1207 m; this was comparable to the average summer home range radius of 1287 m. For males, 14 observations yielded a mean distance of 1520 m. Average male summer home range radius (3579 m) was larger ($P < .0001$) than the mean distance between centers of activity and trap site locations. The pattern of female distances approaching the mean home range radius and male distances approximating half the average home range radius held for both annual and overall home range estimates (Appendix B).

Study Area Definition

Radii of the circles circumscribed around trapsites were 1.3 km for females and 2.5 km for males. Distances correspond to the average summer home range radius for females and approximately two-thirds of the average summer home range radius for males (van Manen 1994). Cumulative area sampled totaled 433.9 km^2 for males and 240.5 km^2 for females (Figure 2.2). Annual study area size averaged 203.5 km^2 (SE = 53.3) for males and 90.4 km^2 (SE = 25.9) for females, but varied from year to year (Table 4.1) due to changes in trap lines (Table 4.2). Graphic representations of annual study areas are presented in Appendix C. Effective study

Table 4.1. Area effectively trapped annually in Great Smoky Mountains National Park determined from proximity analysis in ERDAS.

Year	Km^2	
	Males	Females
1972	90.9	42.4
1973	275.5	133.6
1974	244.4	118.4
1975	274.3	119.5
1976	269.0	121.7
1977	239.4	110.2
1978	174.5	80.5
1979	174.5	80.5
1980	167.0	69.8
1981	193.1	83.8
1982	134.8	53.6
1983	134.8	53.6
1984	188.7	89.0
1985	156.4	68.0
1986	149.1	62.2
1987	206.7	83.1
1988	232.8	99.8
1989	254.7	112.6
1990	254.7	112.6
1991	254.7	112.6
Mean	203.5	90.4
SE	53.3	25.9

Table 4.2. Trap lines used for black bear population monitoring in Great Smoky Mountains National Park, 1972-1991.

Trap Line	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	Y†	N‡	
Bent Arm		X	X	X	X	X			X												6	24	
Bote Mtn.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	20	200	(25)
Bunker Hill					X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16	84	(9)
Coalen Ground					X																1	5	(1)
Curry Mtn.																		X	X	X	3	29	(2)
Defeat Ridge		X	X	X	X	X	X	X		X			X								9	51	(5)
Ekaneetlee Gap				X																	1	4	
Green Camp Gap				X	X											X	X	X	X	X	7	39	(3)
Hannah Mtn.									X	X	X	X			X						5	18	(5)
Hornet Tree Top							X														1	4	
Jakes' Ck.-Miry		X	X																		2	7	
Little Bald		X																			1	2	
Lumber Ridge					X												X	X	X	X	5	22	
Old Tremont	X					X		X					X								4	13	(1)
Parson's Branch		X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16	96	(15)
Rabbit Creek		X	X	X	X	X				X						X	X	X	X	X	11	72	(4)
Schoolhouse Gap														X							1	5	
Spence Field	X	X																			2	5	(2)
Sugarland Mtn.		X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	18	160	(10)
Turkey Pen													X	X	X	X	X	X	X	X	8	34	(2)
Upper Sugarland			X	X																	2	7	
																					---	-----	-----
																						881	(84)

† Number of years trap line was used for summer monitoring of black bears.

‡ Cumulative number of captures on each trap line; within-year recaptures in parentheses.

areas for discrete time intervals ranged in size from 130.7 to 254.7 km^2 for males and 50.7 to 112.6 km^2 for females (Table 4.3). Graphic representations of effective study areas are presented in Appendix D.

Capture

Summer trapping resulted in 887 captures of 558 individual bears. For males, 335 individuals were captured 501 times, including 51 within-year recaptures. For females, 223 individuals were captured 386 times with 32 within-year recaptures. Most (88%) within-year recaptures occurred prior to 1984 (44♂; 29♀). Sex ratio was 150♂:100♀ for initial captures and 130♂:100♀ for total captures. Males were captured an average of 1.50 times (range = 1 - 8) and females were captured an average of 1.73 times (range = 1 - 9). Average time between captures for males and females did not differ (1.8 and 2.1 years, respectively, $P = 0.25$). For females, the mean time interval between first and second captures ($\bar{x}$ = 2.38 years, SD = 1.85, n = 78) was longer (t' = 3.01, df = 127, $P = 0.0031$) than the average time interval between subsequent captures ($\bar{x}$ = 1.61 years, SD = 1.09, n = 54). For males, the mean time interval between first and second captures ($\bar{x}$ = 1.89 years, SD = 1.65, n = 164) was not different (t' = 0.63, df = 70.2, $P = 0.5304$) than the average time interval between subsequent captures ($\bar{x}$ = 1.71 years, SD = 1.08, n = 28). Ages of bears at time of last capture ranged from 0.5 to 21.5 years ($\bar{x}$ = 5.64, SD = 3.09, n = 532). Females were older ($\bar{x}$ = 6.80 years, SD = 3.46, n = 211) than males ($\bar{x}$ = 4.85 years, SD = 2.51, n = 321) (t' = 7.04, df = 351, $P < 0.001$).

Table 4.3. Effective study area sizes determined by proximity analysis in ERDAS for males and females in Great Smoky Mountains National Park during consistent sampling intervals.

Period	Sex	Km^2	SE
1973-1977	M	150.9	
	F	63.8	
1977-1991	M	130.7	
	F	50.7	
1980-1983	M	134.8	
	F	53.6	
1984-1991	M	145.0	
	F	59.2	
1987-1991	M	206.7	
	F	83.1	
1988-1991	M	232.8	
	F	99.8	
1989-1991	M	254.7	
	F	112.6	
Mean	M	179.4	47.2
	F	74.7	22.4

Composite Population Estimates

The calendar of captures method produced an average estimate of 174 bears (SD = 30.3) and ranged from 137 to 251 animals. This estimator indicated consistent population growth (Figure 4.1) at an average annual rate of 2.7%. The number of known females ranged from 61 to 95 ($\bar{x}$ = 78.5, SD = 9.5) and increased from 65 in 1972 to an estimated 93 individuals in 1991, an annual increase of 1.9%. The number of known males ranged from 69 to 162 ($\bar{x}$ = 95.6) and exhibited greater fluctuations (SD = 25.5) than did females. Males increased from 72 in 1972 to an estimated 134 in 1991, an annual increase of 3.3%. The proportion of the population estimate attributed to captures occurring during the year of the estimate was 0.216 (SE = 0.072). Nearly half ($\bar{x}$ = 0.457, SE = 0.106) of the estimate was attributed to animals captured during the first 2 years. Estimates for the years 1988-1991 were projected from these values (Table 4.4).

Lincoln-Petersen estimates ranged from 45 to 319 ($\bar{x}$ = 163.8, SD = 74.5) and increased 8.9% from 1973 to 1991. Estimate fluctuations coincided with JOLLY estimates. Lincoln-Petersen estimates were hampered by few animals captured in consecutive years (n_{max} = 7) (Table 4.5).

The nonparametric estimator ranged from 51 to 795 individuals and displayed an increase every year. The annual growth rate of 16.4% was a function of the inability of the model to estimate the uncaptured portion of the population.

Population estimates from program JOLLY were conducted for each sex separately and for all bears combined. Models A and B provided adequate fit to the

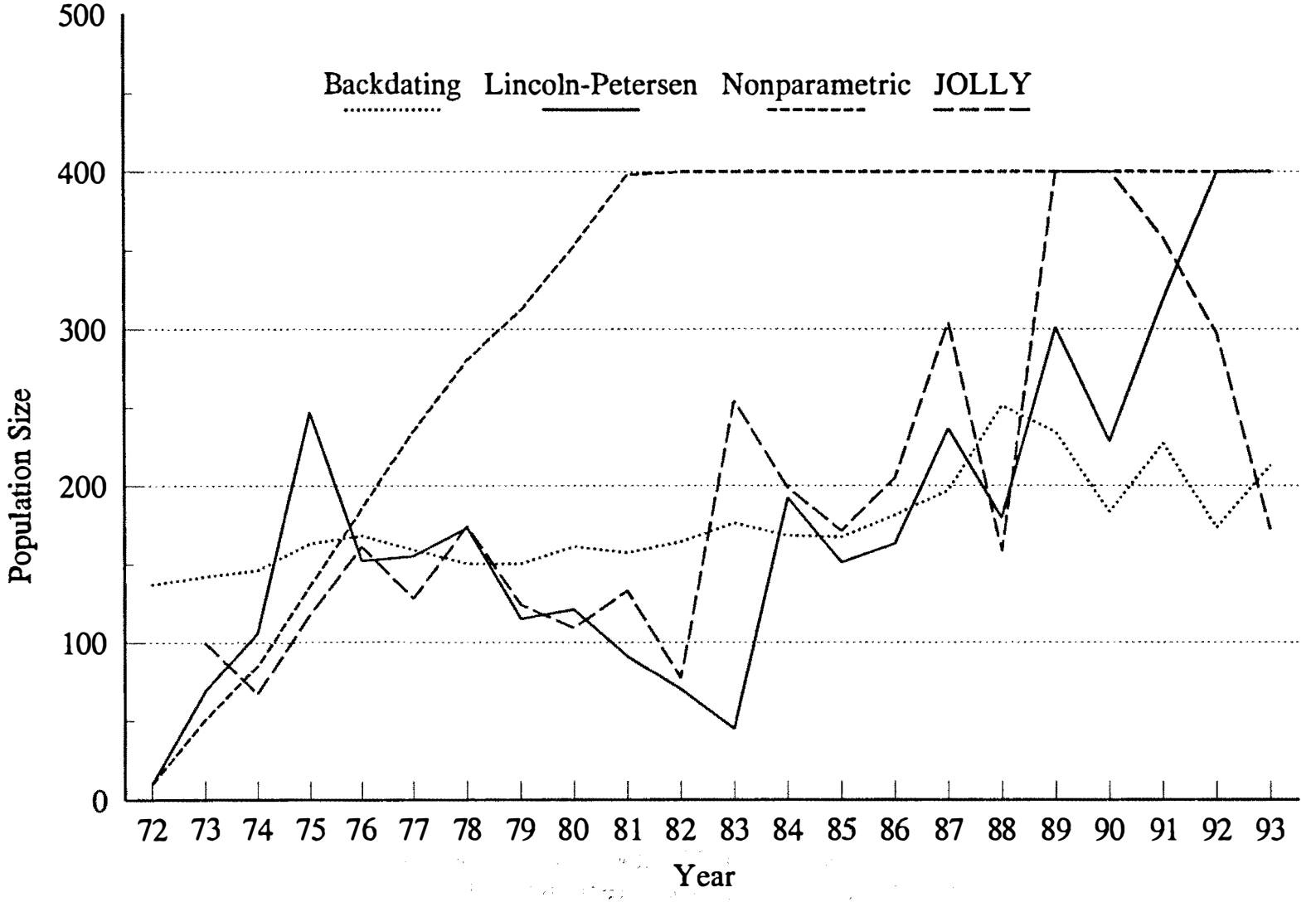


Figure 4.1. Four estimators of population size for cumulative Great Smoky Mountains National Park data set, 1972-1991.

Table 4.4. Population estimates for Great Smoky Mountains National Park data set using the calendar of captures method, 1972-1991.

Year	Female	Male	Total
1972	65	72	137
1973	65	77	142
1974	63	83	146
1975	73	90	163
1976	73	95	168
1977	74	85	159
1978	68	82	150
1979	70	80	150
1980	85	76	161
1981	88	69	157
1982	90	74	164
1983	95	81	176
1984	82	86	168
1985	76	91	167
1986	80	101	181
1987	84	113	197
1988	89	162	251
1989	83	151	234
1990	74	109	183
1991	93	134	227
Mean	78.5	95.6	174.1
SD	9.8	26.1	31.1

Table 4.5. Population estimates for Great Smoky Mountains National Park data set using the Lincoln-Petersen method, 1972-1991.

Year	Inital	Recapture	Marks Lost	L-P Estimate	COY's	Yearlings	Population Estimate
1972	6	0	0	66	3	1	70
1973	26	2	1	106	0	3	109
1974	25	7	0	246	0	0	246
1975	34	3	0	143	0	1	144
1976	25	7	1	149	3	6	158
1977	30	5	3	167	2	4	173
1978	25	4	1	106	2	4	112
1979	23	6	1	110	0	2	112
1980	23	5	1	84	1	4	89
1981	19	6	0	35	0	4	39
1982	4	4	0	40	1	1	42
1983	29	3	1	182	0	2	184
1984	16	2	2	149	0	0	149
1985	18	1	0	151	0	2	153
1986	21	2	1	230	0	0	230
1987	30	2	2	168	0	3	171
1988	29	5	0	289	1	1	291
1989	52	5	1	220	0	6	226
1990	26	7	1	311	0	0	311
1991	33	2	-	------	0	0	------
Mean	24.7	3.9	0.84	155.4	0.65	2.2	158.4
SD	10.1	2.1	0.83	77.9	1.04	2.0	77.0

female data, but estimates from model A were more precise. Estimates averaged 71.8 (SD = 10.6) and ranged from 25 to 146 (Table E.1 - all population parameters available from program JOLLY are presented in Appendix E by time interval and sex). The female population increased from 27.6 in 1973 to 123.3 in 1990, an average annual increase of 9.2%. Estimated mean number of marks remaining in the population was 27.1 (SD = 3.1, range = 2.9 - 58.0). Annual estimated recruitment averaged 22.3 (SD = 4.9, range = -60.8 - 112.2). The likelihood-ratio test indicated differential survival between newly-captured and previously-captured animals (χ^2 = 17.25, df = 9, P = 0.0449). Annual survival rate was lower for newly-captured animals ($\bar{x}$ = 0.73, range = 0.18 - 1.49) than previously-captured animals ($\bar{x}$ = 0.84, range = 0.00 - 2.20). Capture probability varied between 0.00 and 0.63 ($\bar{x}$ = 0.25).

Male data conformed adequately to all models. Model A' was most precise, but the estimates were not realistic ($\bar{x}$ = 594.3, SD = 58.0, range = 265.0 - 1133.0). Model A provided more realistic population estimates ($\bar{x}$ = 101.3, SD = 21.5, range = 34.5 - 256.3) (Table E.2). The male population increased from 56 in 1973 to 256 in 1990, an average annual increase of 9.4%; this compares favorably with the reported rate for females (Figure 4.2). Estimated mean number of marks remaining in the population was 27.5 (SD = 5.5, range = 8.0 - 82.0). Annual estimated recruitment averaged 44.4 (SD = 9.7, range = -45.4 - 165.2). No difference was detected in survival rates between newly-captured and previously-captured bears (χ^2 = 3.73, df = 6, P = 0.71), but males exhibited lower survival

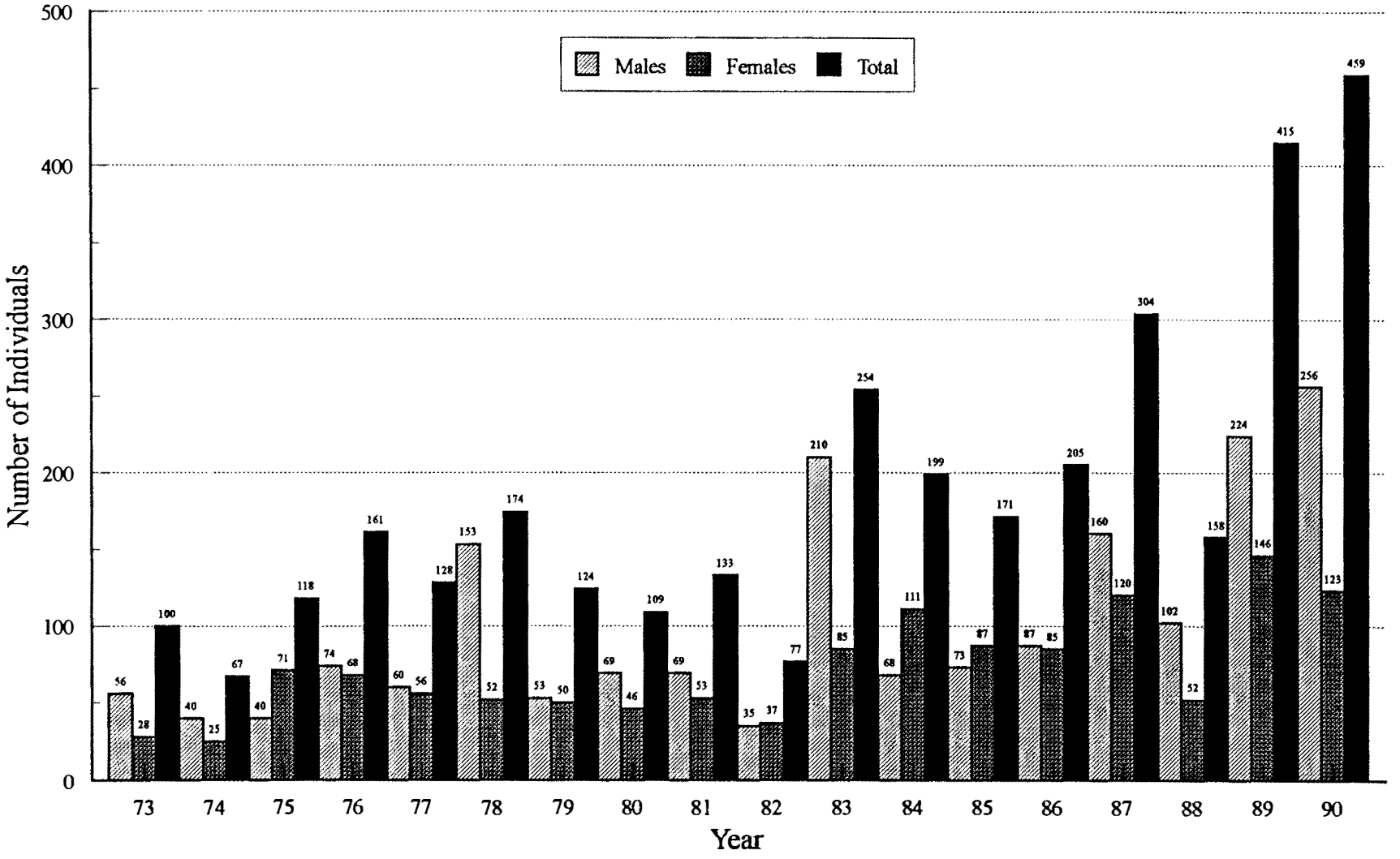


Figure 4.2. Jolly-Seber population estimates for cumulative Great Smoky Mountains National Park data set, 1972-1991.

rates than females ($\bar{x}$ = 0.71, SD = 0.09, range = 0.15 - 1.60). Probability of capture averaged 0.26 (SD = 0.03, range = 0.08 - 0.63).

For data from both sexes combined, model A provided the best fit, although evidence suggested a poor fit at best (P = 0.0775). Population size estimates ($\bar{x}$ = 186.4, SD = 22.7, range = 66.6 - 458.5) (Table E.3) were consistent with the combined results of the female and male analyses ($\bar{x}$ = 173.1, range = 64.7 - 379.5). Estimated mean number of marks remaining in the population was 57.9 (SD = 6.3, range = 9.4 - 167.8). Annual estimated recruitment averaged 62.8 (SD = 8.3, range = -49.1 - 270.8). Survival rates for newly-captured bears ($\bar{x}$ = 0.92, SD = 0.20, range = 0.11 - 2.31) were higher (χ^2 = 25.96, df = 15, P = 0.0385) than those of previously-captured bears ($\bar{x}$ = 0.90, SD = 0.25, range = 0.15 - 2.52). Probability of capture averaged 0.25 (SD = 0.02, range = 0.08 - 0.48).

JOLLY population estimates corresponded with a mean population density of 0.30 females/km^2. Male population estimates corresponded to an average density of 0.23 bears/km^2. Density determination for combined data was problematic. Using the effective study area for females resulted in a mean density of 0.72 bears/km^2 that was biased upwards because of failure to compensate for larger male home ranges. Conversely, using the effective study area for males produced an average density of 0.40 bears/km^2, which is less than the combined density of 0.53 bears/km^2 when estimates were calculated by sex.

Effective population size based on estimated parameters (Table 4.6) averaged 163.6 with a minimum of 60.9. Effective size of the mean estimate was 94.5% of the total.

Interval Estimates

Mean population estimate for females across all 7 time intervals was 79.7 (SD = 39.1, range = 34.7 - 117.0) (Table 4.7). Estimated mean number of marks remaining in the population was 20.0 (SD = 5.0, range = 14.3 - 26.7). Annual estimated recruitment averaged 1.5 (SD = 24.8, range = -47.5 - 18.4). Mean annual survival was 0.89 (SD = 0.20, range = 0.68 - 1.18) and mean capture probability was 0.24 (SD = 0.14, range = 0.10 - 0.49).

Mean population estimate for males was 105.4 (SD = 121.9, range = 31.9 - 375.8) (Table 4.8). Estimated mean number of marks remaining in the population was 21.2 (SD = 15.7, range = 10.1 - 55.0). Annual estimated recruitment averaged 29.6 (SD = 17.6, range = 5.9 - 55.9). Mean annual survival was 0.61 (SD = 0.22, range = 0.35 - 1.04) and mean capture probability was 0.30 (SD = 0.18, range = 0.03 - 0.59).

Combining male and female results produced an average population estimate of 185.1 (SD = 144.5, range = 66.8 - 487.1) (Table 4.9). Estimated mean number of marks remaining in the population was 41.2 (SD = 19.3, range = 26.7 - 81.7). Annual estimated recruitment averaged 31.1 (SD = 20.2, range = 6.1 - 57.4). Mean

Table 4.6. Parameter estimates for calculating effective genetic population size of black bears in Great Smoky Mountains National Park.

Parameter	Male	Female
Number of Breeders	0.34N†	0.59N†
Young/Adult/Year	1.04	0.63
Probability of Breeding	0.28	0.50
Generation Length	6.76	7.63

† N = JOLLY population estimate.

Table 4.7. Mean population parameters from program JOLLY for female black bears in Great Smoky Mountains National Park.

Interval	N[a]	M[b]	B[c]	Φ[d]	p[e]	Model
1973-1977	34.7	14.3	8.9	1.16	0.49	D,2
1977-1991	45.2	18.7	15.0	0.71	0.30	A
1980-1983	34.9	17.0	0.2	0.68	0.33	A
1984-1991	102.7	15.2	18.4	0.78	0.14	A'
1987-1991	117.0	23.0	13.7	0.83	0.16	A'
1988-1991	111.8	25.2	-47.5	0.92	0.17	A'
1989-1991	111.3	26.7	------	1.18	0.10	A'
$\bar{x}$	79.7	20.0	1.5	0.89	0.24	
SD	39.1	5.0	24.8	0.20	0.14	
range	34.7-117.0	14.3-26.7	-47.5-18.4	0.68-1.18	0.10-0.49	

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Value for the interval 1973-1977 is mean of newly-captured (0.61) and previously-captured (1.71) animals (Model 2).

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table 4.8. Mean population parameters from program JOLLY for male black bears in Great Smoky Mountains National Park.

Interval	N[a]	M[b]	B[c]	Φ[d]	p[e]	Model
1973-1977	40.3	12.4	23.3	0.64	0.38	A
1977-1991	62.0	18.4	25.2	0.60	0.24	D
1980-1983	31.9	11.2	5.9	0.40	0.42	A
1984-1991	69.5	17.1	23.6	0.61	0.19	A
1987-1991	48.5	10.1	43.7	0.35	0.59	A
1988-1991	110.0	24.0	55.9	0.60	0.23	A
1989-1991	375.8	55.0	------	1.04	0.03	A'
$\bar{x}$	105.4	21.2	29.6	0.61	0.30	
SD	121.9	15.7	17.6	0.22	0.18	
range	31.9-375.8	10.1-55.0	5.9-55.9	0.35-1.04	0.03-0.59	

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table 4.9. Mean population parameters from program JOLLY for combined results of male and female black bear models in Great Smoky Mountains National Park.

Interval	N[a]	M[b]	B[c]	Φ[d]	p[e]
1973-1977	75.0	26.7	32.2	0.90	0.44
1977-1991	107.2	37.1	40.2	0.66	0.27
1980-1983	66.8	28.2	6.1	0.54	0.38
1984-1991	172.2	32.3	42.0	0.70	0.17
1987-1991	165.5	33.1	57.4	0.59	0.38
1988-1991	221.8	49.2	8.4	0.76	0.20
1989-1991	487.1	81.7	------	1.11	0.07
$\bar{x}$	185.1	41.2	31.1	0.75	0.27
SD	144.5	19.3	20.2	0.20	0.13
range	66.8-487.1	26.7-81.7	6.1-57.4	0.54-1.11	0.07-0.44

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

annual survival was 0.75 (SD = 0.20, range = 0.54 - 1.11) and mean capture probability was 0.27 (SD = 0.13, range = 0.07 - 0.44).

Female densities for consistent sampling intervals ranged from 0.54 bears/km^2 for the interval 1973-1977 to 1.73 bears/km^2 for the interval 1984-1991 ($\overline{x}$ = 1.05, SD = 0.39). Male densities for the same intervals averaged 0.52 bears/km^2 (SD = 0.41, range = 0.23 - 1.48). Total densities ($\overline{x}$ = 1.57, SD = 0.57) ranged from 0.81 bears/km^2 for the interval 1973-1977 to 2.47 bears/km^2 for the interval 1989-1991 (Table 4.10).

Comparison of estimates from cumulative data set to those of defined sampling intervals revealed inconsistencies in calculated densities. For any given year, female interval densities were higher than the female density estimate calculated from the cumulative data set for that year (Table 4.11). The same pattern held for male densities with the exception of years 1988-1990 (Table 4.12) and total densities with the exception of 1989 and 1990 (Table 4.13). Annual trends in densities were comparable between cumulative and interval estimates, although the magnitude of change was greater for interval estimates. However, when cumulative densities were calculated using the area trapped annually, rather than the total area trapped, density estimates, annual trends, and the magnitude of annual changes were consistent with interval estimates.

Table 4.10. Mean annual black bear densities in Great Smoky Mountains National Park study area. Estimates are based on population estimates from program JOLLY for consistent sampling intervals.

Sampling Interval	Density (Bears/km^2)		
	Female	Male	Total
1973-1977	0.54	0.27	0.81
1977-1991	0.89	0.47	1.36
1980-1983	0.65	0.24	0.89
1984-1991	1.73	0.48	2.21
1987-1991	1.41	0.23	1.64
1988-1991	1.12	0.47	1.59
1989-1991	0.99	1.48	2.47
Mean	1.05	0.52	1.57
SD	0.39	0.41	0.57

Table 4.11. Comparison of cumulative and interval female black bear densities (bears/km^2) calculated from computer program JOLLY population estimates in Great Smoky Mountains National Park.

Interval	Year																	
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
1972-1991 (Total area)	0.11	0.10	0.30	0.28	0.23	0.22	0.21	0.19	0.22	0.15	0.35	0.46	0.36	0.35	0.50	0.22	0.61	0.51
1972-1991 (Annual)	0.21	0.21	0.60	0.55	0.51	0.65	0.62	0.65	0.63	0.69	1.59	1.24	1.27	1.36	1.45	0.52	1.30	1.09
1973-1977		0.45	0.60	0.69	0.44													
1977-1991						0.52	0.89	0.56	0.72	0.49	0.87	0.73	1.24	1.26	1.86	0.81	1.03	0.59
1980-1983									0.78	0.52								
1984-1991												2.36	3.18	1.50	2.04	1.64	0.79	0.64
1987-1991															1.94	1.91	0.76	1.01
1988-1991																1.45	0.78	1.13
1989-1991																	0.88	1.10

Table 4.12. Comparison of cumulative and interval male black bear densities (bears/km^2) calculated from computer program JOLLY population estimates in Great Smoky Mountains National Park.

Interval	Year																	
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
1972-1991 (Total area)	0.13	0.10	0.10	0.17	0.13	0.35	0.12	0.15	0.16	0.08	0.48	0.16	0.17	0.20	0.36	0.24	0.52	0.59
1972-1991 (Annual)	0.20	0.16	0.15	0.27	0.25	0.88	0.30	0.39	0.36	0.26	1.56	0.36	0.47	0.58	0.77	0.44	0.88	1.01
1973-1977		0.17	0.30	0.33														
1977-1991						0.55	0.30	0.30	0.55	0.15	1.05	0.37	0.43	0.65	0.63	0.49	0.33	0.37
1980-1983									0.30	0.17								
1984-1991													0.66	0.38	0.66	0.37	0.42	0.39
1987-1991																0.11	0.32	0.27
1988-1991																	0.50	0.45
1989-1991																	1.37	1.58

Table 4.13. Comparison of cumulative and interval total black bear densities (bears/km^2) calculated from computer program JOLLY population estimates in Great Smoky Mountains National Park.

Interval	Year																	
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
1972-1991 (Total area)	0.24	0.20	0.40	0.45	0.36	0.57	0.33	0.34	0.38	0.23	0.83	0.62	0.53	0.55	0.86	0.46	1.13	1.10
1972-1991 (Annual)	0.41	0.37	0.75	0.82	0.76	1.53	0.92	1.04	0.99	0.95	3.15	1.60	1.74	1.94	2.22	0.96	2.18	2.10
1973-1977		0.62	0.90	1.02														
1977-1991						1.07	1.19	0.86	1.27	0.64	1.92	1.10	1.67	1.91	2.49	1.30	1.36	0.96
1980-1983									1.08	0.69								
1984-1991													3.84	1.88	2.70	2.01	1.21	1.03
1987-1991																2.02	1.08	1.28
1988-1991																	1.28	1.58
1989-1991																	2.25	2.68

Sex and Age Distribution

Sex and age distribution of bears was summarized from the calendar of captures population estimate. The proportion of females in the population varied between 0.35 and 0.56, and was negatively correlated with population size (P = 0.00228). The average age of known females ranged between 4.08 (1972) and 7.54 (1991) while male ages ranged between 2.82 (1972) and 5.72 (1991) (Appendix F). Trapping bias against young age classes was responsible for the apparent increase in the age of bears near the end of the study.

Cub Production and Survival

Investigation of 184 female winter dens yielded information on 98 litters. Females between the ages of 4 and 17 produced cubs. Telemetry contact was lost with a 23-year-old female that failed to produce cubs for 2 consecutive years. The size of 74 litters ranged from 1 to 4 and averaged 2.24. Litters of 2 (n = 36) and 3 (n = 25) were most common while 1 (n = 11) and 4 cubs (n = 2) were relatively rare. Gender was determined for 89 cubs from 36 litters. Sex ratio was 102♂:100♀.

Fates of 75 cubs from 31 litters were determined from winter den observations between 1978 and 1992. Overall cub survival was 61.3% (n = 46), with no difference (χ^2 = 0.62; $P > 0.1$) between females (71.4%, 15 of 21) and males (52.4%, 11 of 21). Fourteen complete litters with a total of 32 cubs survived the first year in addition to 14 of 27 cubs (51.9%) from 9 partial litters. Eight complete litters

(16 cubs) were lost or assumed dead when no yearlings were found in the den the following winter or the female produced litters in 2 consecutive years.

Population Dynamics

Deterministic models predicted population declines of 33% (density independent) and 59% (density dependent, K = 300) between 1991 and 1996 based on population parameters obtained from program JOLLY (adult survival rates) and calculated from the GSMNP data set (Table 4.14). The starting population of 227 animals was estimated for 1991 by the calendar of captures method. Stochastic models exhibited the same trends, with the mean projected decrease from 25 density independent simulations being 44%. Population estimates for 1992 and 1993 seemed to contradict the predicted decline. The inability of the model to account for immigration and questionable estimates of subadult and adult survival may have been responsible for the predicted decline.

Population Indices

Indices to annual changes in population size and structure were formulated from trapping data. Trap nights per capture, bear robberies per capture, percentage of trap nights with no activity, percentage of trap nights with bear activity (captures plus robberies), average age of females in the capture, percentage of females lactating, percentage of females in estrus, and percentage of reproductively active (lactating or estrus) females were calculated for each year. Trap nights per capture

Table 4.14. Demographic parameter estimates used in ANURSUS simulations of black bear population dynamics in Great Smoky Mountains National Park.

Parameter	Mean	Standard Deviation
COY Survival	0.61	0.38
Litter Survival	0.45	0.46
Subadult Survival (♂)	0.87	0.05
Subadult Survival (♀)	0.93	0.03
Adult Survival (♂ 4+)	0.61	0.21
Adult Survival (♀ 4+)	0.84	0.16
Litter Production Rate (3 year olds)	0.02	0.04
Litter Production Rate (Adults)	0.61	0.31
Probability Litter Size 1	0.15	0.27
Probability Litter Size 2	0.49	0.27
Probability Litter Size 3	0.34	0.27
Probability Litter Size 4	0.03	0.03
Mean Litter Size Yearlings†	1.62	0.39

†Calculated by ANURSUS

averaged 12.5 (SD = 3.59) and ranged from a low of 7.4 in 1981 to a high of 19 in 1988, with peak years (lowest trapping success) occurring every 4 to 5 years (Table 4.15). Robbery to capture ratio averaged 5.5 (SD = 3.48) with a low of 1.3 in 1980 and a high of 11.4 in 1988. Percentage of trap nights with no activity averaged 36.5 (SD = 15.9, range = 14.6 - 58.9), while the percentage of trap nights with bear activity averaged 49.3 (SD = 16.8, range = 23.2 - 69.6). Mean age of females in the capture ranged from 5.3 in 1986 to 7.6 in 1980. Percentage of females lactating ranged from 0 in 1978 to 0.54 in 1988, while the percentage of females in estrus ranged from 0.07 in both 1980 and 1984 to 0.79 in 1985, and the percentage of reproductively active (lactating or estrus) females ranged between 0.17 (1987) and 1.0 (1986) (Table 4.16).

Analyses indicated a high degree of autocorrelation among the 4 capture success indices. All 4 indices were correlated with the calendar of captures and Lincoln-Petersen population estimates, but only the percentage of trap nights with no activity and the percentage of trap nights with bear activity were correlated with Jolly-Seber population estimates (Table 4.17). Backdating and Jolly-Seber estimates were not highly correlated, but both were correlated with Lincoln-Petersen estimates. Surprisingly, female characteristics were not highly correlated, with the only relationship approaching significance being between mean age and the percentage of estrus females ($P = 0.06345$) in the capture. Female characteristics were not highly correlated with population estimators, although the percentage of lactating females exhibited some correlation with the calendar of captures and Lincoln-Petersen

Table 4.15. Indices of population size calculated with summer trapping data from Great Smoky Mountains National Park.

Year	A	B	C	D
1976	13.7	3.6	58.0	33.3
1977	8.5	1.5	58.9	29.2
1978	8.5	1.6	56.7	30.9
1979	12.5	1.9	53.8	23.2
1980	9.5	1.3	53.1	24.3
1981	7.4	3.1	34.5	54.6
1984	17.6	9.9	28.2	61.8
1985	9.8	4.1	35.8	51.9
1986	14.0	6.0	34.9	50.0
1987	16.6	10.4	21.0	68.4
1988	19.0	11.4	14.6	65.1
1989	9.2	5.0	21.6	65.3
1990	13.9	7.7	18.9	62.8
1991	14.6	9.1	20.3	69.6
$\bar{x}$	12.5	5.5	36.5	49.3
SD	3.6	3.5	15.9	16.8

A = Trap nights per capture

B = Robberies per capture

C = Percentage of trap nights with no activity

D = Percentage of trap nights with bear activity

Table 4.16. Indices to female reproductive status calculated from Great Smoky Mountains National Park summer trapping data.

Year	A	B	C	D
1976	5.9	13	20	33
1977	6.8	38	11	42
1978	5.3	0	27	27
1979	5.3	20	56	67
1980	7.6	35	7	32
1981	6.2	7	18	24
1982	6.1	50	0	33
1983	6.7	12	36	45
1984	6.4	43	7	47
1985	6.3	8	79	86
1986	5.3	36	64	100
1987	6.9	4	13	17
1988	6.8	54	27	73
1989	5.4	33	25	50
1990	5.6	18	29	43
1991	6.1	21	23	44
$\overline{x}$	6.2	25	28	48
SD	0.7	16	22	24

A = Average age of females in the capture

B = Percentage of females lactating

C = Percentage of females in estrus

D = Percentage of reproductively active females (lactating or estrus)

Table 4.17. Correlations between population indices and population estimates for Great Smoky Mountains National Park. Correlations in bold face type are significant. The top number in each pair is the correlation coefficient; the bottom number is the probability.

	JOLLY	Lincoln-Petersen	Calendar of Captures
JOLLY	1.000 0.000	**0.636** **0.019**	0.474 0.102
Lincoln-Petersen	**0.636** **0.019**	1.000 0.000	**0.707** **0.007**
Calendar of Captures	0.474 0.102	**0.707** **0.007**	1.000 0.000
Trap Nights/Capture	0.169 0.580	0.546 0.053	0.501 0.068
Robberies/Capture	0.430 0.142	**0.614** **0.025**	**0.705** **0.005**
Nights with no activity (%)	**-0.643** **0.018**	**-0.608** **0.028**	**-0.775** **0.001**
Nights with bear activity (%)	**0.644** **0.018**	0.533 0.061	**0.729** **0.003**

population estimates. Correlation among population estimators was high, with the exception of the calendar of captures which was correlated only with the Lincoln-Petersen estimate.

Hard Mast

Cumulative

From 1977 to 1991, the Whitehead hard mast production index in GSMNP averaged 2.66 (SD = 0.50, range = 1.34 - 3.35) (Table 4.18). White oak production averaged 2.42 (SD = 0.99, range = 0.36 - 3.80) and red oaks averaged 2.79 (SD = 0.74, range = 1.43 - 4.06). MPPI means were 11.47 (SD = 8.76, range = 2.08 - 31.73) for all species, 7.37 (SD = 8.10, range = 0.75 - 27.11) for white oaks, and 12.55 (SD = 9.83, range = 1.85 - 35.47) for red oaks (Table 4.19).

Interval

Average hard mast production within effective study areas ranged between 3.16 and 3.29 for all species using the Whitehead Index. Average white oak production fluctuated between 3.03 and 3.19, and red oaks varied between 3.21 and 3.46 (Table 4.20). The range of MPPI means was 2.38 - 15.26 for all species, 3.11 - 13.97 for white oaks, and 1.71 - 16.14 for red oaks (Table 4.21). Whitehead and MPPI results for all intervals are presented in Appendix F.

Table 4.18. Whitehead Index hard mast survey results from Great Smoky Mountains National Park, 1977-1991 (Modified from McLean 1991).

Year	White oaks	Red oaks	All oaks
1977	2.05 (21)	3.95 (21)	3.00 (42)
1978	- - -	- - -	- - -
1979	3.29 (65)	2.76 (67)	3.02 (132)
1980	0.39 (46)	4.06 (67)	2.57 (113)
1981	3.80 (55)	2.07 (75)	2.80 (130)
1982	0.36 (44)	1.92 (74)	1.34 (118)
1983	2.67 (9)	1.43 (7)	2.13 (16)
1984	- - -	- - -	- - -
1985	2.97 (72)	2.33 (70)	2.65 (142)
1986	2.11 (74)	2.68 (91)	2.42 (165)
1987	2.69 (84)	2.80 (110)	2.75 (194)
1988	2.12 (86)	2.51 (164)	2.38 (250)
1989	2.96 (73)	3.53 (159)	3.35 (232)
1990	3.11 (100)	3.25 (105)	3.19 (205)
1991	2.91 (98)	2.96 (146)	2.94 (244)

Table 4.19. MPPI hard mast survey results from Great Smoky Mountains National Park, 1977-1991 (Modified from McLean 1991).

Year	White oaks	Red oaks	All oaks
1977	2.00 (15)	23.96 (19)	14.27 (34)
1978	- - -	- - -	- - -
1979	12.77 (51)	19.73 (42)	15.91 (93)
1980	2.92 (7)	35.47 (54)	31.73 (61)
1981	22.46 (52)	21.66 (42)	22.10 (94)
1982	0.75 (11)	9.83 (45)	8.05 (56)
1983	8.43 (9)	2.17 (5)	6.19 (14)
1984	- - -	- - -	- - -
1985	27.11 (55)	17.21 (49)	22.45 (104)
1986	3.79 (67)	8.31 (84)	6.30 (151)
1987	4.76 (77)	5.88 (99)	5.39 (176)
1988	3.26 (72)	8.26 (135)	6.52 (207)
1989	1.10 (45)	5.53 (146)	4.49 (191)
1990	4.00 (74)	3.33 (82)	3.65 (156)
1991	2.41 (51)	1.85 (74)	2.08 (125)

Table 4.20. Whitehead Index hard mast survey means for consistent sampling intervals in Great Smoky Mountains National Park.

Interval	White oaks	Red oaks	All oaks
1977-1991	3.19 (309)	3.37 (429)	3.29 (738)
1980-1983	3.13 (77)	3.46 (74)	3.28 (151)
1984-1991	3.15 (275)	3.30 (329)	3.24 (604)
1987-1991	3.16 (193)	3.31 (262)	3.26 (455)
1988-1991	3.15 (149)	3.29 (210)	3.25 (359)
1989-1991	3.02 (123)	3.21 (140)	3.16 (263)

Table 4.21. MPPI hard mast survey means for consistent sampling intervals in Great Smoky Mountains National Park.

Interval	White oaks	Red oaks	All oaks
1977-1991	6.40 (206)	7.75 (310)	7.21 (516)
1980-1983	13.97 (32)	16.14 (47)	15.26 (79)
1984-1991	3.62 (198)	3.34 (258)	3.46 (456)
1987-1991	3.11 (137)	2.95 (209)	3.01 (346)
1988-1991	3.49 (99)	2.54 (163)	2.90 (262)
1989-1991	3.30 (75)	1.71 (104)	2.38 (179)

Hard Mast Relationships

Cumulative

Correlation analysis was performed on calendar of captures, Lincoln-Petersen, and Jolly-Seber population estimates in addition to indices to population change and structure (see Population Indices) using both the Whitehead method and the MPPI. Time lags in population response to mast production were examined up to 5 years. The Whitehead Index was correlated with only the Jolly-Seber estimates of the same year (r = 0.6083, P = 0.0471). All 3 population estimates were negatively correlated with MPPI results of varying lag times. The calendar of captures estimate was most highly correlated with the MPPI 4 years prior to the population estimate (r = -0.8468, P = 0.0703). Jolly-Seber estimates were correlated with both the index for the year of the estimate (r = -0.6002, P = 0.0509) and the year before (r = -0.6197, P = 0.0560). Lincoln-Petersen estimates were correlated with the index for the year of the estimate (r = -0.6302, P = 0.0377), 1 year before (r = -0.6959, P = 0.0254), and 2 years before (r = -0.6305, P = 0.0687).

Interval

Sampling interval 1977-1991

Male population estimates were significantly correlated with the Whitehead Index for total and white oak production during the year of the estimate (Table 4.22). Male estimates were also correlated with white oak production each of the 3 years

Table 4.22. Correlations between population estimates and mast production (Whitehead Index) in Great Smoky Mountains National Park for the sampling interval 1977-1991. Correlations in bold face type are significant. The top number in a pair is the correlation coefficient; the bottom number is the probability.

Whitehead Mast Index	Male	Total
Total, year of estimate	**0.785** **0.002**	**0.704** **0.016**
White Oak, year of estimate	**0.630** **0.028**	0.586 0.058
White Oak, 1 year prior to estimate	-0.566 0.055	**-0.627** **0.039**
White Oak, 2 years prior to estimate	**0.768** **0.006**	0.626 0.053
White Oak, 3 years prior to estimate	**-0.668** **0.035**	-0.655 0.055

prior to the estimate. Relationships between mast production and total population estimates mirrored those of males. MPPI values were poorly associated with population estimates. Only male estimates were correlated with white oak production during the year of the sample ($r = 0.7238$, $P = 0.0180$). Substituting maximum MPPI values in the analyses produced no significant correlations.

Sampling interval 1984-1991

Female and total population estimates were significantly correlated with the Whitehead index for total production 3 years prior to population estimates (Table 4.23). Male and total estimates were correlated with red oak production 2 years prior to the estimate. All estimates exhibited weak relationships with various aspects of white oak production. The 3 estimates were correlated with MPPI values from 2 years before the estimate. Female and total population estimates exhibited weaker relationships with total mast production 4 years prior to the estimate. Maximum MPPI values were not correlated with population estimates.

Table 4.23. Correlations between population estimates and mast production (Whitehead and MPPI) in Great Smoky Mountains National Park for the sampling interval 1984-1991. Correlations in bold face type are significant. The top number in a pair is the correlation coefficient; the bottom number is the probability.

Mast Index	Female	Male	Total
Total, 3 years prior to estimate†	-0.301 0.562	-0.688 0.199	**-0.891** **0.043**
Total, 4 years prior to estimate‡	0.771 0.072	0.647 0.238	0.836 0.078
Red Oak, 2 years prior to estimate†	-0.789 0.062	**-0.998** **0.000**	-0.863 0.059
Red Oak, 2 years prior to estimate‡	-0.365 0.476	**-0.955** **0.011**	**-0.893** **0.041**
White Oak, 3 years prior to estimate†	-0.194 0.712	-0.836 0.078	-0.838 0.076
White Oak, 4 years prior to estimate†	0.374 0.465	0.835 0.079	0.775 0.124
White Oak, 5 years prior to estimate†	-0.296 0.569	-0.839 0.075	-0.647 0.238
White Oak, 2 years prior to estimate‡	0.443 0.379	0.631 0.254	0.864 0.059

†Whitehead Index
‡MPPI

CHAPTER 5

DISCUSSION

Study Area

Comparison of distances between female centers of activity and trap site locations to home range radii supported the assertion of Caughley (1977) that an area bounded by a circle with radius equal to the average home range radius was effectively sampled by each trap site. Data for males indicated that an area equal to only two-thirds the average home range radius was effectively sampled. This difference between the sexes may have been an artifact of our inability to determine the actual home range of male bears, or male home ranges were, in fact, as large as our estimates indicated and a longer trapping duration was needed to effectively sample the same area relative to home range size. It seems more likely that male home ranges were somewhat over-estimated, as summer distance comparisons indicated the area effectively trapped for males is approximately 3 times larger than for females, not 8 times larger as expected from average home range sizes. Additionally, greater travel rates for males (Garris 1983, Carr 1983) should have negated the need for a longer trapping duration. These data also indicated trap-site baits were not so attractive that they resulted in movements, and therefore captures, outside of an individual's home range.

Caughley (1977) did not expound on his determination of effective sampling area, but a brief explanation will demonstrate the underlying principle. Given a female bear with home range radius r, capture is possible in any trap that is $\leq r$

away from the female's center of activity (Figure 5.1). Logically, some bears may be attracted beyond their normal home range and subsequently captured, while others within r distance of a trap are not captured for various reasons (trap shyness, misses, escapes, etc.). The primary assumption then becomes that captures occurring from long-distance ($> r$) movements are rare and are compensated for by uncaptured bears whose centers of activity are $\leq r$ from the trap site. Potential for bias exists in noncircular home ranges (not evident, or at least not important, in my data), shifting of home ranges with corresponding shifts in centers of activity in response to bait, and the propensity to capture animals whose centers of activity are closest to the trap site. Detecting shifts in home range due to bait is beyond the limits of our current telemetry data and deserves further attention.

Population Estimators

All 4 estimators of population size indicated a population increase from 1972 to 1991, but there was disparity in growth rates and final population size. Zarnoch (1979) found the nonparametric estimator to be more robust than Chapman's (1952) modification of the Schnabel estimator and the geometric estimator (Eberhardt *et al.* 1963, Edwards and Eberhardt 1967, Nixon *et al.* 1967, Eberhardt 1969) under conditions of learned trap response and a probability of capture of 10% or 40%. Experience with trap-wary bears and capture probabilities from JOLLY falling consistently between 5% and 40%, made usage of this estimator very attractive. Problems with the nonparametric estimator quickly became apparent. Population size

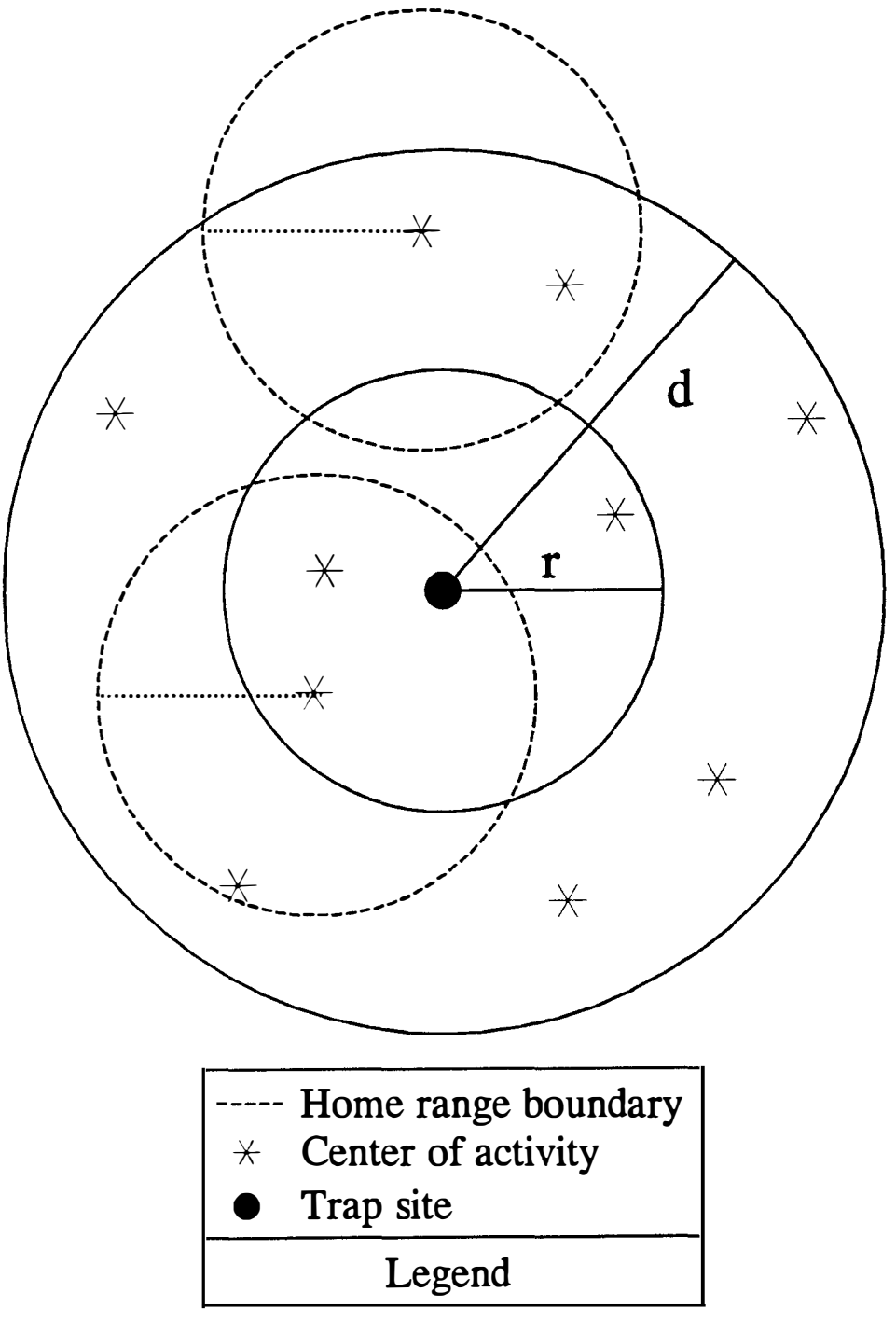


Figure 5.1. Graphic representation of effective study area concept. Individuals whose centers of activity are located within *r* distance of a trap site are effectively sampled. Average home range diameter and radius are represented by d and r, respectively.

increased steadily, as expected and consistent with the other estimators, but the trajectory was much steeper than observed for the other estimates. Contrary to other observations, the estimate never decreased from one year to the next, with the resulting graph approximating exponential growth (Figure 4.1). The nonparametric estimator does not compensate for mortality and is therefore not appropriate for time scales sufficiently long to allow significant changes in population size or composition. However, analysis with the nonparametric estimator may prove useful for short-term, localized, intensive trapping schemes or as the within-year estimator under the robust design model of Pollock *et al.* (1990).

Lincoln-Petersen and JOLLY estimates exhibited the same population trajectories, with Lincoln-Petersen estimates consistently more conservative and often tracking 1 year behind JOLLY trajectories. Periods of lag time in Lincoln-Petersen estimates may indicate bias in the recapture sample that JOLLY is able to detect from estimates of mortality and recruitment *via* inter-capture interval (individual capture history is unimportant in the Lincoln-Petersen model, bias is therefore possible if the recapture sample is systematically biased). JOLLY estimates near the end of an estimation interval (*e.g.* 1990 and 1991) tend to be inflated because of the long inter-capture interval of black bears. This problem was confounded by the high rate of mortality exhibited by marked bears during the fall of 1992.

Backdating, Lincoln-Petersen, and JOLLY estimates were all highly correlated, with the strongest correlation occurring between calendar of captures and Lincoln-Petersen estimates. Weaker correlation between backdating and JOLLY

estimates can be attributed to annual changes in trap lines that bias estimates of survival, recruitment, capture probability, and, ultimately, population size. Lincoln-Petersen estimates were probably not influenced as much by altered trap lines because changes occurred gradually (*i. e.* 1 or 2 new lines were adopted each year with a corresponding abandonment of 1 or 2 lines). Because the Lincoln-Petersen estimator is a 2-sample model, the gradual changing of lines ensured enough lines were trapped in consecutive years to allow a consistent sample of recaptures. Jolly-Seber models were more easily influenced by inconsistent trapping because they are multiple-sample models that integrate mortality (with emigration) and immigration.

The Lincoln-Petersen model is similar to the nonparametric estimator with respect to mortality and long inter-sample intervals, but it offers the advantages of requiring only 2 samples and 1 recapture of individuals to produce estimates. The nonparametric model is most accurate with high capture probabilities and multiple, inter-seasonal samples, 2 requirements that are diametrically opposed with respect to black bears. Relative to current Park trapping, the number of areas trapped would have to be halved to produce Lincoln-Petersen estimates within a trapping season, but this would double the annual trapping intensity in the remaining areas. Further, the data collected under this regime could also be used in a robust design (Pollock *et al.* 1990) with Jolly-Seber models used for yearly estimates.

Interestingly, the other estimators did not exceed the minimum number known alive (backdating) until the 4th or 5th year of data, indicating that estimates produced

with <5 years of data may be too low; this may be due to the low capture rate of young (1.5 and 2.5 years) age classes and low capture probabilities.

Backdating is useful as a baseline population estimate assuming net emigration is greater than or equal to net immigration and the number of animals that leave the study area for periods greater than 1 year and return is not unacceptably high. These assumptions appear realistic for our study area. The Park population has historically been considered a source population for adjacent habitat. The apparent stability of the population and no evidence of immigration support this view. Additionally, it seems unlikely that an animal could disperse from the Park and successfully return after a period of years in such a stable, high-density population. However, periodic population declines such as exhibited in the fall of 1992 may provide windows for immigration. Bears returning to natal ranges is also possible in this scenario and may partially explain the relatively large number of unmarked bears in the 1994 capture. Subadults forced to disperse from high-density areas such as Sugarland Mountain and Bote Mountain may establish home ranges in more marginal areas of the Park but return to their maternal ranges when the opportunity arises.

Pollock *et al.* (1990) recommended Jolly-Seber estimates for the open population portion of a robust design. The variety of models available in JOLLY diminish concerns over assumption violations. JOLLY does not reduce violations *per se*, but rather provides estimates of population parameters that can be independently tested. Discrepancies can then be explained or examined in more detail. The array of models in JOLLY simulate various types of dynamics, allowing an unbiased

approximation that may have been misinterpreted using age structures (Garshelis 1993).

Under circumstances similar to those in the Park, research conducted to estimate black bear density should utilize a robust design with the Lincoln-Petersen estimator used for within-year estimates and program JOLLY for among-year estimates. A minimum of 5 years data collection should be used to avoid bias due to long inter-capture intervals. Population estimates, particularly in program JOLLY, should be calculated by sex to account for differences in behavior and life history patterns. However, if capture probabilities are high ($\geq$ .9), the length of study may be shortened and the robust design may be abandoned to allow twice as much area to be trapped annually.

Population Size and Density Estimates

Data indicate our true study area in GSMNP is significantly smaller than previously reported (McLean 1991, Pozzanghera 1990), especially for females. Cumulative density estimates were therefore higher than previously reported (McLean 1991, Marcum 1974) although population estimates were consistent with earlier findings (McLean 1991). When calculated using cumulative area trapped, density estimates were comparable to other populations in the Southern Appalachians (Carney 1986, Warburton 1984), but, when calculated using the area trapped annually, density estimates were consistent with interval estimates. Cumulative data indicate our study

area supports a viable population of black bears (Schaffer 1978) as defined by the minima (Franklin 1980).

Model selection in JOLLY for data from both sexes combined indicated a poor fit. Data analyzed by sex produced adequate fits with males and females exhibiting divergent dynamics as shown by the selection of different models.

Disparity in model selection between time intervals and between sexes within time intervals indicates that males and females have different population dynamics. Dominance of the death but no immigration model (Model A') for females demonstrates the stability of the female population and may indicate dispersal of subadult females as an important population regulation force. The predominance of Model A (death and immigration) for male data supports a density-dependent view of black bear population regulation (Mech 1970, Stringham 1983).

Estimating population size using consistent sampling intervals provides some distinct advantages over lumping all the data. By eliminating changes in trap lines from year to year, the assumption of equal catchability is more closely met. Consequently, rates of migration, recruitment, and survival and capture probabilities are not biased by new areas with no marked bears or marked bears that are uncatchable due to abandoned trap lines. However, the consistency exhibited between cumulative and interval densities indicates that changes in trap lines from year to year do not necessarily invalidate the data. Interval estimates also allow examination of the effects of study duration and altered trapping regime on population estimates. For example, time interval 1977-1991 utilized data from Bote Mountain, Bunker Hill,

Parson's Branch Road, and Sugarland Mountain. Time intervals 1980-1983 and 1984-1991 both used the same data as 1977-1991, but data from Hannah Mountain was added to 1980-1983 and data from Turkey Pen was added to 1984-1991. Adding approximately 20% more data produced disparate results; estimates for the time interval 1980-1983 were 50% less than the corresponding years from the 1977-1991 interval. Conversely, estimates for 1984-1991 were approximately 30% greater than the corresponding yearly estimates from the interval 1977-1991. The above trends, but not the magnitudes, held for densities as well. These disparities can be attributed not only to additional data, but also, and perhaps more importantly, to the length of the estimation interval. Longer time intervals allow for the greatest probability of recapture; this is especially important in populations such as ours where annual capture probabilities are very low and inter-capture interval is often several years.

Interval densities were higher than previous reports in the literature (Table 5.1), and were exceeded only by estimates from Alaska (McIlroy 1972). Carlock *et al.* (1983) reported a density range of 0.08 - 0.59 bears/km^2 using various techniques and Eagar (1977) concluded the density of one watershed was 1.49 bears/km^2. Although some of the difference in density estimates was caused by a population increase that lasted until the late 1980's, the usage of home range data to define study areas revealed poorer coverage of the study area than was previously thought (Carlock *et al.* 1983, McLean 1991). Disparity in home range sizes led to significantly smaller study areas and higher densities for females than males, but that was compensated for somewhat by apparently-inflated male home ranges. Our study area has traditionally

Table 5.1. Estimated densities of selected North American black bear populations (adapted from McLean 1991 and Clark 1991).

Location		Source	Density (bears/km^2)
Alaska		McIlroy 1972	3.12
Alberta		Kemp 1976	0.38
Arizona		LeCount 1982	0.33
Arkansas	(Ozark)	Clark 1991	0.08
	(Ouachita)	Clark 1991	0.09
Great Dismal Swamp NWR		Hellgren & Vaughan 1989	0.53
GSMNP		This Study (Cumulative - Cumulative area)	0.53
		This Study (Cumulative - Annual area)	1.38
		This Study (Interval)	0.81 - 2.47
		McLean 1991	0.29
		Marcum 1974	0.37
Idaho		Beecham 1980	0.77
Maine		Hugie 1982	0.06 - 0.18
Massachusetts		Elowe 1987	0.13
Michigan		Erickson & Petrides 1964	0.11
Minnesota		Garshelis 1988	0.19
		Rogers 1987	0.22
Montana		Jonkel & Cowan 1971	0.23 - 0.48
New York		McCaffrey *et al.* 1976	0.05 - 0.06
North Carolina		Warburton 1984	0.16 - 0.23
Shenandoah NP		Carney 1986	0.71 - 1.04
Washington		Lindzey & Meslow 1977	1.12 - 1.49

been considered to have the highest bear density in the Park and one of the highest nationwide. These estimates support that claim, but they should not be extrapolated beyond the boundaries of the study area. Little is known about the interaction of our study area bears with the rest of the park population. It is possible that substantial segments of the population shift their home ranges seasonally, and these density estimates may not be valid on an annual basis, much less outside the study area.

Population Dynamics

Sex and age distribution

ANURSUS simulations predicted population decrease from 1991 to 1996 regardless of the type of simulation. Drastic population declines predicted by the model illustrate the problems associated with obtaining population parameters from reconstructed capture data. Low capture rates of young age-classes (1.5 and 2.5 years) ensure high estimates of subadult survival and young population structures. The effect of reconstructed distributions is seen in comparison of mean age of females obtained from capture ($\bar{x}$ = 6.2) and backdating ($\bar{x}$ = 5.2). Failure of female age distributions to converge with reproductive parameters and biased subadult survival rates may partially explain the predicted decline.

Reconstructed age structures may indicate males are exploited more than females (Hellgren 1988), although age structures obtained from backdating are strongly biased against older animals. Capture structures indicate little or no exploitation although trapping is biased against young age-classes as evidenced by the

paucity of 1.5 and 2.5 year-old bears in the sample. Higher travel rates, larger home ranges, shorter denning periods, and intra-gender social intolerance contribute to higher rates of male mortality. Additionally, adult male panhandlers may be relocated to less protected areas as they are perceived to be less important to population dynamics than are females.

McLean (1991) found no conclusive evidence of density-dependence in the Park population. Data from this study are not conclusive either, but several results point in that direction. Significant negative correlation between the percentage of females in the population and population size, combined with the predominant influence of males on effective population sizes, gives strong evidence of rapid male responses to local variation coupled with female stability.

Backdating can be a useful tool for examining sex and age structure, assuming a representative yearly capture sample and insignificant immigration. As reported earlier, our capture sample was biased against young age-classes resulting in reconstructed age structures significantly younger than the capture and immigration would produce the same results. If these assumptions are met, reliable population structure and parameters can be obtained.

Cub Production and Survival

Litter size was smaller than early reports for this population (Eiler 1981, Wathen 1983), but larger than a more recent estimate (McLean 1991). Wathen's (1983) estimate was produced from a smaller data set, most of which was collected

the winter following a fall of abundant hard mast (McLean 1991). Differences in Eiler's (1981) results may have been due to estimated litter sizes instead of minimum counts (McLean 1991). Average litter size of 2.24 compares favorably with the range of values (1.5 - 2.4) reported elsewhere (Collins 1973, LeCount 1982, Rogers 1987, Clark 1991). Overall cub survival was consistent with earlier reports (Eiler 1981, Wathen 1983) and lay in the mid-range of values (31% - 90%) reported elsewhere (Erickson and Petrides 1964, Jonkel and Cowan 1971, Kemp 1972, Rogers 1976, LeCount 1980, Lindzey and Meslow 1980, Alt 1982, Wathen 1983, Smith 1985, Elowe 1987, Kolenosky 1990, Clark 1991). There was some evidence of higher survival rates of female cubs, but annual sample sizes were insufficient to test statistically. Differential survival may function as a fitness-enhancing mechanism, with female survival favored in a low-density or growing population with high recruitment rates and male survival favored in stable or high-density populations with little or no recruitment and high intra-specific intolerance. Litters that survived the first year intact were larger than those lost entirely and smaller than litters with partial survival. Loss of small litters as a whole was probably due to poor maternal nutrition which resulted in smaller litter size and decreased ability to successfully raise offspring or inexperienced young females. Excellent maternal condition may account for larger litter size while poor spring or summer food supply and the difficulty of protecting a large litter may explain partial survival of large litters. Causes of mortality were usually unknown. Although most mortality in the Southern Appalachians has been attributed to poor nutrition (Wathen 1983), other potential

sources include cannibalism (Lindzey and Meslow 1977, LeCount 1982) and young females with no maternal experience (Alt 1982).

Population indices

Cyclical tendencies in trap success imply the same pattern in the GSMNP bear population. Estimates of population size did not exhibit a classical cyclical pattern, but peaks tended to occur at fairly regular intervals. No regular patterns were obvious in troughs; this was perhaps due to consistent, long-term population growth with expected troughs becoming plateaus. Production of hard mast tends to be cyclical (Zahner 1991 *in* McLean 1991:109) and corresponding fluctuations in bear numbers may occur in response. This relationship may be dampened by alternative food sources (Southern 1970 *in* Krebs 1985:295), but data thus far are unclear (Pelton 1989).

Although trend indicators alone are often inadequate (Garshelis 1993), strong correlation between indices of bear activity and population estimates demonstrate the ability of trapping data to provide accurate insights into bear population trends. The percentage of nights with no activity was the best indicator of population size. The percentage of trap nights with bear activity was marginally weaker than percentage of nights with no activity, indicating errors in discriminating between bear and raccoon visits at trap sites. These indices are also robust as trapping intensity did not bias the results. Lack of relationships between female reproductive parameters and population

estimates confirms the relative stability of the female segment of the population and the importance of males to population change.

Hard Mast

Whitehead index values for cumulative mast production fluctuated with no regular pattern. MPPI values seemed to vary randomly also, although production was markedly higher prior to 1986. Relationships between overall mast production and population estimates were erratic and confusing. Most correlations were negative, seemingly indicating a detrimental relationship between bears and mast. Existence of a relationship between population size and mast production during the same year may indicate a common response to environmental or climatic conditions.

Reducing the data set to survey routes associated with effective study areas produced nearly uniform Whitehead values among intervals. Segregating the data set greatly reduced sample sizes. Survey routes are widely dispersed and located approximately uniformly throughout the park. Our study areas are clustered in the northwest quadrant with the same general mast survey routes within each effective study area. In fact, most intervals used the same data for years of overlap. Density of survey routes needs to be increased to develop meaningful data sets associated with effective study areas. Correlation analysis emphasizes the importance of long-term data sets, as only 2 of 7 intervals were sufficiently long to conduct analyses.

Correlations for time intervals 1977-1991 and 1984-1991 indicate Whitehead values are more closely related to population estimates than are MPPI values,

although those relationships are dubious at best. Interestingly, relationships between both male and total population estimates and Whitehead values for the time interval 1977-1991 switched signs every year, indicating male population responses to mast production may be exaggerated.

Collection, calculation, and interpretation of mast data was highly questionable. Numerous field personnel, variable weather conditions, nonstandardized data collection, and limited data for our study area raised questions about the data, while different approaches to calculation and no information regarding acorn quality plagued the technique. Personnel of the NPS have essentially standardized all aspects of data collection possible, but the quality of several years of data remains questionable and several more years will be necessary to develop a sufficient amount of data.

I eliminated nonproductive trees from the sample for calculation of the MPPI (Pozzanghera 1990), but numerous trees with values between 0.001 and 0.1 biased the results. However, using the maximum value for each year failed to produce any relationships. A minimum MPPI value for inclusion into analyses should be set based on useful productivity, rather than on the presence of a few acorns.

PART 2

Age Prediction

CHAPTER 6

INTRODUCTION

The distance required for the successful relocation of a nuisance black bear is dependant upon the individual's age (Stiver 1991). The current method of aging bears is time consuming (Eagle and Pelton 1978) and results are not available for several months. A technique for quick age-estimation in the field could potentially save the National Park Service (NPS), Tennessee Wildlife Resources Agency (TWRA), and other agencies a significant amount of time and transportation costs as well as ensure a successful relocation effort. Because reproductive and behavioral characteristics such as dispersal, age at first reproduction, and reproductive rate are primarily functions of age, such a method could prove useful to researchers in determining if a captured individual should be radiocollared.

Body measurements have long been used to estimate the weight of such animals as domestic pigs and cattle and, more recently, bear researchers have found similar correlations between morphometrics and weight and have used these correlations to develop models to estimate weight from a standardized set of measurements (McLean 1991).

Statistical analyses of body measurements have proven reliable with animals of known age (Mee, pers. comm.). The short birthing period of black bears (approximately 3 weeks) (Pelton 1982) make them a prime candidate for age estimation based upon calibration (Aitchison and Dunsmore 1975, Mee pers. comm.).

The objectives of this study were:

1. To determine if correlations between morphometrics and age exist.
2. To determine differences in correlations among study areas, sexes, and bear status (panhandler versus wild).
3. Given correlations, to develop appropriate age prediction models for each class.
4. To test models for each class.
5. To interpret research and management implications from model results.

CHAPTER 7

MATERIALS AND METHODS

Data Collection

Body measurements collected from bears captured in GSMNP from 1972-1991 were used to develop the models. Only data from captures occurring between May and September were used to develop the models; deleting animals captured in the fall allowed us to circumvent biased measurements caused by seasonal weight gain. Bears captured in Cherokee National Forest (CNF) and Pisgah National Forest (PNF) within this same time interval were used to determine whether or not the models were applicable beyond the study area. Morphological measurements considered for the model and the method of measurement for each are as follows:

chest circumference - girth of chest directly behind shoulder blades at point of least expansion

forearm circumference - girth of front leg at widest point below the elbow (NOTE: do not measure capture leg, this could create biased measurements due to swelling)

front foot length - length of the longest portion of the front foot pad, not including toe pads

front foot width - length of the widest portion of the front foot pad, not including toe pads

head length - distance from the tip of the nose to the occipital condyle along the contour of the head

head width - distance from one temporomandibular joint to the other with tape held tightly across the top of the skull. (NOTE: calipers may also be used, but make sure that measurements from the 2 methods are not mixed)

height at shoulder - front leg (non-capture), distance from the last joint on the longest digit to the tip of the scapula adjacent to the spine; measurement is taken from the end of the longest digit to the elbow, up the outside of the upper foreleg to the tip of the scapula

hind foot length - length of the longest portion of the hind foot pad, not including toe pads

hind foot width - length of the widest portion of the hind foot pad, not including toe pads

neck circumference - girth of neck mid-way between skull and shoulders

total length - with the tape held tightly, distance from the tip of the nose to the tip of the last vertebra in the tail along the contour of the body

between ears - distance between the base of the ears using the closest point across the top of the head

For a detailed explanation of biological data collection see LeCount (1986). A premolar was extracted from each bear for age determination; teeth were sectioned, stained, and aged according to the protocol of Eagle and Pelton (1978).

Model Development

Separate models were generated for wild Park bears, panhandlers, and National Forest bears by sex based upon sexual dimorphism and differences in growth rates (McLean 1991). Bears were grouped into 1-year age intervals based on summer ages (*i.e.* 1.5, 2,5, *etc.*) up to 4.5 years. Bears $\geq$ 5.5 years were pooled because morphological growth after this age was indistinguishable. Both univariate and multivariate models were produced. Univariate models were generated for ease of usage in the field; multivariate models were developed because the combination of 2 or more measurements often produces a better model (Mee, pers. comm.). Model development was treated as a natural calibration problem (Aitchison and Dunsmore 1975). The technique is based upon a normal distribution of body measurements for each age class, with a resulting probability of a given measurement or set of measurements belonging to each age class.

Pearson correlation coefficients were calculated, by group, using PROC CORR in SAS (SAS 1989). Body measurements most highly correlated with age were then used as independent variables in multivariate regression (GLM) to obtain slopes and intercepts for each variable. A multivariate analysis of variance (MANOVA) was then conducted using the same variables to obtain the covariance matrix of residuals. Slopes, intercepts, and covariance matrices of residuals were then incorporated into the models. Testing was accomplished by reconstructing models using a random sample of 75% of the data. The remaining 25% of the data was classified using the reconstructed model.

CHAPTER 8

RESULTS

Total length was the single most reliable estimator of age for both male (R^2 = 0.72) and female (R^2 = 0.84) panhandlers. Multivariate models for both panhandler groups were constructed using total length, height at shoulder, and chest circumference (Table 8.1).

The univariate model for males correctly predicted 19 of 45 ages (42.2%) with 19 other observations (42.2%) classified within 1 age class. The multivariate model correctly classified 24 of 45 (53.3%) observations with 17 (37.8%) others within 1 age class. For females, the univariate model correctly classified 67% (n = 20) with 7 (23.3%) of the remaining 10 within 1 age class. The female multivariate model predicted 22 (73.3%) correctly with 6 (20.0%) of the remaining 8 classified within 1 age class.

Total length was the most reliable estimator of age for backcountry female (R^2 = 0.48) and male (R^2 = 0.49) bears. Multivariate models for both wild groups were constructed using total length, height at shoulder, and chest circumference (Table 8.2). For females, the univariate model correctly predicted 47.1% (40 of 85) of the ages with an additional 28 (32.9%) within 1 age class. The multivariate model was within 1 age class for 30 individuals (35.3%) with 50.6% (N = 43) being classified correctly. Of 105 individual males, the univariate model correctly predicted 45.7% (N = 48). An additional 40 (38.1%) observations were within 1 age class. Results

Table 8.1 Correlations between age and morphological measurements for male and female panhandler black bears in Great Smoky Mountains National Park. Correlations in bold face type were used to construct multivariate age prediction models. The top number in each pair is the correlation coefficient; the bottom number is the probability.

	Male	Female
Total Length	**0.873** **< 0.0001**	**0.916** **< 0.0001**
Height at Shoulder	**0.825** **< 0.0001**	**0.886** **< 0.0001**
Chest Circumference	**0.808** **< 0.0001**	**0.903** **< 0.0001**
Weight	0.757 < 0.0001	0.899 < 0.0001
Neck Circumference	0.828 < 0.0001	0.887 < 0.0001

Table 8.2 Correlations between age and morphological measurements for male and female backcountry black bears in Great Smoky Mountains National Park. Correlations in bold face type were used to construct multivariate age prediction models. The top number in each pair is the correlation coefficient; the bottom number is the probability.

	Male	Female
Total Length	**0.770** **<0.0001**	**0.696** **<0.0001**
Height at Shoulder	**0.728** **<0.0001**	**0.645** **<0.0001**
Chest Circumference	**0.750** **<0.0001**	**0.616** **<0.0001**
Weight	0.713 <0.0001	0.660 <0.0001
Neck Circumference	0.741 <0.0001	0.588 <0.0001
Distance Between Ears	0.576 <0.0001	0.407 <0.0001

for the multivariate model were comparable to the univariate, 55 correct (52.4%) and 35 (33.3%) within 1 age class.

The variable most highly correlated with age for both male (r = 0.67) and female (r = 0.85) national forest bears was weight. Both multivariate models included weight and neck circumference, but the female model included distance between ears while the male model used height at shoulder (Table 8.3).

Table 8.3 Correlations between age and morphological measurements for male and female black bears in Cherokee and Pisgah National Forests. Correlations in bold face type were used to construct multivariate age prediction models. The top number in each pair is the correlation coefficient; the bottom number is the probability.

	Male	Female
Total Length	0.597 <0.0001	0.588 <0.0001
Height at Shoulder	**0.631** **<0.0001**	0.521 <0.0001
Chest Circumference	0.551 <0.0001	0.653 <0.0001
Weight	**0.669** **<0.0001**	**0.849** **<0.0001**
Neck Circumference	**0.621** **<0.0001**	**0.690** **<0.0001**
Distance Between Ears	0.600 <0.0001	**0.723** **<0.0001**

CHAPTER 9

DISCUSSION

Although female models proved fairly accurate, the models have some serious problems. The most obvious problem is lack of age differentiation after 4.5 years; this method, therefore, will not replace tooth sectioning. These models also require relatively large data sets, with a minimum of 45-50 observations per group that accurately represent each age class. As our correlation matrices indicate, there is apparently too much phenotypic plasticity to apply a model developed for GSMNP to the neighboring national forest bears, much less to bears that inhabit significantly different habitat. Another problem with the models is that outputs are probabilities, not definitive ages, and the age class with the highest probability often does not exceed 0.35. Finally, the full multivariate model is limited to computer usage and is generally not available to be used in the field.

Models provided fairly accurate age discrimination up to 4.5 years. Univariate models were fairly accurate and easy to apply. Although models are not applicable to other populations, the technique is. Researcher with data sets of at least 45 observations per group can develop their own models. These models provide an estimate of age that would not be available otherwise.

There are 4 primary applications of these models. Ages can be estimated for observations in data sets that have no age for one reason or another. Our data set has 234 observations of 180 individual bears that have no corresponding ages, a considerable amount of missing information. Extracted teeth can sometimes be

misplaced or lost, and these models could at least supply an estimate of the bear's age. Perhaps the most important applications are for field work. Telemetry studies on bears are often limited by the number of radiocollars researchers can afford and monitor. By being able to estimate an animal's age in the field, better decisions can be made regarding which animals should be radiocollared. For example, females older than 3 years for reproductive studies or 1.5 and 2.5 year-olds for dispersal studies. Relocation of nuisance bears may also be improved. The ability of a bear to home after translocation is directly related to age. If age can be accurately estimated in the field, then a determination of how far the animal needs to be moved can be made, thus making the process more time and cost efficient.

CHAPTER 10

SUMMARY AND CONCLUSIONS

1. Home range sizes should be taken into account when establishing trapping regimes and telemetry data should be used to verify effective coverage of the area.
2. Emphasis should be placed on effectively sampling females, as male home range estimates appear to be inflated.
3. For females, the area effectively sampled at each trap site was equal to the average summer home range size.
4. For males, the area effectively sampled at each trap site was equal to a circle defined by a radius of 2.5 km.
5. Research needs to be conducted on the attractiveness of baits and detecting shifts in home range in response to baits.
6. Backdating, Lincoln-Petersen, and JOLLY population estimates were highly correlated.
7. The nonparametric population estimator is inappropriate for long-term data, but may be useful for short-term studies or robust design models where capture probabilities are high.
8. The Lincoln-Petersen estimator is ideally suited for inter-seasonal population estimates in a robust design.
9. Backdating can be used as a reliable baseline population estimate.

10. Using backdating data, the proportion of females in the population was negatively correlated with population size ($P = 0.00228$).

11. Jolly-Seber models are the most reliable and best-suited for long-term black bear population studies, especially when capture probabilities are low.

12. Population estimates produced with <5 years of data may be inaccurate, especially if capture probabilities are low.

13. Disparity in model selection in program JOLLY indicates males and females exhibit different population dynamics. The death but no immigration model (A') predominated female population estimates, whereas model A (death and immigration) was indicative of male population estimates.

14. Estimating population size for time intervals with consistent trapping efforts provided the opportunity to examine the effects of study duration and altered trapping regimes. Longer time intervals provided more reliable population estimates. Our data indicate inconsistent trapping does not necessarily invalidate the usage of such data to estimate population size.

15. Density estimates ranged between 0.81 and 2.47 bears/km^2, although estimates of population size were consistent with earlier findings.

16. ANURSUS simulations predicted severe population declines from 1991-1996 using both stochastic (44% - density independent) and deterministic models (33% - density independent; 59% - density dependent). Population estimates for 1992 and 1993 contradicted a drastic decline. Estimates of subadult and adult survival were suspect and may have been responsible for the predicted decline.

17. Average size of 74 litters was 2.24 with a sex ratio of 102♂:100♀.

18. Overall cub survival was 61.3% with females and cubs from intermediate-size litters exhibiting slightly higher survival rates.

19. The percentage of trap nights with no activity and the percentage of trap nights with bear activity were the best indices to population size.

20. Indices of female reproductive status were not significantly correlated with population estimates.

21. The bear population and hard mast production appear to respond to the same environmental and climatic conditions, rather than the bear population responding to hard mast production.

22. Failure of population estimates to correspond to hard mast indices may indicate that current hard mast index methodology is irrelevant to bear biology.

23. Total length, height at shoulder, chest circumference, neck circumference, weight, and distance between ears were significant ($P < 0.0001$) predictors of age.

24. Bears $\geq$ 5.5 years were indistinguishable with morphometric models.

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APPENDICES

APPENDIX A

COMPUTER DATA SHEET

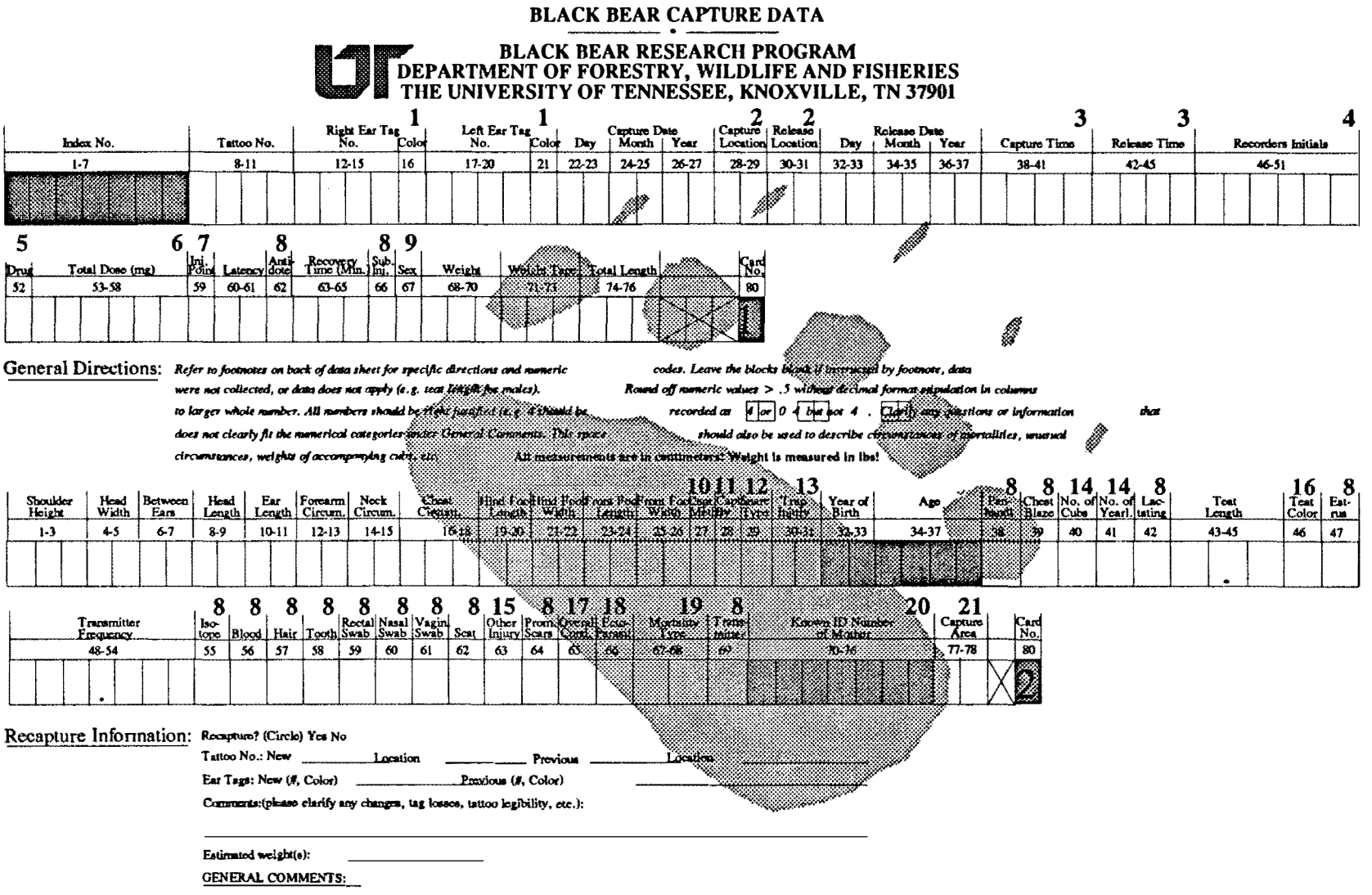


Figure A.1. Computer data sheet used by black bear research program at The University of Tennessee, Knoxville (Front).

■ Will be filled out by field project leader.

1 M=Silver Metal, B=Blue, R=Red, Y=Yellow, O=Orange, G=Green, W=White.

2
1=Bote Mtn. Rd.
2=Defeat Rdg.
3=Rabbit Ck. Rd.
4=Parson's Br. Rd.
5=Bunker Hill Rd.
6=Colen Ground Rdg.
7=Ekaneetlee Gap Loop
8=Sugarland Mtn.-Huskey Gap
9=Rough Ck.-Upper Sugarland Mtn.
10=Bent Arm
11=Green Camp Gap
12=Tremont Rd.-Long Br.
13=Jakes Ck.-Miry Rdg.-Derrick Loop
14=Lumber Rdg.
15=Hornet Tree Top
16=Tellico WMA
17=Dead End Rd.-Falls Br.
18=Double Camp
19=Cowcamp Rdg.
20=Sawmill Rd.-Bivens Br.
21=Citico
22=Gatlinburg
23=Cades Cove
24=Cataloochee
25=Hwy 441, TN
26=Collins Ck.
27=20-Mile
28=Chimney Tops
29=Tremont Turnaround
30=Smokemont
31=Walnut Bottoms
32=Oconaluftee
33=Cosby
34=Hazel Ck.
35=Cataloochee Divide
36=Mining Property, NC
37=Mt. Sterling Gap
38=Indian Camp Ck.
39=Collins Gap
40=Balsam Mtn. CG.
41=Upper Tremont Rd.
42=Little Bald
43=Sugarlands Vis. Ctr.
44=Clingmans Dome Rd.
45=Greenbrier
46=Elkmont
47=Indian Camp Rd.
48=Old Tremont
49=Spence Field
50=Forge Ck.
51=Cooper Ck.
52=Cooper Rd.
53=Tremont Env. Ed. Ctr.
54=Davenport Gap
55=Ramsay Cascades
56=Silers Bald
57=Hwy. 129
58=Little Cataloochee
59=Schoolhouse Gap
60=Cocke Co., TN
61=Hwy. 441, NC
62=Avery Co., NC
63=Greene Co., TN
64=McMinn Co., TN
65=Coastal, NC
66=Henderson Co., TN
67=Polk Co., TN
68=Indian Boundary
69=Horse Ck. Rec. Area
70=Green Cove
71=Big Ck., GSMNP
72=Hannah Mtn. Tr.
73=Unicoi Co., TN
74=Other, please specify _____
75=Mt. LeConte
76=Harmon Den Mtn.
77=Hurricane Rdg.
78=12-Mile Strip
96=Turkey Pen
00=Curry Mtn.

3 Time of capture is defined as time of initial injection and release time is defined as when the bear leaves the site under its own power or is left to recover. Use military time (e.g. 6:30 PM = 18:30).

4 Use 2 initials of up to 3 recorders, in order of seniority.

5 1=M99; 2=Sernylan; 3= =Succinylcholine Chloride (Sucostrin); 4=Ketamine; 5=Ketamine-Xylazine; 6=Ketamine-Xylazine-Mepivacaine; 7=Other: _____

6 M99, 1cc=1mg; Sernylan, 1cc=100mg; Ketamine, 1cc=100mg; Ketamine-Xylazine, 1cc=200mg of Ketamine and 100mg of Xylazine (add dosages together, e.g. 2cc=600mg); Ketamine-Xylazine-Mepivacaine, 1cc=200mg Ketamine and 100mg Xylazine and 20mg Mepivacaine (add dosages together and enter the total, e.g. 2cc=640mg; Other, please specify _____

7 1=Hip; 2=Flank; 3=Front shoulder; 4=Neck; 5=Other, please specify _____

8 1=Yes; 2=No.

9 1=Male; 2=Female

10 1=Snare; 2=Trailer-mounted culvert; 3=Free-ranging; 4=Other, please specify _____; 5=Killed (see *Mortality Type*); 6=Barrel Trap; 7=Den Capture.

11 1=Right front paw; 2=Left front paw; 3=Right rear paw; 4=Left rear paw.

12 1=Wooden cubby; 2=Burlap cubby; 3=Other natural materials cubby; 4=Trailset; 5=Trickset outside cubby, 6=Double set.

13 0=None; 1=Broken Teeth; 2=Swelling; 3=Cable cut on paw; 4=Cut and swelling; 5=Broken bones, 6=Dislocation; 7=Broken toes; 8=Killed by another bear.

14 Leave blank if undetermined. 0=None; 1=One; 2=Two; etc.

15 0=None, 1=Battle injuries or scars; 2=Collar Injury; 3=Other, please specify _____

16 1=Pink, 2=Black.

17 1=Excellent; 2=Good; 3=Fair; 4=Poor.

18 0=None; 1=Ticks; 2=Lice; 3=Other, please specify _____

19 0 or . =Alive; 1=Natural death; 2=Bear killed by other bear in trap; 3=Legal harvest; 4=Illegal harvest; 5=Vehicle collission; 6=Euthanasia; 7=Nuisance activity control; 8=Damage control; 9=Unknown; 10=bear killed by other bear in natural circumstances; 11=Drug overdose (OD).

20 Use ID# of KNOWN mother.

21 01=GSMNP; 02=Tellico; 03=Pisgah.

Figure A.1. Continued (Back).

APPENDIX B

EFFECTIVE STUDY AREA VALIDATION

Table B.1. Comparison of distance between capture location and summer center of activity to summer home range radius for male and female black bears in GSMNP, 1977-1981.

Male			Female		
ID	Radius†	Distance†	ID	Radius†	Distance†
185	3660.7	1584.3	182	1236.1	1343.2
185	3660.7	1160.3	182	1236.1	735.0
185	3660.7	922.1	182	1236.1	1163.3
185	3660.7	725.3	201	1370.4	1568.7
226	2876.8	2502.9	201	1370.4	1568.7
226	2876.8	931.9	201	1370.4	1135.9
226	2876.8	2502.9	201	1370.4	1568.7
255	3699.6‡	1275.4	201	1370.4	582.5
257	4399.2	2415.9	243	1183.5	570.9
294	3699.6‡	2204.6	243	1183.5	570.9
294	3699.6‡	2408.3	243	1183.5	527.5
338	3699.6‡	678.1	243	1183.5	54.6
338	3699.6‡	1656.0	269	1370.4	2024.1
362	3699.6‡	310.2	269	1370.4	1528.9
			303	1286.6‡	174.8
			303	1286.6‡	357.6
			309	1286.6‡	1577.8
			309	1286.6‡	1437.3
			309	1286.6‡	4438.0
Mean	3562.1	1519.9		1287.8	1206.8
SD	417.1	770.2		74.3	966.6

† All distances are in meters
‡ For bears with no summer home range estimate, the mean radius of all bears of the respective sex was used

Table B.2. Comparison of distance between capture location and annual center of activity to annual home range radius for male and female black bears in GSMNP, 1977-1981.

Male			Female		
ID	Radius†	Distance†	ID	Radius†	Distance†
5	3929.1‡	2683.0	60	3079.9	520.7
12	3929.1‡	3941.5	136	1236.1	2546.0
185	3929.1‡	830.3	151	1555.4‡	1590.0
185	2628.2	742.1	182	1896.6	595.1
185	3929.1‡	2212.1	201	1702.0	1506.8
226	4693.3	317.8	201	1142.4	999.2
255	4199.3	1645.0	201	1142.4	1377.8
257	4573.6	3591.8	201	1142.4	691.7
334	3929.1‡	2684.7	243	874.0	806.8
334	3929.1‡	755.1	243	1210.1	817.6
338	3477.9	4161.7	243	1106.7	761.1
338	3477.9	4788.0	243	1236.1	110.4
350	2729.2	265.7	269	1041.7	1141.1
350	2729.2	505.2	303	1393.5	456.3
373	3929.1‡	1789.6	309	1298.9	4485.9
453	3929.1‡	219.0	312	1555.4‡	584.5
453	3929.1‡	893.4	336	2426.7	1523.7
Mean	3757.1	1883.9		1473.0	1206.7
SD	571.3	1468.1		540.3	992.1

† All distances are in meters
‡ For bears with no annual home range estimate, the mean radius of all bears of the respective sex was used

Table B.3. Comparison of distance between capture location and overall center of activity to overall home range radius for male and female black bears in GSMNP, 1977-1981.

Male			Female		
ID	Radius†	Distance†	ID	Radius†	Distance†
5	2786.9	2794.7	40	1692.6	1130.8
5	2786.9	4645.6	40	1692.6	1070.1
12	9361.1‡	3941.5	40	1692.6	2408.5
168	9361.1‡	2154.6	60	3079.9	1531.4
185	8902.8	776.3	60	3079.9	520.7
185	8902.8	444.1	136	3496.2	2652.1
185	8902.8	219.1	136	3496.2	647.8
185	8902.8	1527.0	136	3496.2	2804.0
226	4915.3	650.8	151	2298.7‡	1710.6
226	4915.3	966.2	151	2298.7‡	1589.8
226	4915.3	650.8	165	2723.3	2062.1
255	12171.3	7371.4	182	1482.0	614.6
257	11295.1	1876.8	182	1482.0	1460.7
294	10202.3	3499.0	182	1482.0	424.9
294	10202.3	5138.1	201	1460.4	1263.0
301	18255.7	13131.9	201	1460.4	1263.0
301	18255.7	14305.3	201	1460.4	872.1
334	9361.1‡	2684.7	201	1460.4	1263.0
334	9361.1‡	755.1	201	1460.4	516.2
338	6120.9	1075.3	243	1471.2	615.8
338	6120.9	1720.4	243	1471.2	615.8
350	3027.8	185.4	243	1471.2	487.4
350	3027.8	1497.2	243	1471.2	9.5
350	3027.8	582.7	269	2915.3	2142.4
350	3027.8	185.4	269	2915.3	1588.7
362	8904.5	1907.9	303	1575.7	456.5
373	9361.1‡	1789.6	303	1575.7	653.7
453	3691.0	794.4	309	1370.4	1577.8
453	3691.0	320.2	309	1370.4	1437.4
			309	1370.4	4437.8
			310	2298.7‡	1231.3
			312	2298.7‡	1306.3
			336	2393.7	1347.4
Mean	7715.8	2675.6		2023.2	1324.6
SD	4090.8	3437.3		716.8	861.6

† All distances are in meters
‡ For bears with no overall home range estimate, the mean radius of all bears of the respective sex was used

APPENDIX C

EFFECTIVE AREA TRAPPED ANNUALLY

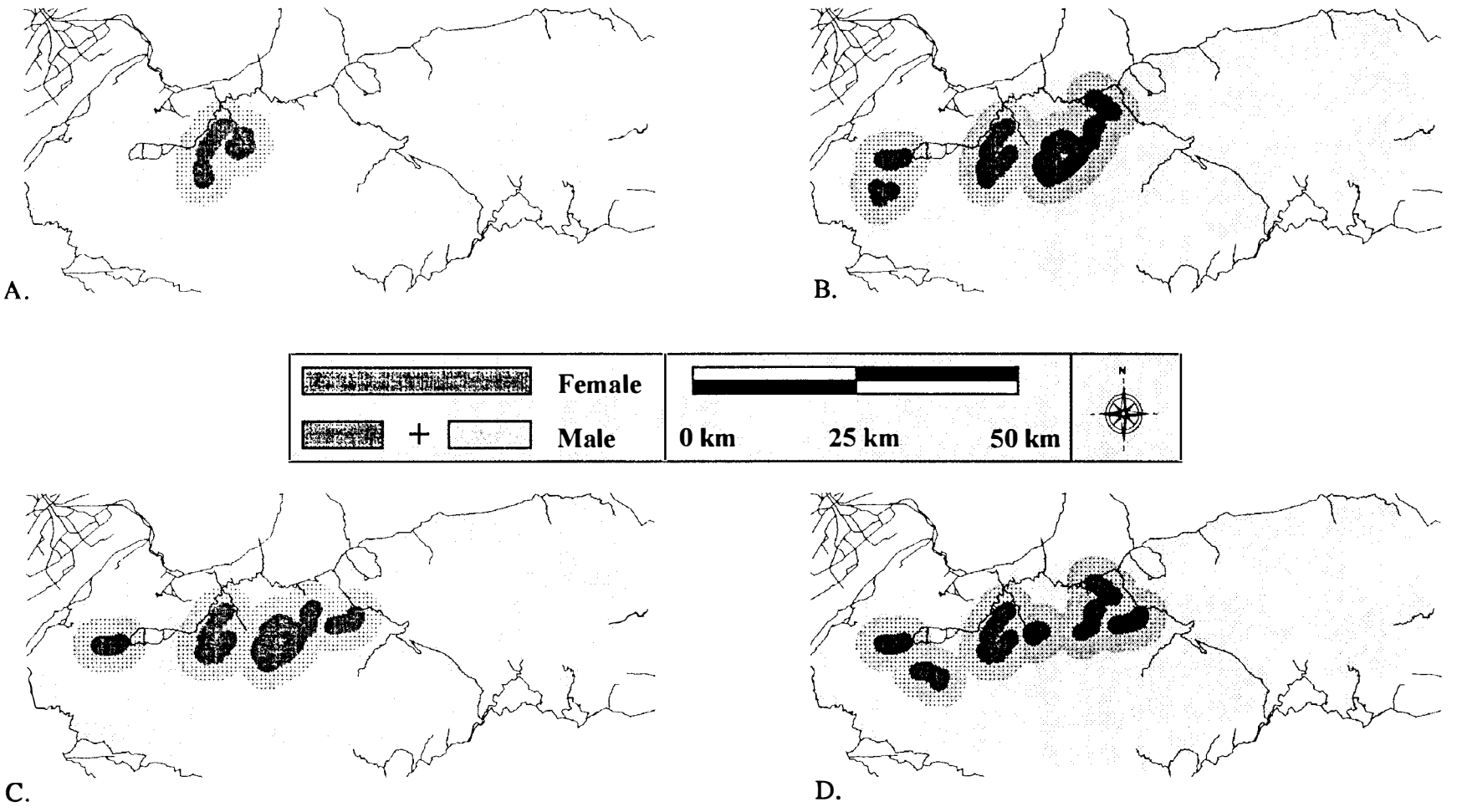
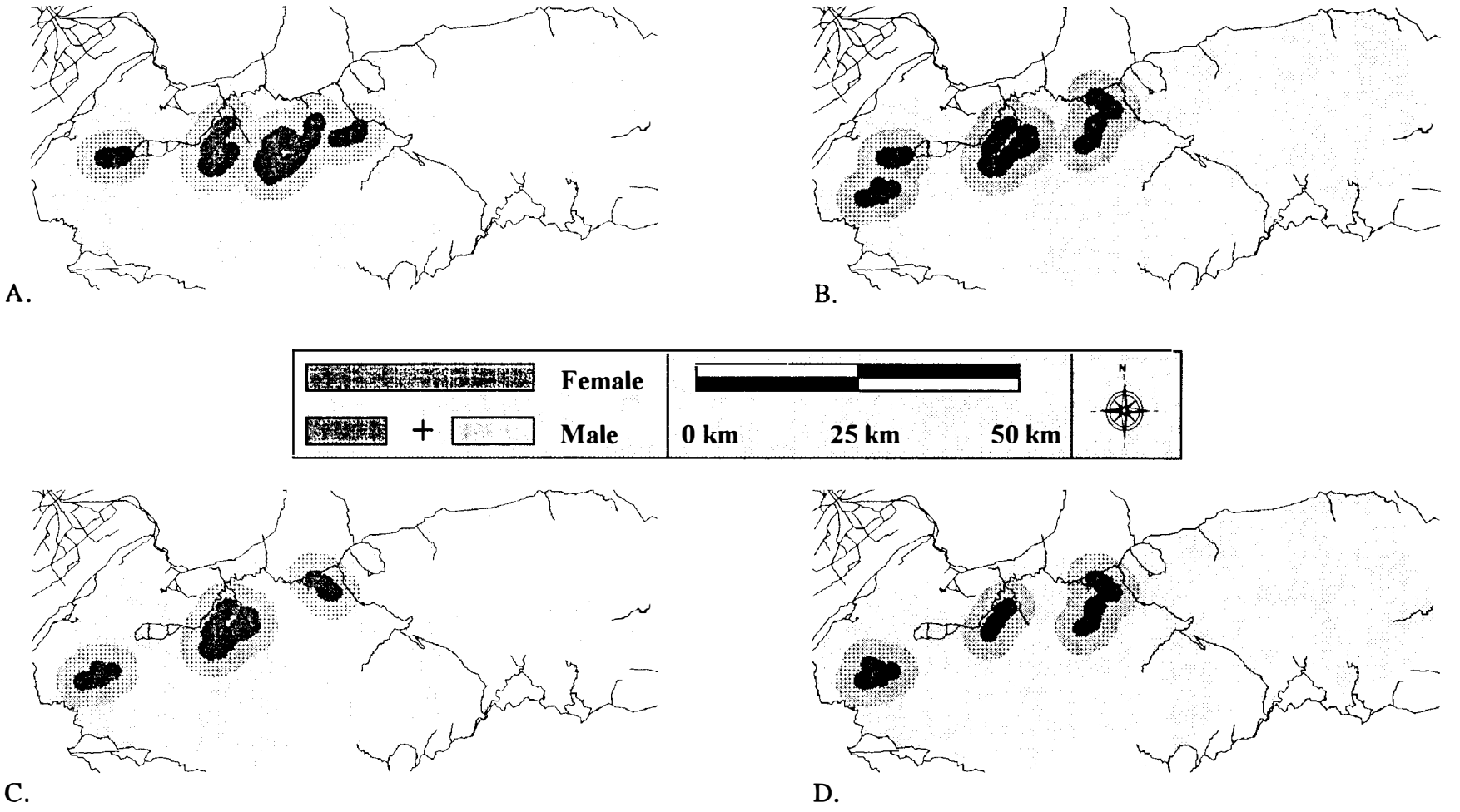
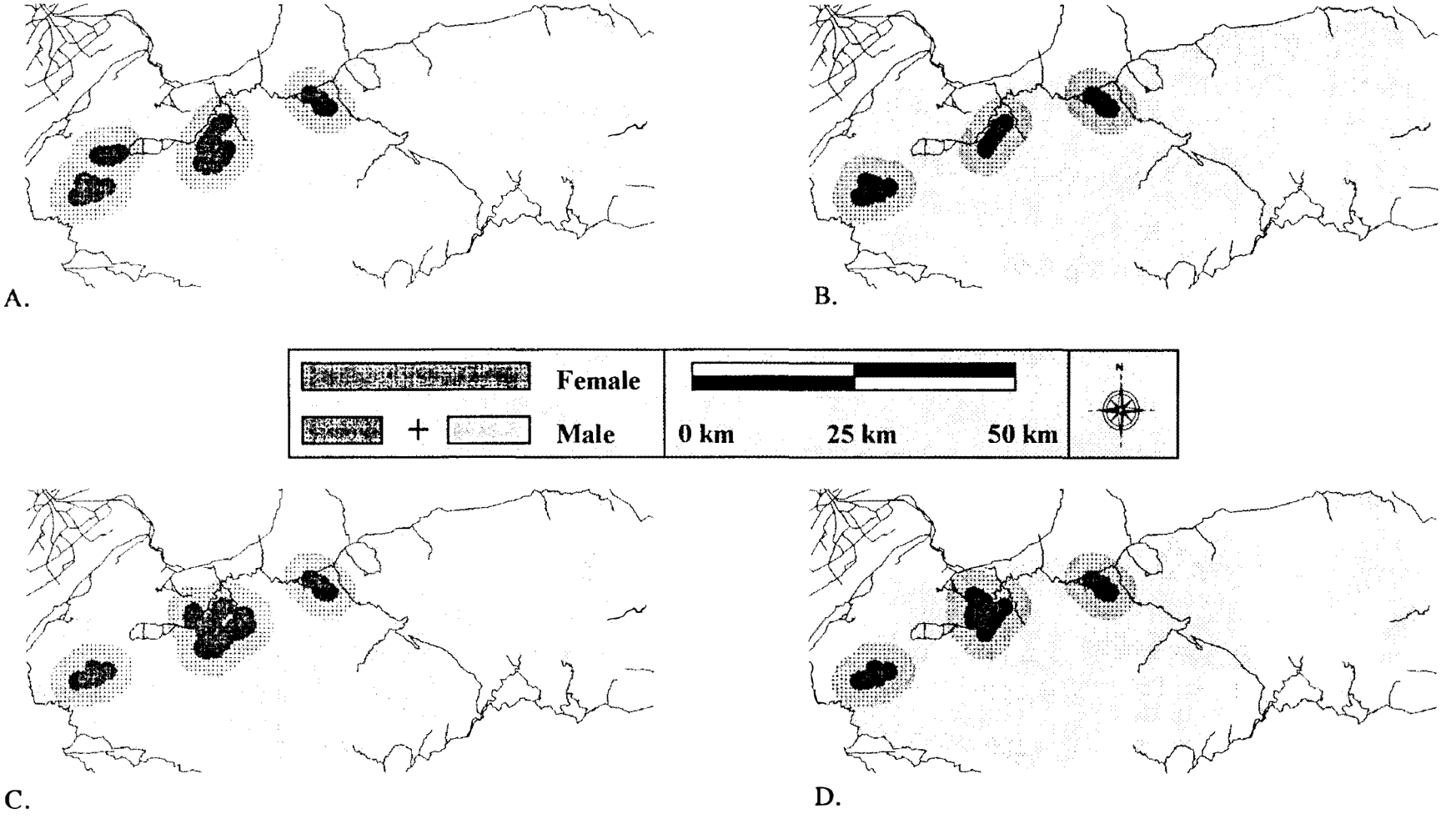


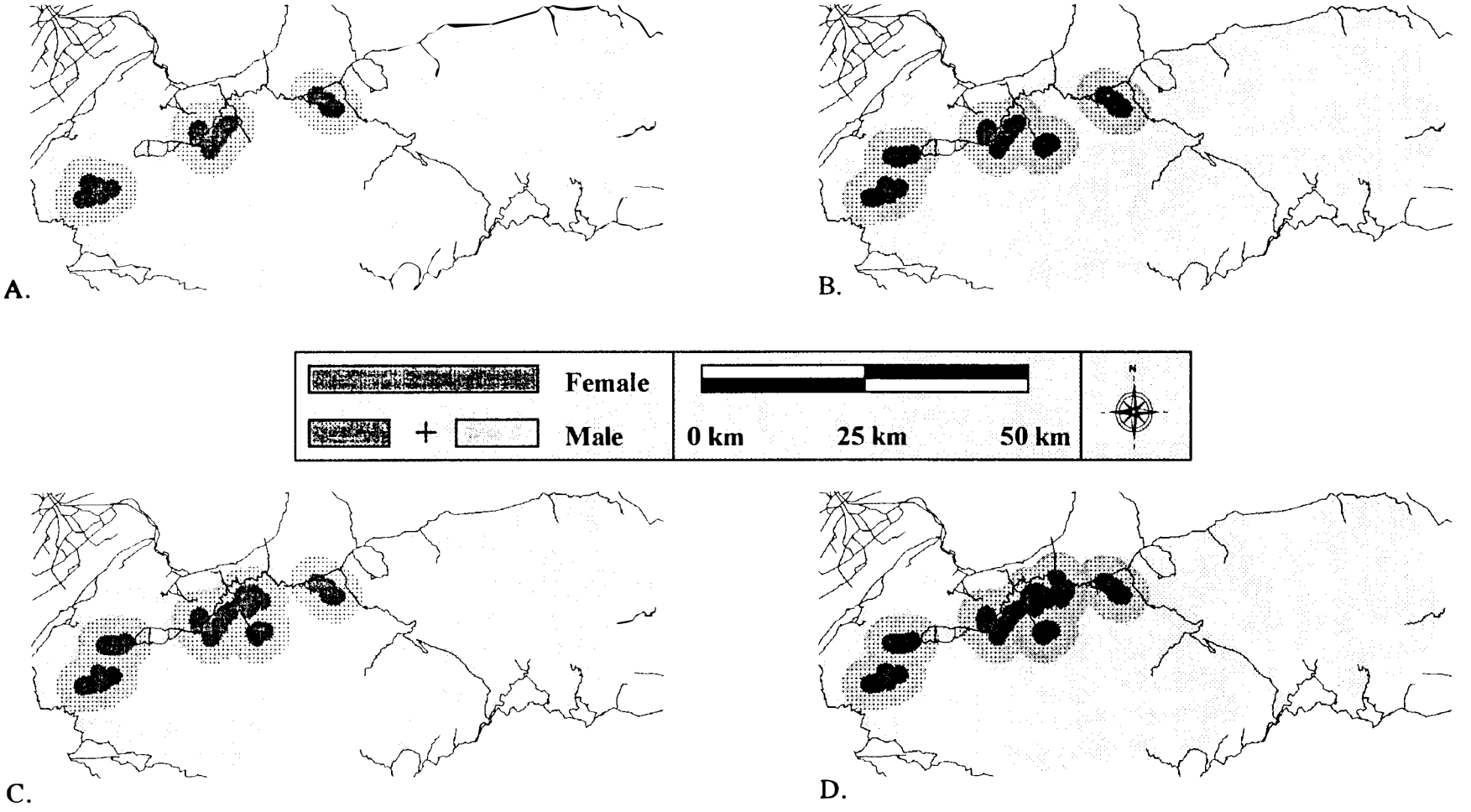
Plate C.1. Effective sampling areas for 1972 (A), 1973 (B), 1974 (C), and 1975 (D).



C.2 Effective sampling areas for 1976 (A), 1977 (B), 1978-1979 (C), and 1980 (D).



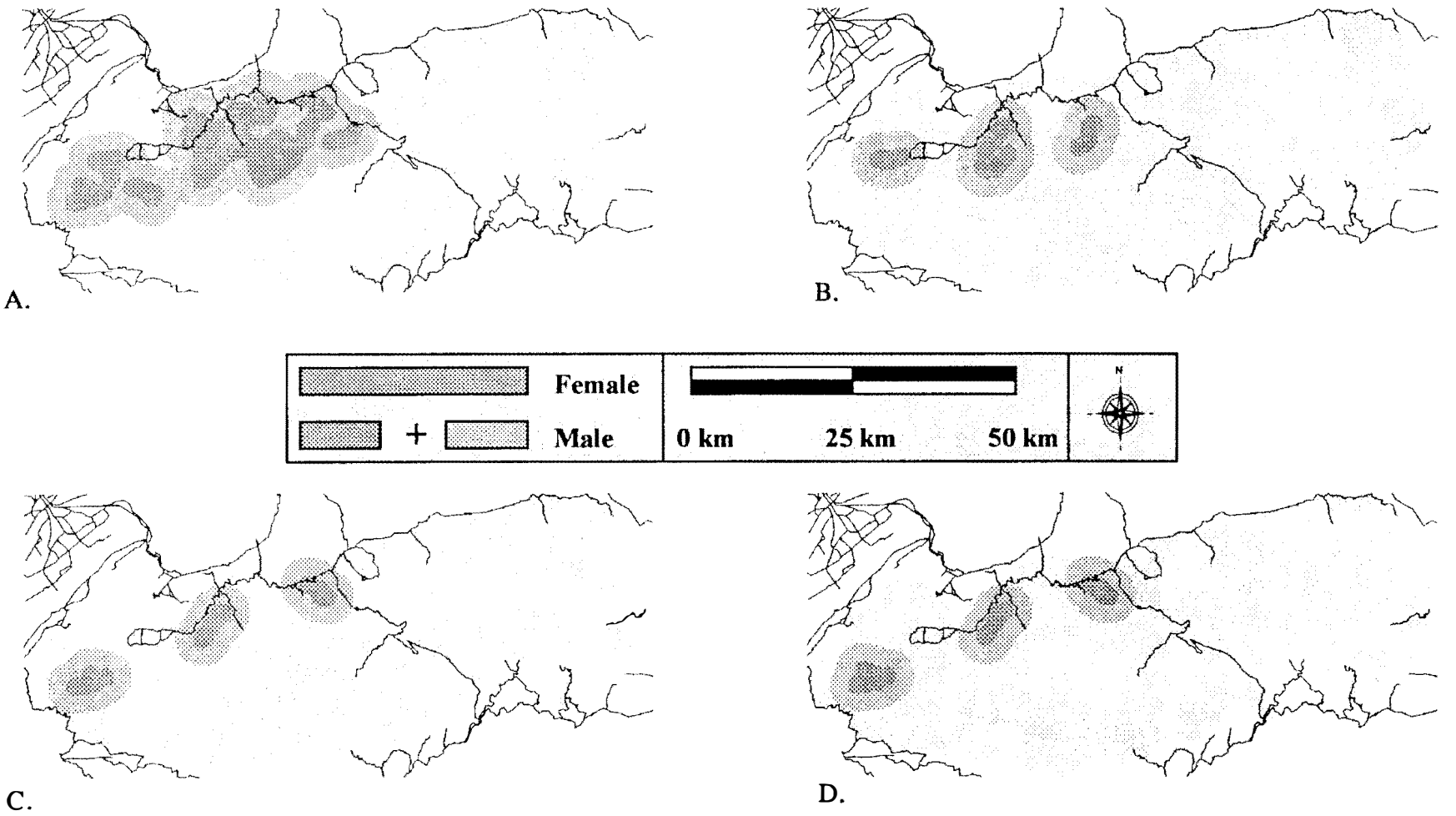
C.3 Effective sampling areas for 1981 (A), 1982-1983 (B), 1984 (C), and 1985 (D).



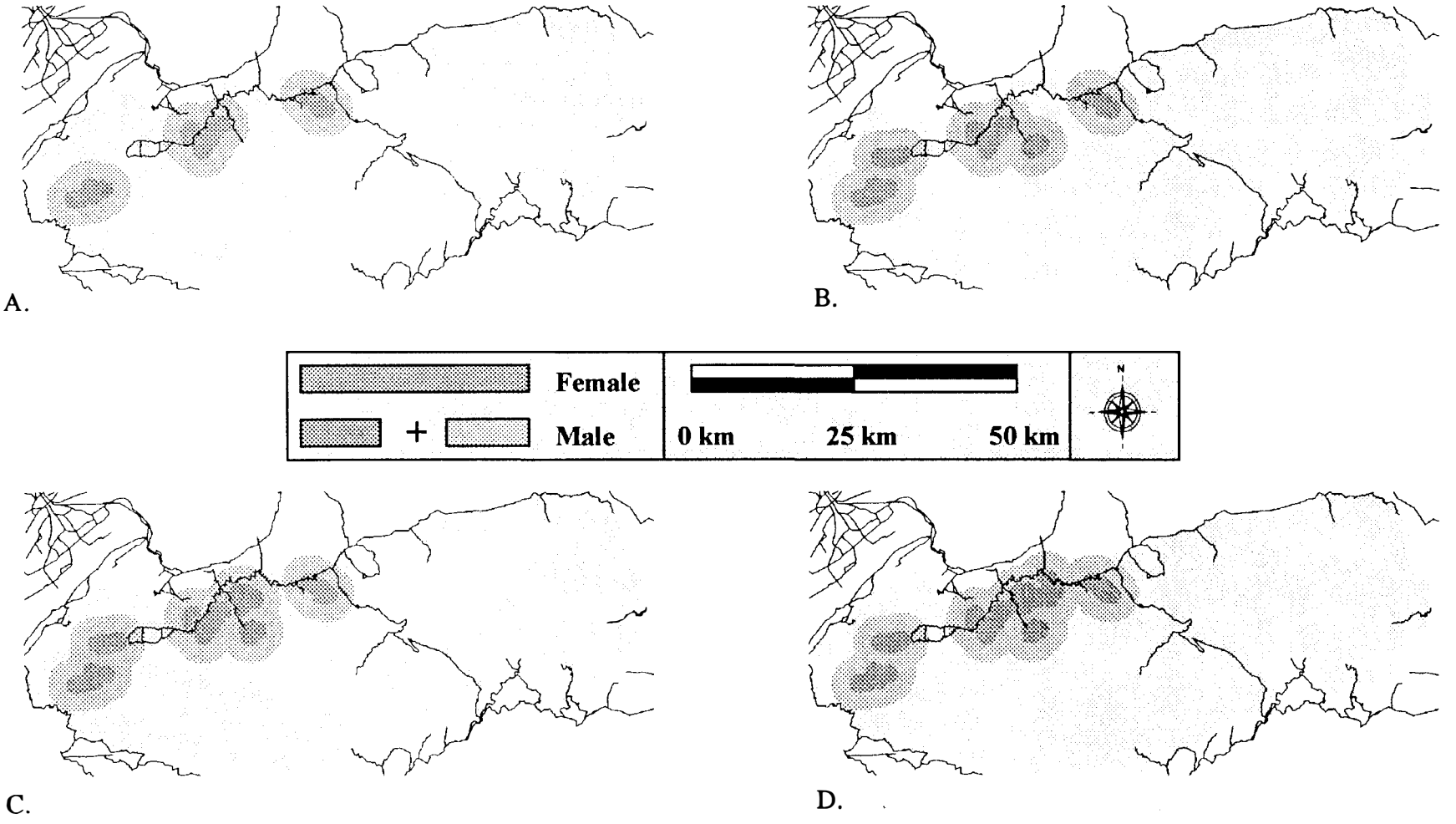
C.4 Effective sampling areas for 1986 (A), 1987 (B), 1988 (C), and 1989-1991 (D).

APPENDIX D

EFFECTIVE STUDY AREAS



D.1 Effective study areas for the sampling intervals 1972-1991 (A), 1973-1977 (B), 1977-1991 (C), and 1980-1983 (D).



D.2 Effective study areas for the sampling intervals 1984-1991 (A), 1987-1991 (B), 1988-1991 (C), and 1989-1991 (D).

APPENDIX E

JOLLY POPULATION PARAMETERS

Table E.1. Female population parameters in GSMNP derived from program JOLLY, models A and 2, for the time interval 1972-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[c]	SD	95% CI
1973	27.6	18.5	-8.7 - 63.8	2.9	1.5	0.1 - 5.7	7.7	19.2	-29.9 - 45.2	0.59	0.15	0.30 - 0.88	0.00	----	----------
										0.00	---	----------			
1974	24.7	7.0	10.9 - 38.4	12.3	2.5	7.4 - 17.3	48.9	30.8	-11 - 109	0.45	0.23	0.01 - 0.90	0.63	0.17	0.29 - 0.96
										0.87	0.27	0.33 - 1.40			
1975	71.4	34.2	4.3 - 138.5	18.8	5.8	7.4 - 30.2	10.4	28.2	-44.9 - 65.7	0.50	0.21	0.08 - 0.92	0.30	0.14	0.02 - 0.58
										1.05	0.39	0.29 - 1.81			
1976	67.5	26.9	14.7 - 120.3	27.0	8.4	10.6 - 43.4	17.4	16.0	-14.0 - 48.7	0.45	0.27	-0.09 - 0.99	0.33	0.14	0.07 - 0.60
										1.03	0.49	0.07 - 1.99			
1977	56.2	18.6	19.8 - 92.5	23.4	6.0	11.6 - 35.2	23.1	14.8	-5.8 - 52.1	0.60	0.23	0.15 - 1.05	0.33	0.16	0.03 - 0.64
										0.47	0.24	-0.01 - 0.95			
1978	52.3	16.2	20.5 - 84.1	19.9	3.8	12.5 - 27.3	8.1	15.4	-22.1 - 38.3	0.78	0.22	0.35 - 1.20	0.33	0.14	0.07 - 0.60
										0.72	0.27	0.20 - 1.24			
1979	49.7	15.1	20.1 - 79.3	26.5	5.1	16.5 - 36.5	5.9	10.5	-14.7 - 26.4	0.69	0.24	0.22 - 1.15	0.28	0.11	0.07 - 0.48
										0.86	0.22	0.42 - 1.30			
1980	45.6	9.5	27.0 - 64.1	27.3	3.9	19.8 - 34.9	11.3	9.3	-6.9 - 29.5	1.18	0.61	-0.01 - 2.38	0.53	0.12	0.29 - 0.77
										1.52	0.69	0.17 - 2.87			
1981	52.7	15.1	23.1 - 82.2	34.2	8.1	18.3 - 50.2	6.6	9.7	-12.5 - 25.6	1.49	0.80	-0.08 - 3.05	0.23	0.12	0.00 - 0.46
										0.52	0.36	-0.19 - 1.23			
1982	36.8	13.4	10.5 - 63.0	24.5	6.3	12.1 - 36.9	39.2	23.8	-7.5 - 85.9	1.30	0.21	0.89 - 1.70	0.13	0.09	-0.04 - 0.31
										0.52	0.30	-0.06 - 1.10			
1983	85.1	32.6	21.3 - 148.9	36.0	11.7	13.1 - 58.9	48.6	45.1	-40 - 137	0.24	0.31	-0.36 - 0.85	0.43	0.13	0.17 - 0.69
										2.20	1.90	-1.52 - 5.92			
1984	110.5	62.4	-12 - 233	39.0	17.9	4.0 - 74.0	10.7	34.7	-57.4 - 78.8	0.61	0.43	-0.22 - 1.45	0.09	0.09	-0.08 - 0.26
										0.45	0.46	-0.45 - 1.35			
1985	86.6	51.0	-13 - 187	38.5	20.5	-1.6 - 78.6	52.4	54.8	-55 - 160	0.18	0.21	-0.22 - 0.58	0.22	0.14	-0.05 - 0.49
										0.51	0.45	-0.36 - 1.39			
1986	84.8	61.6	-36 - 206	21.2	9.6	2.4 - 40.0	48.9	62.6	-74 - 172	1.11	1.03	-0.91 - 3.14	0.11	0.10	-0.09 - 0.32
										1.67	1.78	-1.82 - 5.16			
1987	120.3	61.8	-0.9 - 241.4	27.8	10.6	7.0 - 48.5	-10.5	28.2	-65.7 - 44.7	0.69	0.41	-0.12 - 1.49	0.13	0.12	-0.10 - 0.35
										0.46	0.47	-0.46 - 1.37			
1988	52.0	22.3	8.3 - 95.7	26.0	9.4	7.5 - 44.5	112.2	81.8	-48 - 273	0.82	0.71	-0.58 - 2.22	0.25	0.15	-0.05 - 0.55
										0.61	0.59	-0.54 - 1.76			

Table E.1. Continued.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1989	146.0	87.7	-26 - 318	24.3	8.8	7 - 42	-60.8	109.6	-258 - 154				0.11	0.10	-0.09 - 0.32
1990	123.3	87.6	-49 - 295	58.0	38.7	-18 - 134							0.00	----	----------
Mean	71.8	10.6	51.1 - 92.5	27.1	3.1	21.1 - 33.1	22.3	4.9	12.8 - 31.9	0.73 0.84	---- ----	---------- ----------	0.25	----	----------

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals. Values in the second line are for previously-captured animals (Model 2).

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.2. Male population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1972-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1973	56.0	18.5	-8.7 - 63.8	1.9	1.5	0.1 - 5.7	7.7	19.1	-19.9 - 45.1	0.59	0.15	0.30 - 0.88	0.00	----	----------
1974	40.0	7.0	10.9 - 38.4	11.3	1.5	7.4 - 17.3	48.9	30.8	-11 - 109	0.45	0.13	0.01 - 0.90	0.63	0.17	0.19 - 0.96
1975	40.4	34.1	4.3 - 138.5	18.8	5.8	7.4 - 30.1	10.4	18.1	-44.9 - 65.7	0.50	0.11	0.08 - 0.91	0.30	0.14	0.01 - 0.58
1976	74.0	16.9	14.7 - 110.3	17.0	8.4	10.6 - 43.4	17.4	16.0	-14.0 - 48.7	0.45	0.17	-0.09 - 0.99	0.33	0.14	0.07 - 0.60
1977	59.5	18.6	19.8 - 91.5	13.4	6.0	11.6 - 35.1	13.1	14.8	-5.8 - 51.1	0.60	0.13	0.15 - 1.05	0.33	0.16	0.03 - 0.64
1978	151.6	16.1	10.5 - 84.1	19.9	3.8	11.5 - 17.3	8.1	15.4	-11.1 - 38.3	0.78	0.11	0.35 - 1.20	0.33	0.14	0.07 - 0.60
1979	52.7	15.1	20.1 - 79.3	16.5	5.1	16.5 - 36.5	5.9	10.5	-14.7 - 16.4	0.69	0.14	0.11 - 1.15	0.18	0.11	0.07 - 0.48
1980	64.8	9.5	27.0 - 64.1	17.3	3.9	19.8 - 34.9	11.3	9.3	-6.9 - 19.5	1.18	0.61	-0.01 - 1.38	0.53	0.11	0.19 - 0.77
1981	69.0	15.1	23.1 - 81.1	34.1	8.1	18.3 - 50.1	6.6	9.7	-11.5 - 15.6	1.49	0.80	-0.08 - 3.05	0.13	0.12	0.00 - 0.46
1981	34.5	13.4	10.5 - 63.0	14.5	6.3	11.1 - 36.9	39.1	13.8	-7.5 - 85.9	1.30	0.11	0.89 - 1.70	0.13	0.09	-0.04 - 0.31
1983	110.1	31.6	11.3 - 148.9	36.0	11.7	13.1 - 58.9	48.6	45.1	-40 - 137	0.24	0.31	-0.36 - 0.85	0.43	0.13	0.17 - 0.69
1984	68.0	62.4	-12 - 233	39.0	17.9	4.0 - 74.0	10.7	34.7	-57.4 - 78.8	0.61	0.43	-0.21 - 1.45	0.09	0.09	-0.08 - 0.16
1985	73.0	51.0	-13 - 187	38.5	10.5	-1.6 - 78.6	51.4	54.8	-55 - 160	0.18	0.11	-0.11 - 0.58	0.12	0.14	-0.05 - 0.49
1986	86.0	61.6	-36 - 106	11.2	9.6	2.4 - 40.0	48.9	61.6	-74 - 172	1.11	1.03	-0.91 - 3.14	0.11	0.10	-0.09 - 0.31
1987	159.6	61.8	-0.9 - 241.4	27.8	10.6	7.0 - 48.5	-10.5	18.1	-65.7 - 44.7	0.69	0.41	-0.11 - 1.49	0.13	0.11	-0.10 - 0.35
1988	101.7	22.3	8.3 - 95.7	16.0	9.4	7.5 - 44.5	112.1	81.8	-48 - 173	0.81	0.71	-0.58 - 2.21	0.25	0.15	-0.05 - 0.55
1989	224.1	87.7	-16 - 318	14.3	8.8	7 - 41	-60.8	109.6	-158 - 154				0.11	0.10	-0.09 - 0.32
1990	256.3	87.6	-49 - 195	58.0	38.7	-18 - 134							0.00	----	----------
Mean	101.3	21.3	59.2 - 143.3	27.5	5.5	16.8 - 38.2	44.4	9.7	25.5 - 63.4	0.71	0.09	0.53 - 0.89	0.26	0.03	0.02 - 0.15

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.3. Population parameters in GSMNP, for data with both sexes combined, derived from program JOLLY, models A and 2, for the time interval 1972-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1973	100.1	18.5	-8.7 - 73.8	1.9	1.5	0.1 - 5.7	7.7	19.2	-19.9 - 45.1	0.59	0.15	0.30 - 0.88	0.00	----	----------
										0.00	----	----------			
1974	66.6	7.0	10.9 - 38.4	11.3	1.5	7.4 - 17.3	48.9	30.8	-11 - 109	0.45	0.13	0.01 - 0.90	0.63	0.17	0.19 - 0.97
										0.87	0.17	0.33 - 1.40			
1975	118.4	34.1	4.3 - 138.5	18.8	5.8	7.4 - 30.1	10.4	18.1	-44.9 - 75.7	0.50	0.11	0.08 - 0.91	0.30	0.14	0.01 - 0.58
										1.05	0.39	0.19 - 1.81			
1976	161.1	27.9	14.7 - 110.3	17.0	8.4	10.6 - 43.4	17.4	17.0	-14.0 - 48.7	0.45	0.17	-0.09 - 0.99	0.33	0.14	0.07 - 0.70
										1.03	0.49	0.07 - 1.99			
1977	127.5	18.7	19.8 - 91.5	13.4	7.0	11.7 - 35.1	13.1	14.8	-5.8 - 51.1	0.60	0.13	0.15 - 1.05	0.33	0.17	0.03 - 0.64
										0.47	0.14	-0.01 - 0.95			
1978	174.5	17.1	10.5 - 84.1	19.9	3.8	11.5 - 17.3	8.1	15.4	-11.1 - 38.3	0.78	0.11	0.35 - 1.10	0.33	0.14	0.07 - 0.60
										0.71	0.17	0.10 - 1.14			
1979	123.6	15.1	10.1 - 79.3	16.5	5.1	17.5 - 37.5	5.9	10.5	-14.7 - 16.4	0.69	0.14	0.11 - 1.15	0.18	0.11	0.07 - 0.48
										0.86	0.11	0.41 - 1.30			
1980	109.3	9.5	27.0 - 64.1	27.3	3.9	19.8 - 34.9	11.3	9.3	-7.9 - 19.5	1.18	0.61	-0.01 - 1.38	0.53	0.12	0.19 - 0.77
										1.51	0.69	0.17 - 2.87			
1981	132.7	15.1	13.1 - 81.1	34.1	8.1	18.3 - 50.1	7.7	9.7	-12.5 - 15.6	1.49	0.80	-0.08 - 3.05	0.13	0.12	0.00 - 0.47
										0.52	0.36	-0.19 - 1.23			
1982	76.8	13.4	10.5 - 63.0	14.5	7.3	11.1 - 37.9	39.2	13.8	-7.5 - 85.9	1.30	0.21	0.89 - 1.70	0.13	0.09	-0.04 - 0.31
										0.51	0.30	-0.06 - 1.10			
1983	254.0	32.6	11.3 - 148.9	37.0	11.7	13.1 - 58.9	48.6	45.1	-40 - 137	0.24	0.31	-0.37 - 0.85	0.43	0.13	0.17 - 0.69
										1.10	1.90	-1.51 - 5.92			
1984	198.9	62.4	-11 - 133	39.0	17.9	4.0 - 74.0	10.7	34.7	-57.4 - 78.8	0.71	0.43	-0.22 - 1.45	0.09	0.09	-0.08 - 0.16
										0.45	0.46	-0.45 - 1.35			
1985	171.0	51.0	-13 - 187	38.5	20.5	-1.7 - 78.6	51.4	54.8	-55 - 160	0.18	0.11	-0.22 - 0.58	0.11	0.14	-0.05 - 0.49
										0.51	0.45	-0.37 - 1.39			
1986	204.8	61.7	-36 - 206	21.1	9.7	2.4 - 40.0	48.9	72.6	-74 - 172	1.11	1.03	-0.91 - 3.14	0.11	0.10	-0.09 - 0.32
										1.77	1.78	-1.81 - 5.16			
1987	303.6	61.8	-0.9 - 141.4	17.8	10.7	7.0 - 48.5	-10.5	18.1	-65.7 - 44.7	0.69	0.41	-0.12 - 1.49	0.13	0.12	-0.10 - 0.35
										0.47	0.47	-0.46 - 1.37			
1988	157.5	21.3	8.3 - 95.7	17.0	9.4	7.5 - 44.5	112.1	81.8	-48 - 173	0.81	0.71	-0.58 - 1.21	0.25	0.15	-0.05 - 0.55
										0.61	0.59	-0.54 - 1.76			

Table E.3. Continued.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[c]	SD	95% CI
1989	415.4	87.7	-27 - 318	14.3	8.8	7 - 41	-70.8	109.6	-258 - 154				0.11	0.10	-0.09 - 0.31
1990	458.5	87.6	-49 - 195	58.0	38.7	-18 - 134							0.00	----	----------
Mean	186.4	22.7	141.8 - 230.9	57.9	6.3	45.5 - 70.3	62.8	8.3	46.5 - 79.0	0.75 0.90	0.05 0.25	0.65 - 0.84 0.42 - 1.38	0.25	0.02	0.04 - 0.13

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals. Values in the second line are for previously-captured animals (Model 2).

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.4. Female population parameters in GSMNP derived from program JOLLY, models D and 2, for the time interval 1973-1977.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1974	28.6	8.7	11.6 - 45.6	9.0	2.1	4.9 - 13.1	15.5	8.5	-1.3 - 32.2	0.77	0.10	0.57 - 0.98	0.36	0.09	0.17 - 0.54
										0.33	0.21	-0.07 - 0.74	0.83	0.15	0.53 - 1.13
1975	38.1	11.1	16.3 - 59.9	12.8	3.1	6.9 - 18.8	12.7	8.8	-4.6 - 29.9	0.77	0.10	0.57 - 0.98	0.36	0.09	0.17 - 0.54
										1.00	0.91	-0.78 - 2.78	0.43	0.19	0.06 - 0.80
1976	44.0	12.6	19.2 - 68.7	18.7	5.0	8.9 - 28.6	-1.4	8.0	-17.0 - 14.3	0.77	0.10	0.57 - 0.98	0.36	0.09	0.17 - 0.54
													0.20	0.18	-0.15 - 0.55
1977	28.0	10.0	8.4 - 47.7	16.8	6.9	3.4 - 30.3				0.77	0.10	0.57 - 0.98	0.36	0.09	0.17 - 0.54
Mean	34.7	17.5	0.4 - 69.0	14.3	6.8	1.0 - 27.7	8.9	4.7	-0.3 - 18.1	0.77	0.10	0.57 - 0.98	0.36	0.09	0.17 - 0.54
										0.67	0.31	-0.00 - 1.23			

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals. Values in the second line are for previously-captured animals (Model 2).

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.5. Male population parameters in GSMNP derived from program JOLLY, model A, for the sampling interval 1973-1977.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1973										0.53	0.30	-0.05 - 1.11			
1974	25.5	13.4	-0.7 - 51.7	4.3	1.9	0.5 - 8.0	27.4	20.2	-12.2 - 67.0	0.70	0.30	0.12 - 1.28	0.47	0.31	-0.14 - 1.09
1975	45.2	21.2	3.7 - 86.8	13.6	5.2	3.4 - 23.8	19.2	19.7	-19.4 - 57.8	0.68	0.40	-0.11 - 1.48	0.37	0.19	0.002 - 0.74
1976	50.1	29.9	-8.5 - 108.8	19.5	10.6	-1.3 - 40.3							0.31	0.19	-0.06 - 0.68
Mean	40.3	13.1	14.6 - 66.0	12.4	4.0	4.6 - 20.3	23.3	21.4	-18.6 - 65.2	0.64	0.16	0.32 - 0.96	0.38	0.21	-0.09 - 0.71

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.6. Female population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1977-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1978	26.1	16.2	20.5 - 84.1	14.9	3.8	12.5 - 27.3	6.1	15.4	-22.1 - 38.3	0.68	0.22	0.35 - 1.20	0.23	0.14	0.17 - 0.63
1979	45.3	15.1	20.1 - 79.3	23.5	5.1	16.5 - 36.5	3.9	10.5	-14.7 - 26.4	0.79	0.24	0.22 - 1.15	0.38	0.11	0.07 - 0.38
1980	28.4	9.5	27.0 - 64.1	22.3	3.9	19.8 - 34.9	13.3	9.3	-6.9 - 29.5	1.08	0.61	-0.01 - 2.38	0.53	0.12	0.29 - 0.57
1981	36.5	15.1	23.1 - 82.2	33.2	8.1	18.3 - 50.2	5.6	9.7	-12.5 - 25.6	1.29	0.80	-0.08 - 3.05	0.33	0.12	0.01 - 0.26
1982	25.0	13.4	10.5 - 63.0	22.5	6.3	12.1 - 36.9	36.2	23.8	-7.5 - 85.9	1.20	0.21	0.89 - 1.70	0.13	0.09	-0.02 - 0.31
1983	44.3	32.6	25.3 - 128.9	35.0	11.7	13.1 - 58.9	43.6	45.1	-40 - 137	0.44	0.31	-0.36 - 0.85	0.53	0.13	0.17 - 0.49
1984	37.1	62.4	-11 - 212	33.0	17.9	4.0 - 74.0	16.7	34.7	-57.4 - 78.8	0.31	0.43	-0.22 - 1.45	0.39	0.09	-0.01 - 0.36
1985	63.0	51.0	-15 - 287	32.5	20.5	-1.6 - 78.6	56.4	54.8	-55 - 160	0.48	0.21	-0.22 - 0.58	0.22	0.14	-0.15 - 0.59
1986	63.8	61.6	-36 - 216	22.2	9.6	2.4 - 40.0	43.9	62.6	-74 - 172	1.31	1.03	-0.91 - 3.14	0.11	0.10	-0.19 - 0.42
1987	94.3	61.8	-1.9 - 141.4	22.8	10.6	7.0 - 48.5	-13.5	28.2	-65.7 - 44.7	0.29	0.41	-0.12 - 1.49	0.33	0.12	-0.10 - 0.35
1988	41.3	22.3	18.3 - 95.7	21.0	9.4	7.5 - 44.5	112.2	81.8	-48 - 273	0.42	0.71	-0.58 - 2.22	0.15	0.15	-0.15 - 0.55
1989	52.0	87.7	-26 - 328	27.3	8.8	7 - 42	-60.8	109.6	-258 - 154				0.21	0.10	-0.09 - 0.32
Mean	45.2	8.3	28.3 - 62.0	18.7	2.6	13.7 - 23.8	15.0	3.4	8.2 - 21.7	0.71	0.07	0.57 - 0.85	0.30	0.04	0.10 - 0.27

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.7. Male population parameters in GSMNP derived from program JOLLY, model D, for the time interval 1977-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1978	73.9	19.8	35.1 - 112.6	19.9	3.8	12.5 - 27.3	55.0	15.4	-22.1 - 38.3						
1979	109.3	25.4	59.5 - 159.1	26.5	5.1	16.5 - 36.5	26.1	10.5	-14.7 - 26.4						
1980	96.4	22.8	51.6 - 141.1	27.3	3.9	19.8 - 34.9	54.8	9.3	-6.9 - 29.5						
1981	119.4	27.0	66.4 - 172.3	34.2	8.1	18.3 - 50.2	-43.3	9.7	-12.5 - 25.6						
1982	29.6	7.8	14.3 - 44.9	24.5	6.3	12.1 - 36.9	89.8	23.8	-7.5 - 85.9						
1983	112.1	26.8	59.6 - 164.6	36.0	11.7	13.1 - 58.9	-17.7	45.1	-40 - 137						
1984	52.9	14.5	24.6 - 81.3	39.0	17.9	4.0 - 74.0	40.3	34.7	-57.4 - 78.8						
1985	73.8	19.7	35.3 - 112.3	38.5	20.5	-1.6 - 78.6	32.0	54.8	-55 - 160						
1986	81.6	20.8	-40.8 - 122.4	21.2	9.6	2.4 - 40.0	-1.5	62.6	-74 - 172						
1987	58.8	15.0	29.4 - 88.3	27.8	10.6	7.0 - 48.5	40.3	28.2	-65.7 - 44.7						
1988	75.0	20.0	35.9 - 114.2	26.0	9.4	7.5 - 44.5	47.4	81.8	-48 - 273						
1989	91.3	23.7	44.8 - 137.8	24.3	8.8	7 - 42	0.7	109.6	-258 - 154						
1990	51.2	16.2	19.4 - 83.0	58.0	38.7	-18 - 134	29.8								
1991	56.5	18.1	21.1 - 91.9	26.0	9.4	7.5 - 44.5									
Mean	77.3	46.7	-14.2 - 168.7	18.9	10.1	-0.76 - 38.6	27.2	12.1	3.5 - 51.0	0.65	0.04	0.57 - 0.73	0.19	0.03	0.13 - 0.26

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.8. Female population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1980-1983.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1980										0.70	0.24	0.24 - 1.17			
1981	42.1	16.5	9.7 - 74.4	15.5	4.8	6.1 - 24.9	0.2	9.8	-18.9 - 19.4	0.65	0.31	0.05 - 1.26	0.39	0.17	0.06 - 0.72
1982	27.8	13.5	1.3 - 54.2	18.5	7.8	3.3 - 33.7							0.27	0.15	-0.02 - 0.56
Mean	34.9	10.8	13.8 - 56.1	17.0	4.6	8.1 - 25.9	0.2			0.68	0.16	0.36 - 1.00	0.33	0.23	-0.17 - 0.71

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.9. Male population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1980-1983.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1980										0.37	0.20	-0.03 - 0.77			
1981	40.4	20.5	0.3 - 80.6	9.3	4.5	0.5 - 18.2	5.9	10.7	-15.0 - 26.8	0.43	0.40	-0.35 - 1.22	0.54	0.29	-0.03 - 1.10
1982	23.4	21.5	-18.8 - 65.6	13.0	11.6	-9.7 - 35.7							0.31	0.27	-0.22 - 0.84
Mean	31.9	14.9	2.7 - 61.2	11.2	6.2	-1.0 - 23.3	5.9			0.40	0.21	-0.01 - 0.82	0.42	0.40	-0.47 - 1.09

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.10. Female population parameters in GSMNP derived from program JOLLY, model A', for the time interval 1984-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1984	139.8	52.2	38 - 242							1.19	0.73	-0.24 - 2.63			
1985	188.0	91.9	8 - 368	9.0	6.0	-2.7 - 20.7	13.0	16.8	-20 - 46	0.39	0.22	-0.05 - 0.83	0.06	0.03	-0.01 - 0.12
1986	88.8	27.1	-36 - 142	7.5	2.9	1.8 - 13.2	43.3	44.4	-44 - 130	1.26	0.63	0.03 - 2.48	0.11	0.10	0.02 - 0.19
1987	120.6	48.5	26 - 216	19.0	9.5	0.3 - 37.7	1.6	24.2	-46 - 49	0.70	0.43	-0.15 - 1.55	0.13	0.12	0.01 - 0.21
1988	97.0	46.0	7 - 187	19.0	9.8	-0.3 - 38.3	51.3	47.8	-42 - 145	0.40	0.23	-0.05 - 0.84	0.25	0.15	-0.01 - 0.23
1989	46.5	15.0	17 - 76	14.5	6.5	1.7 - 27.3	-17.4	39.4	-95 - 60	0.75	0.47	-0.17 - 1.68	0.11	0.10	0.07 - 0.48
1990	38.0	21.3	-4 - 80	22.0	13.3	-4.0 - 48.0							0.17	0.11	-0.04 - 0.38
Mean	102.7	18.7	66 - 139	15.2	3.5	8.2 - 22.1	18.4	9.0	0.8 - 35.9	0.78	0.13	0.53 - 1.03	0.14	0.03	0.08 - 0.20

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.11. Male population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1984-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1984										0.52	0.40	-0.27 - 1.30			
1985	96.3			5.7	4.1	-2.4 - 13.7	-0.6			0.57	0.27	0.03 - 1.10	0.00		
1986	54.0	30.9	-8 - 116	12.7	5.1	2.7 - 22.7	15.0	53.9	-90.6 - 120.5	1.50	1.49	-1.42 - 4.42	0.24	0.15	-0.06 - 0.53
1987	96.0	99.7	-99 - 291	40.0	39.2	-36.9 - 116.9	34.8	27.0	-18.0 - 87.7	0.19	0.19	-0.19 - 0.57	0.10	0.10	-0.10 - 0.30
1988	53.3	32.5	-11 - 117	14.8	7.6	-0.1 - 29.7	33.9	36.3	-37.3 - 105.0	0.52	0.45	-0.37 - 1.40	0.27	0.17	-0.07 - 0.61
1989	61.3	50.9	-38 - 161	15.3	12.5	-9.2 - 39.9	34.8			0.35			0.39	0.30	-0.20 - 0.99
1990	56.0			14.0									0.14		
Mean	69.5			17.1			23.6			0.61			0.19		

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.12. Female population parameters in GSMNP derived from program JOLLY, model A', for the time interval 1987-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[c]	SD	95% CI
1987	161.5	47.4	68.6 - 254.4							0.91	0.52	-0.11 - 1.93			
1988	159.0	78.2	5.8 - 312.2	16.0	9.3	-2.2 - 34.2	100.4	113.4	-121.9 - 322.8	0.33	0.18	-0.03 - 0.68	0.08	0.04	-0.01 - 0.16
1989	63.4	15.6	32.9 - 94.0	12.1	4.9	2.5 - 21.8	-73.0	166.2	-399 - 253	1.26	0.80	-0.31 - 2.84	0.29	0.09	0.12 - 0.45
1990	84.0	50.6	-15.2 - 183.2	41.0	27.1	-12.1 - 94.1							0.13	0.08	-0.04 - 0.29
Mean	117.0	26.5	65.0 - 169.0	23.0	9.7	4.0 - 42.0	13.7	90.2	-163 - 191	0.83	0.29	0.27 - 1.40	0.16	0.04	0.08 - 0.25

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.13. Male population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1987-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1987										0.11	0.07	-0.03 - 0.26			
1988	23.0			2.0	0.0	2.0 - 2.0	52.2	34.2	-14.7 - 119.1	0.63	0.38	-0.12 - 1.37	1.00		
1989	66.6	40.0	-12 - 145	14.4	8.5	-2.2 - 31.0	35.3	46.8	-56.4 - 126.9	0.31	0.38	-0.43 - 1.06	0.49	0.29	-0.09 - 1.06
1990	56.0	66.9	-75 - 187	14.0	16.6	-18.5 - 46.5							0.29	0.30	-0.31 - 0.88
Mean	48.5			10.1	6.2	-2.0 - 22.3	43.7	52.7	-59.6 - 147.0	0.35	0.17	0.02 - 0.68	0.59		

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.14. Female population parameters in GSMNP derived from program JOLLY, model A', for the time interval 1988-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1988	144.7	51.5	44 - 246							0.48	0.21	0.07 - 0.90			
1989	78.3	19.5	40 - 116	10.3	4.5	1.5 - 19.2	-47.5	142.2	-326 - 231	1.36	0.89	-0.38 - 3.11	0.24	0.07	0.10 - 0.39
1990	112.3	69.0	-23 - 248	40.0	27.3	-14 - 93							0.11	0.07	-0.03 - 0.24
Mean	111.8	29.6	54 - 170	25.2	13.8	-1.9 - 52.3	-47.5			0.92	0.43	0.07 - 1.77	0.17	0.05	0.07 - 0.27

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.15. Male population parameters in GSMNP derived from program JOLLY, model A, for the time interval 1988-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1988										0.77	0.47	-0.16 - 1.70			
1989	115.0	75.6	-33 - 263	23.0	14.1	-4.5 - 50.5	55.9	78.1	-97.2 - 208.9	0.43	0.51	-0.56 - 1.42	0.30	0.20	-0.08 - 0.69
1990	105.0	125.1	-140 - 350	25.0	28.6	-31.1 - 81.1							0.16	0.18	-0.18 - 0.50
Mean	110.0	73.1	-33 - 253	24.0	15.9	-7.2 - 55.2	55.9			0.60	0.31	-0.01 - 1.20	0.23	0.26	-0.36 - 0.68

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears >1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

Table E.16. Female population parameters in GSMNP derived from program JOLLY, model A', for the time interval 1989-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1989	99.0	24.9	50 - 148							1.18	0.78	-0.36 - 2.71			
1990	123.7	76.3	-26 - 273	26.7	19.6	-12 - 65							0.10	0.06	-0.03 - 0.22
Mean	111.3	40.1	33 - 190	27.1	3.1	21.1 - 33.1	22.3	4.9	12.8 - 31.9	1.18	0.78	-0.36 - 2.71	0.10	0.06	-0.03 - 0.22

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old.

[e]The probability that a marked bear alive in interval i is captured in i.

Table E.17. Male population parameters in GSMNP derived from program JOLLY, model A', for the time interval 1989-1991.

Year	N[a]	SD	95% CI	M[b]	SD	95% CI	B[c]	SD	95% CI	PHI[d]	SD	95% CI	p[e]	SD	95% CI
1989	349.6	113.5	127 - 572							1.04	1.05	-1.01 - 3.09			
1990	402.0	381.4	-346 - 1150	55.0	62.0	-67 - 177							0.03	0.03	-0.03 - 0.10
Mean	375.8	199.0	-14 - 766	55.0	62.0	-67 - 177				1.04	1.05	-1.01 - 3.09	0.03	0.03	-0.03 - 0.10

[a]Population estimate.

[b]The estimated number of marks in the population.

[c]The estimated number of animals added to the population since the previous year.

[d]Annual survival rate estimate for bears > 1 year old. Values in the first line of a given year are for newly-captured animals.

[e]The probability that a marked bear alive in interval i is captured in i (Model 2).

APPENDIX F

SEX AND AGE STRUCTURE

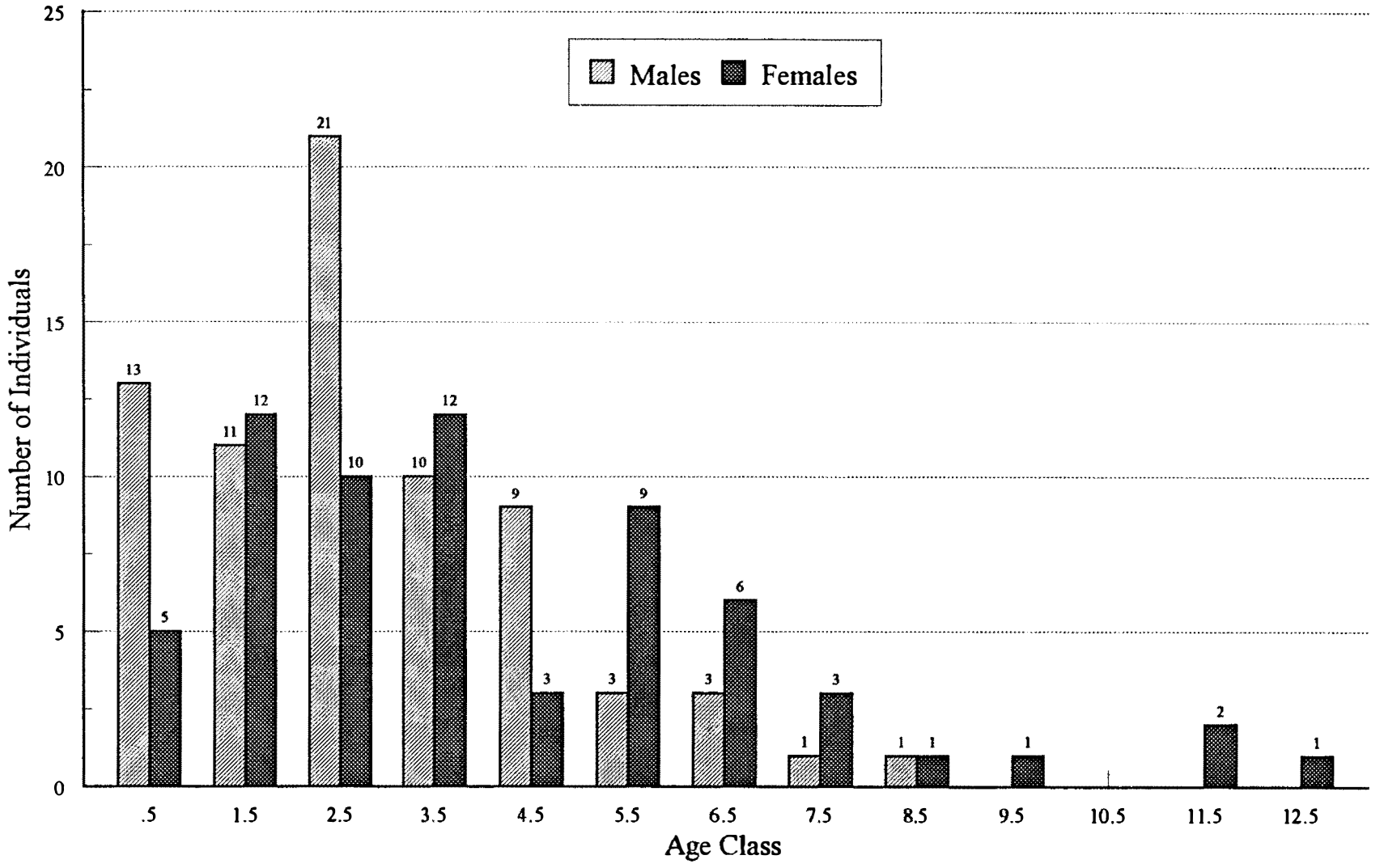


Figure F.1. Sex and age distribution of black bears known to be alive during the summer of 1972.

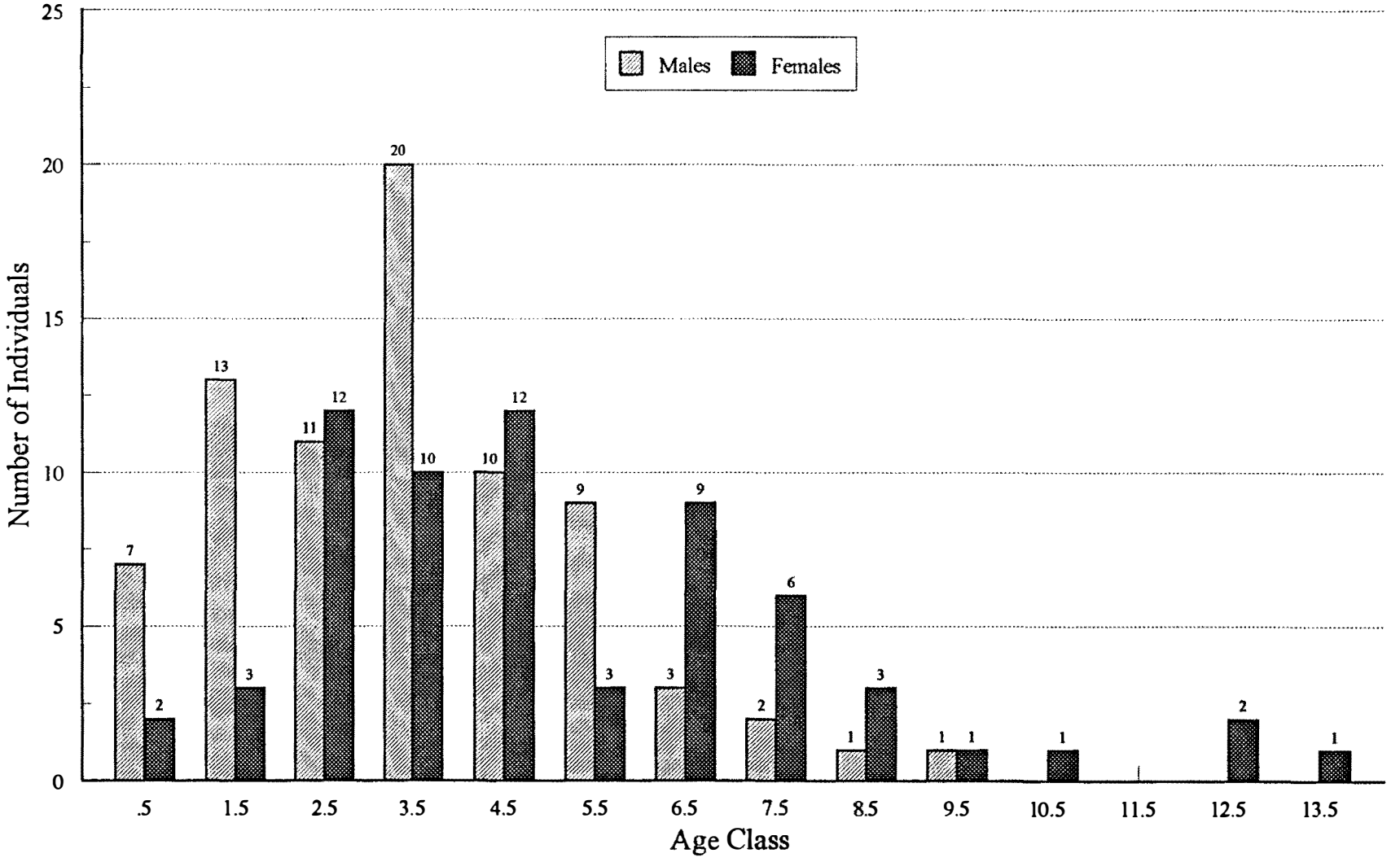


Figure F.2. Sex and age distribution of black bears known to be alive during the summer of 1973.

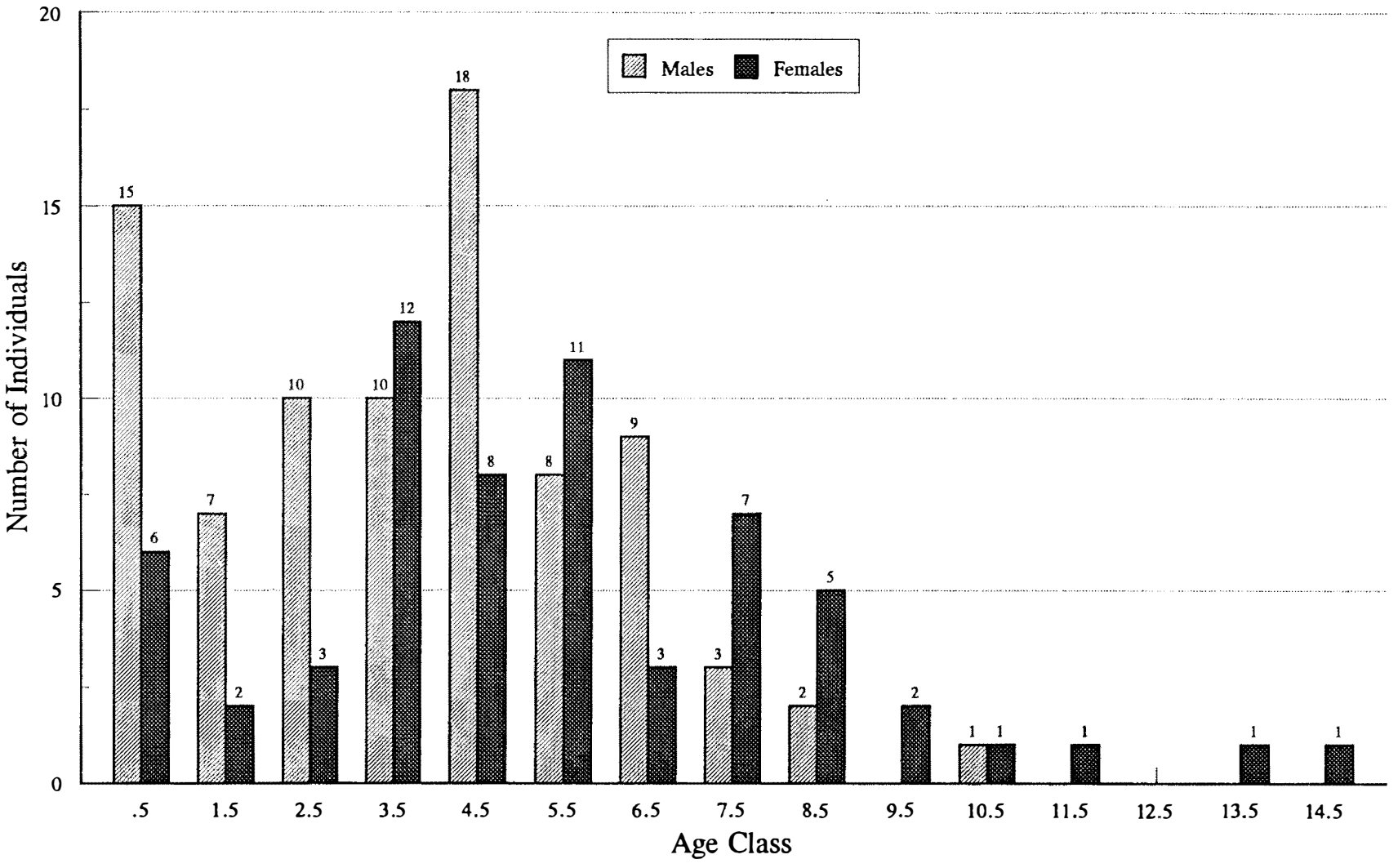


Figure F.3. Sex and age distribution of black bears known to be alive during the summer of 1974.

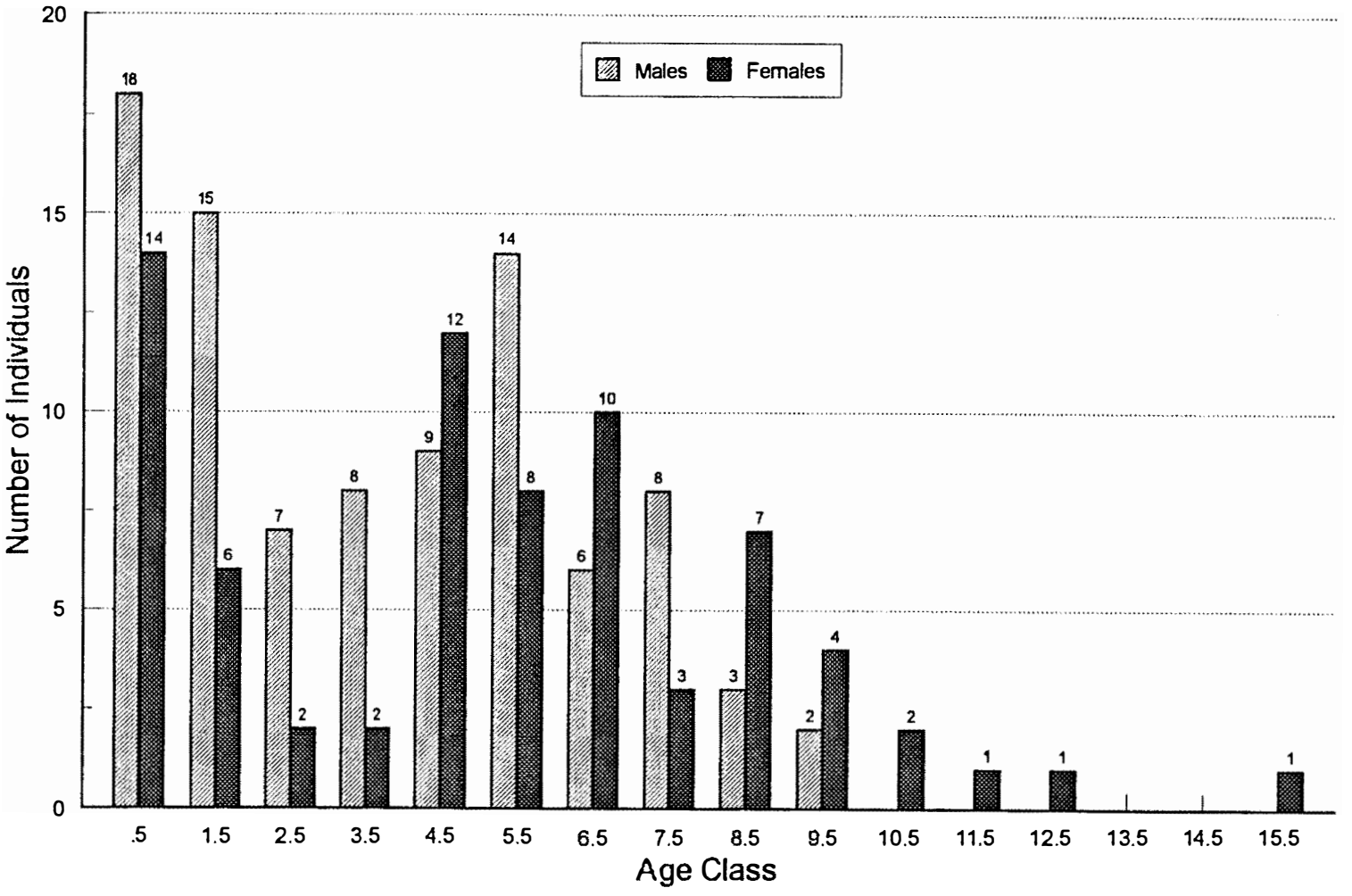


Figure F.4. Sex and age distribution of black bears known to be alive during the summer of 1975.

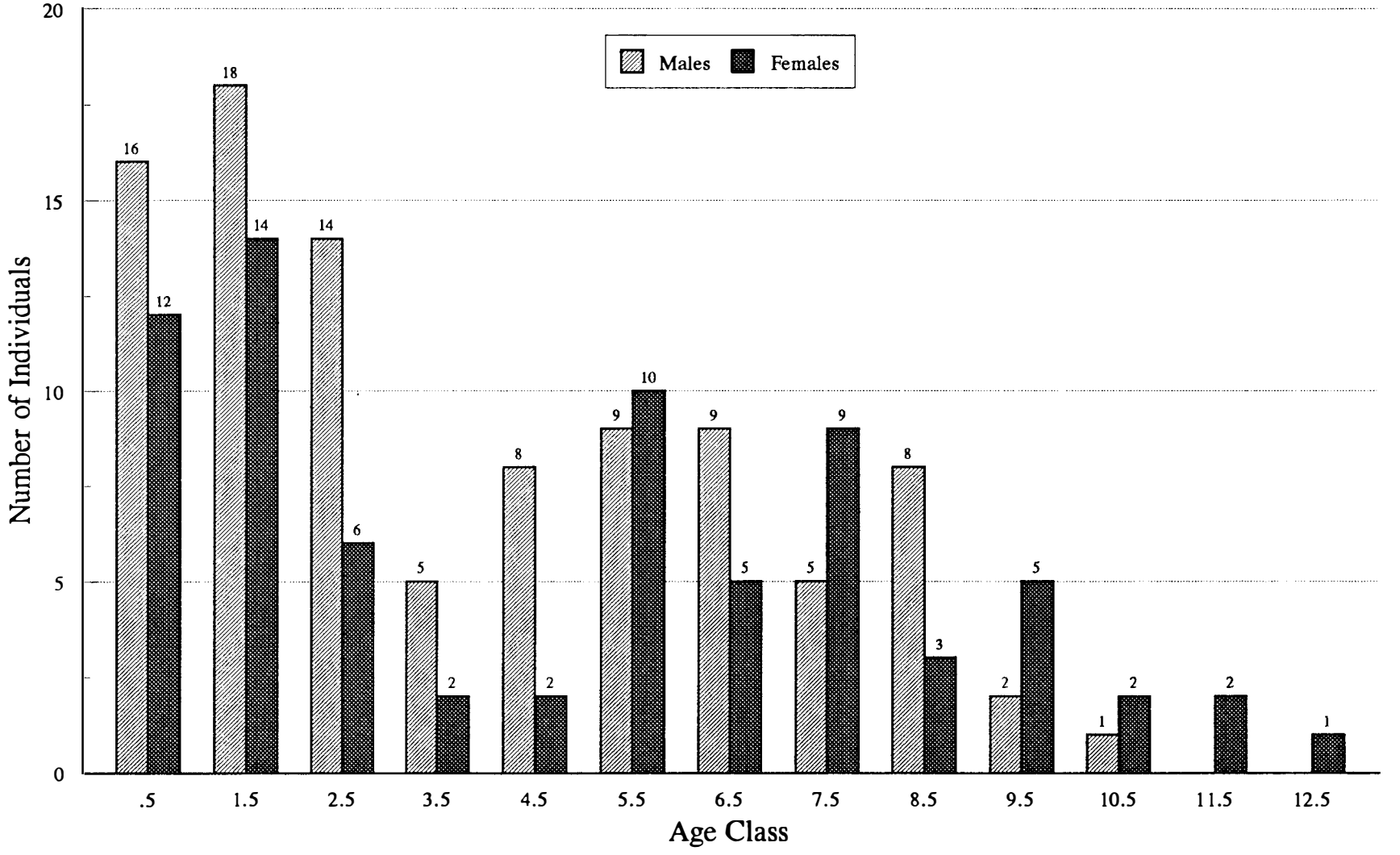


Figure F.5. Sex and age distribution of black bears known to be alive during the summer of 1976.

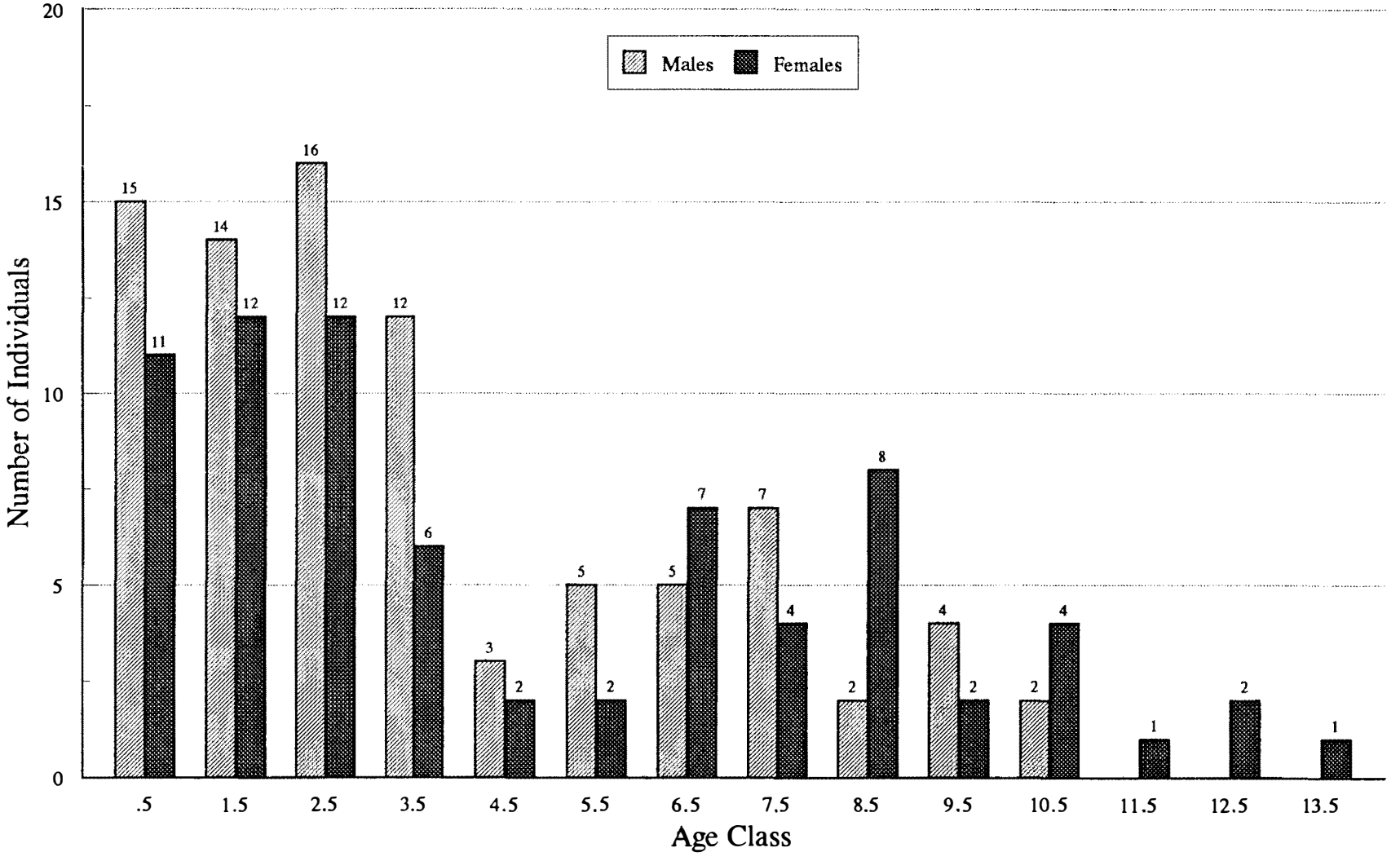


Figure F.6. Sex and age distribution of black bears known to be alive during the summer of 1977.

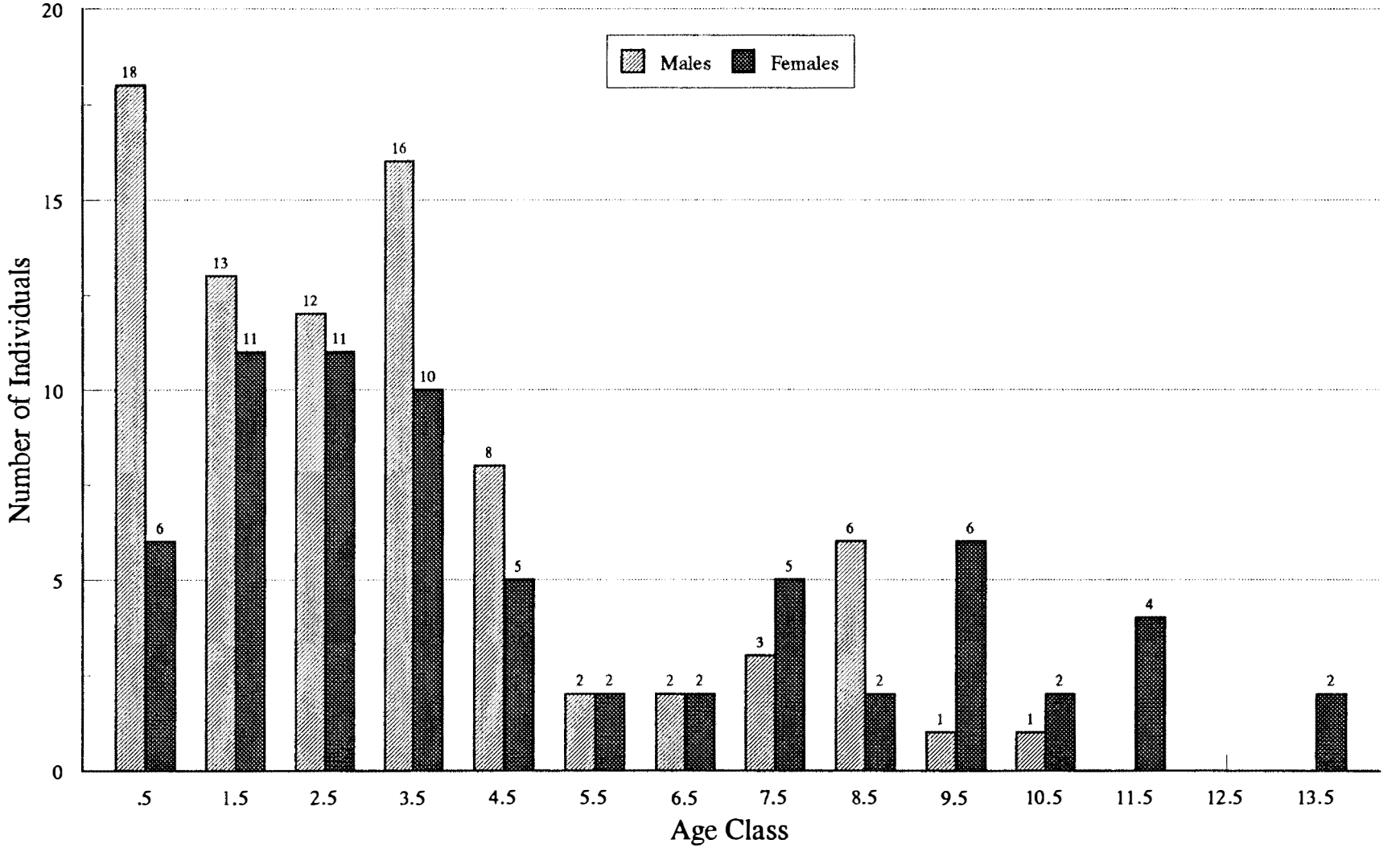


Figure F.7. Sex and age distribution of black bears known to be alive during the summer of 1978.

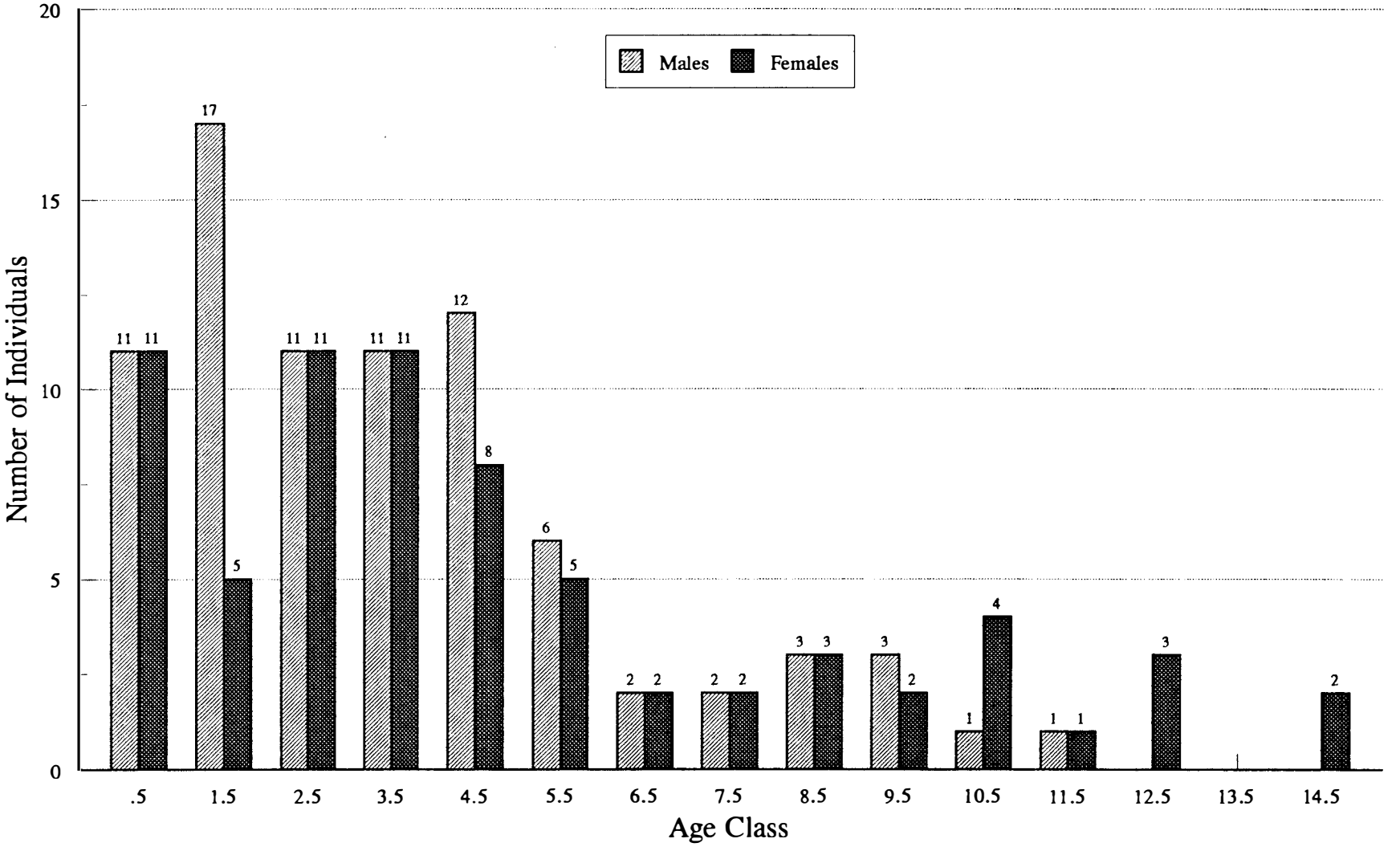


Figure F.8. Sex and age distribution of black bears known to be alive during the summer of 1979.

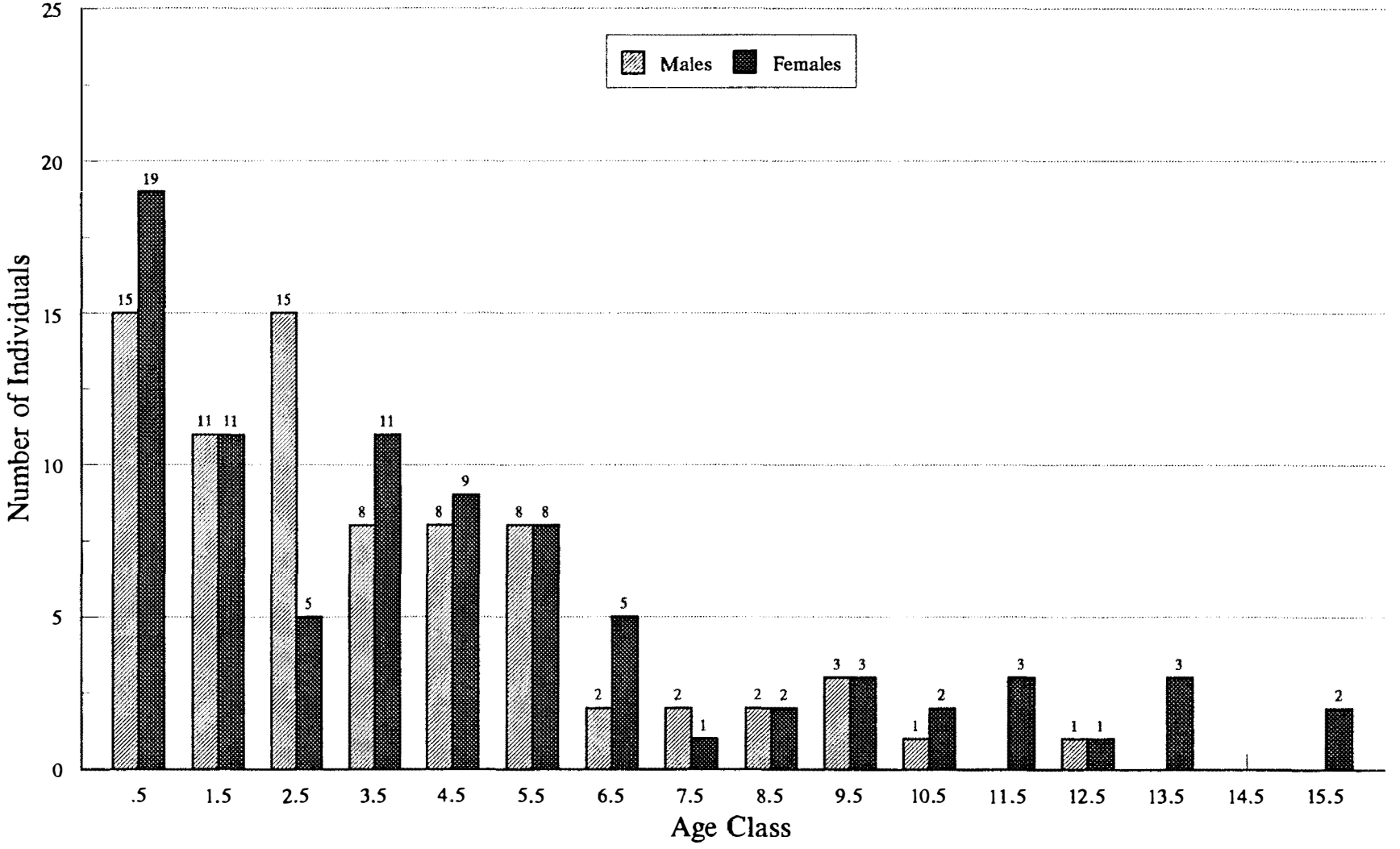


Figure F.9. Sex and age distribution of black bears known to be alive during the summer of 1980.

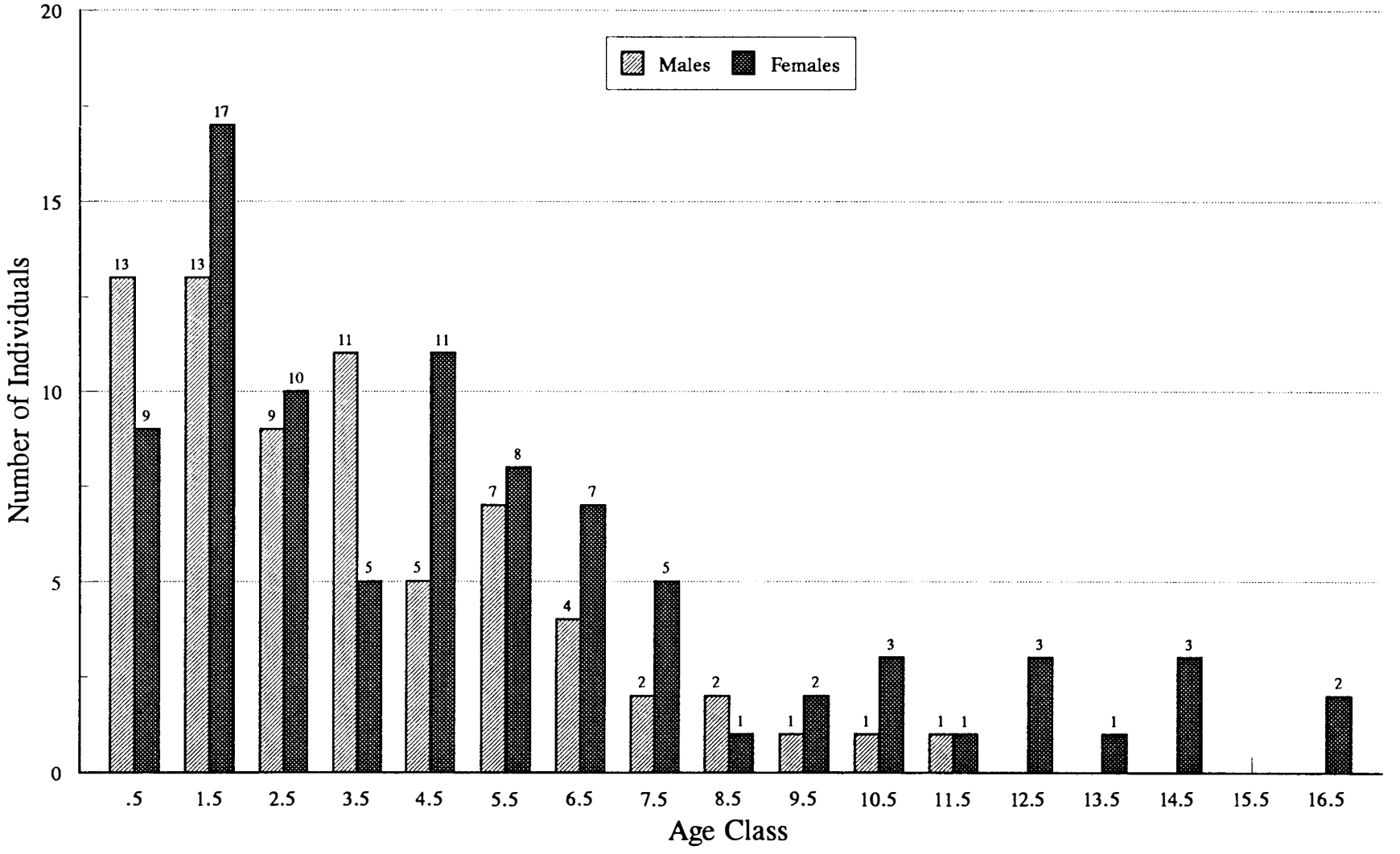


Figure F.10. Sex and age distribution of black bears known to be alive during the summer of 1981.

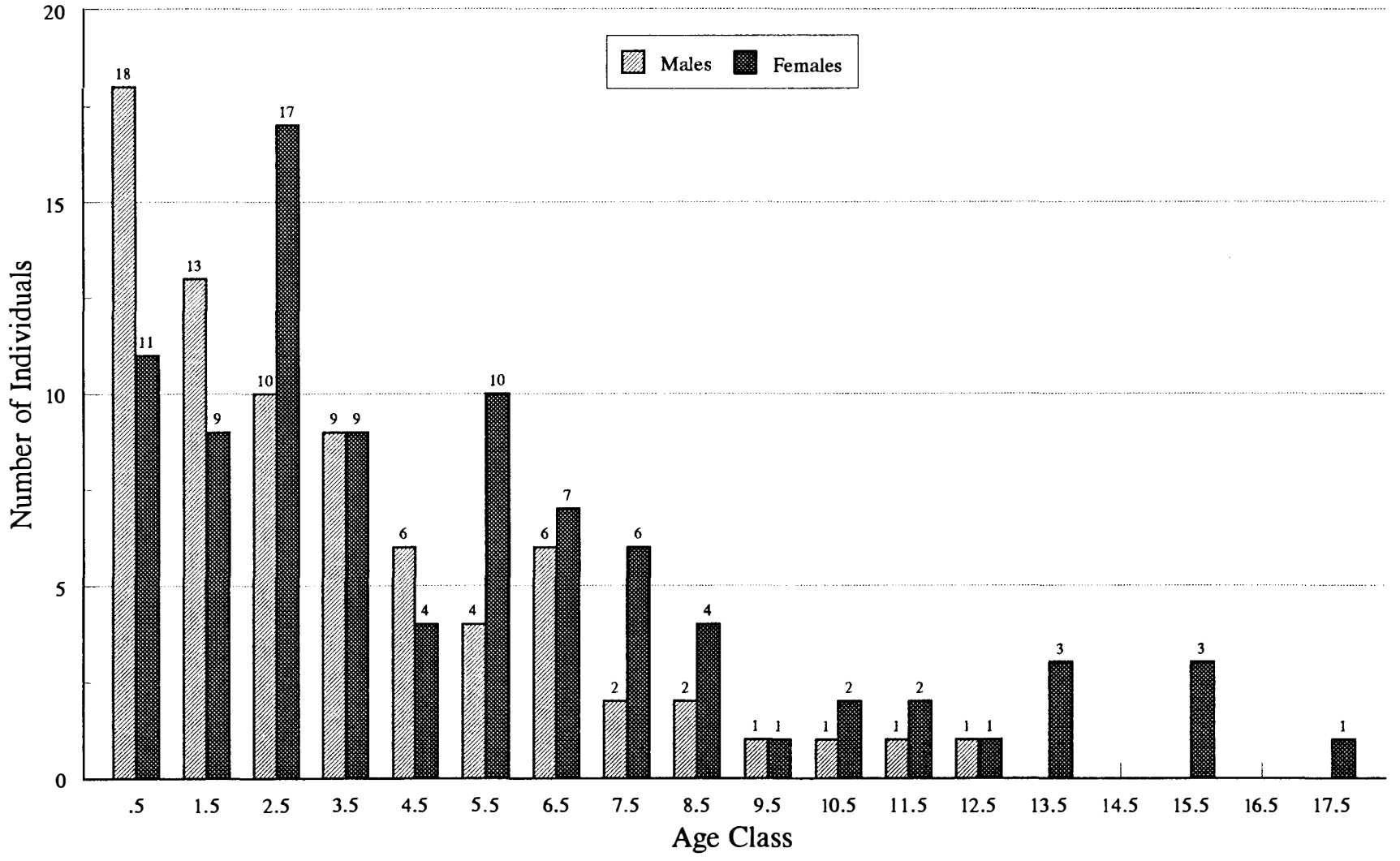


Figure F.11. Sex and age distribution of black bears known to be alive during the summer of 1982.

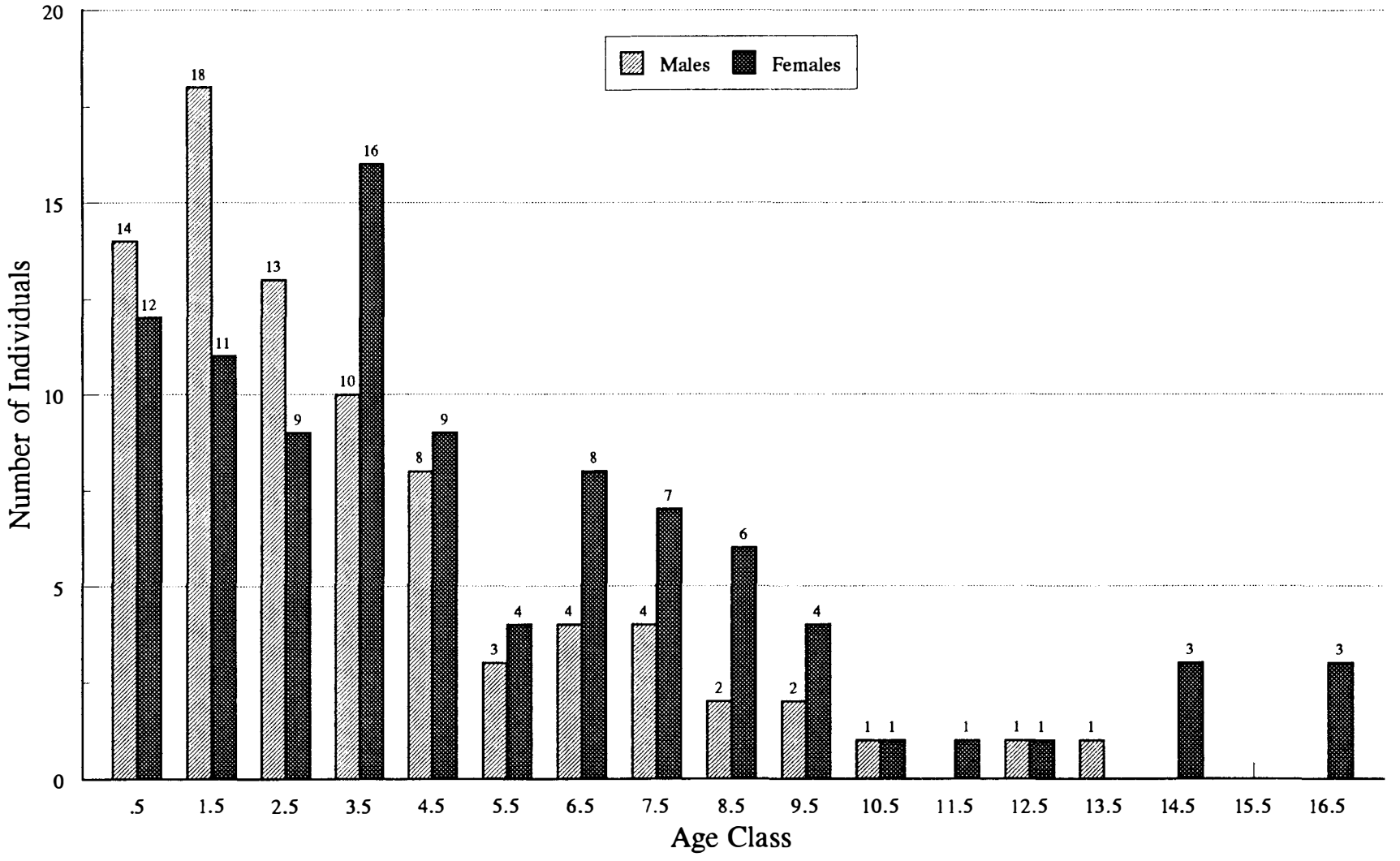


Figure F.12. Sex and age distribution of black bears known to be alive during the summer of 1983.

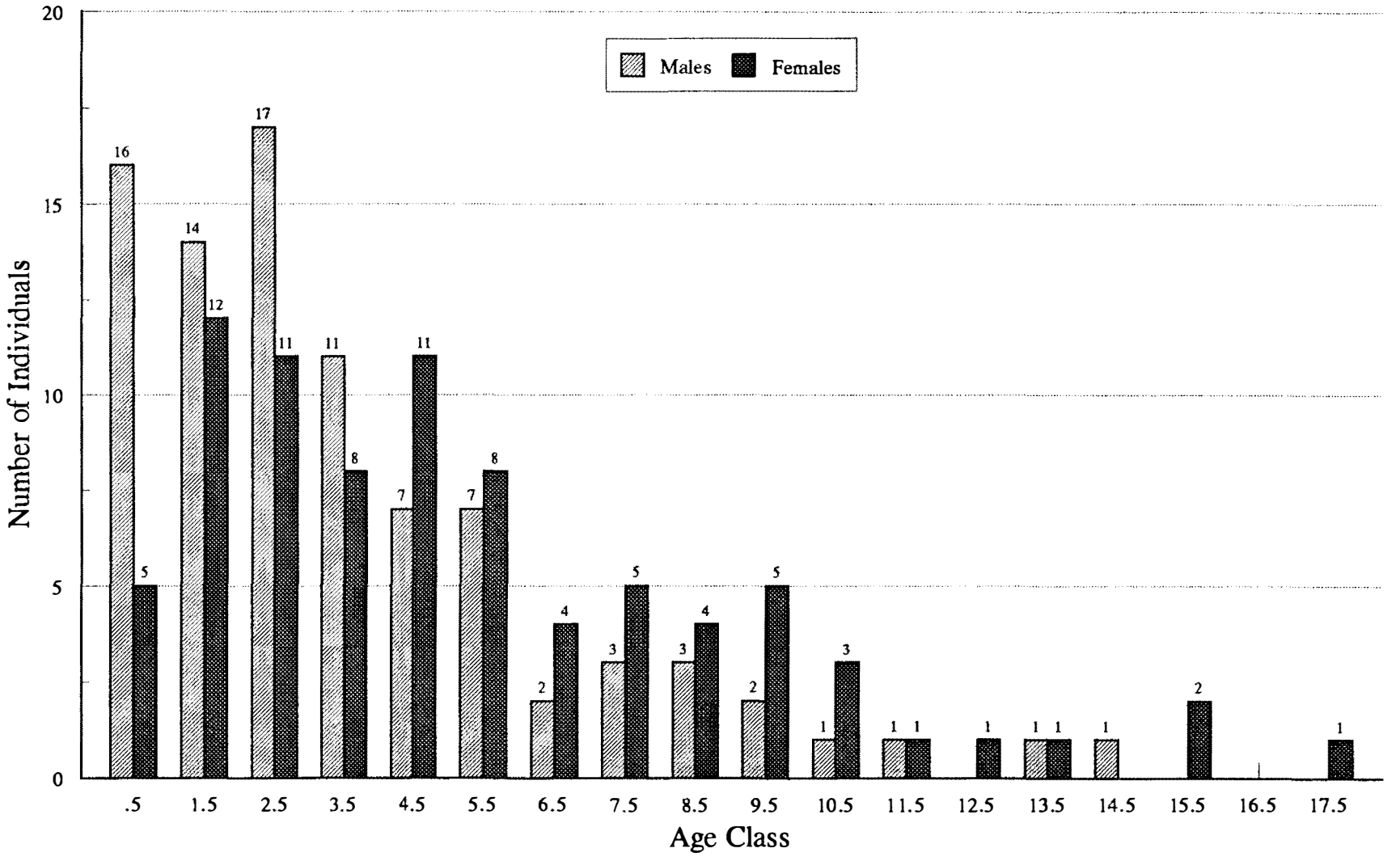


Figure F.13. Sex and age distribution of black bears known to be alive during the summer of 1984.

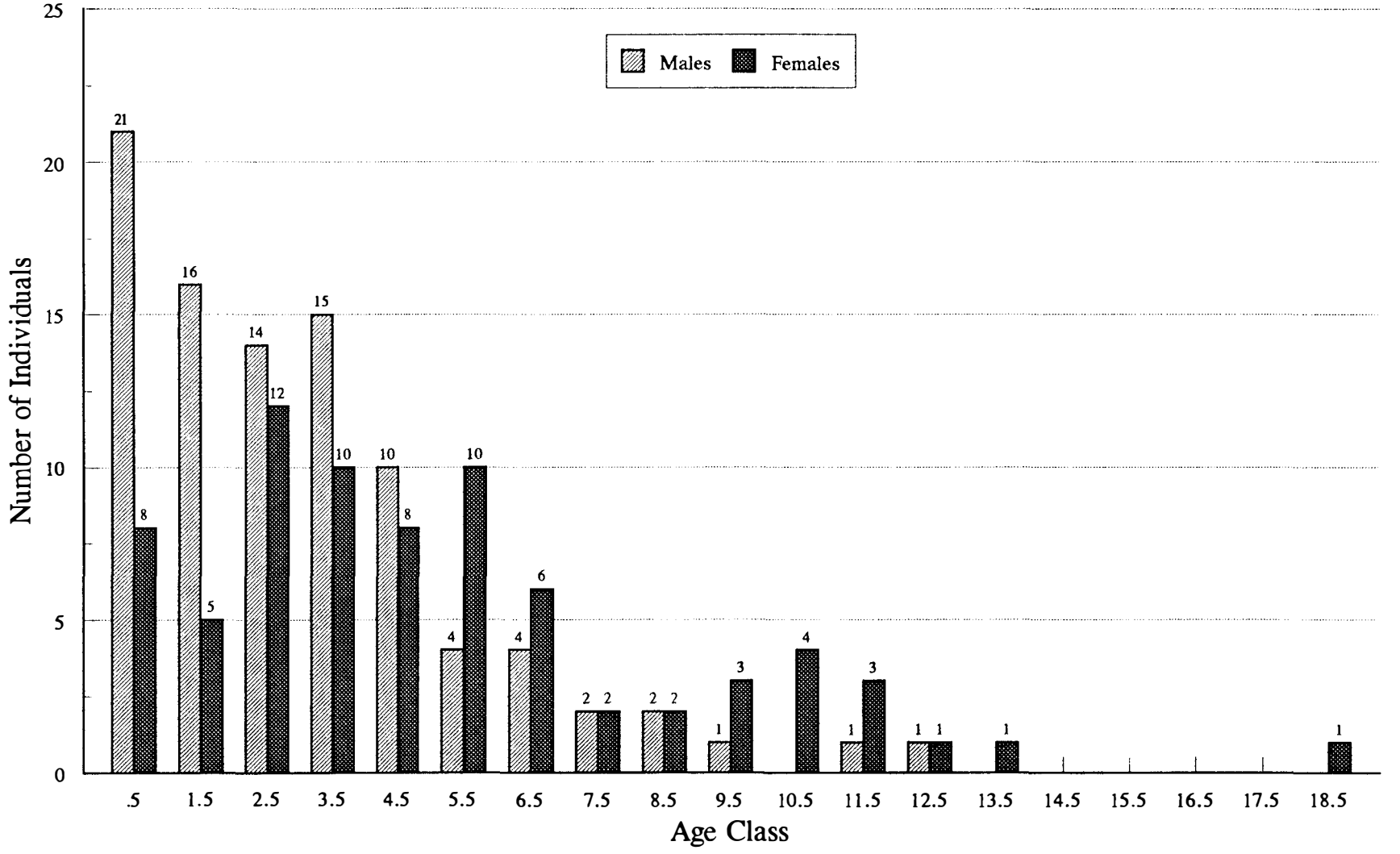


Figure F.14. Sex and age distribution of black bears known to be alive during the summer of 1985.

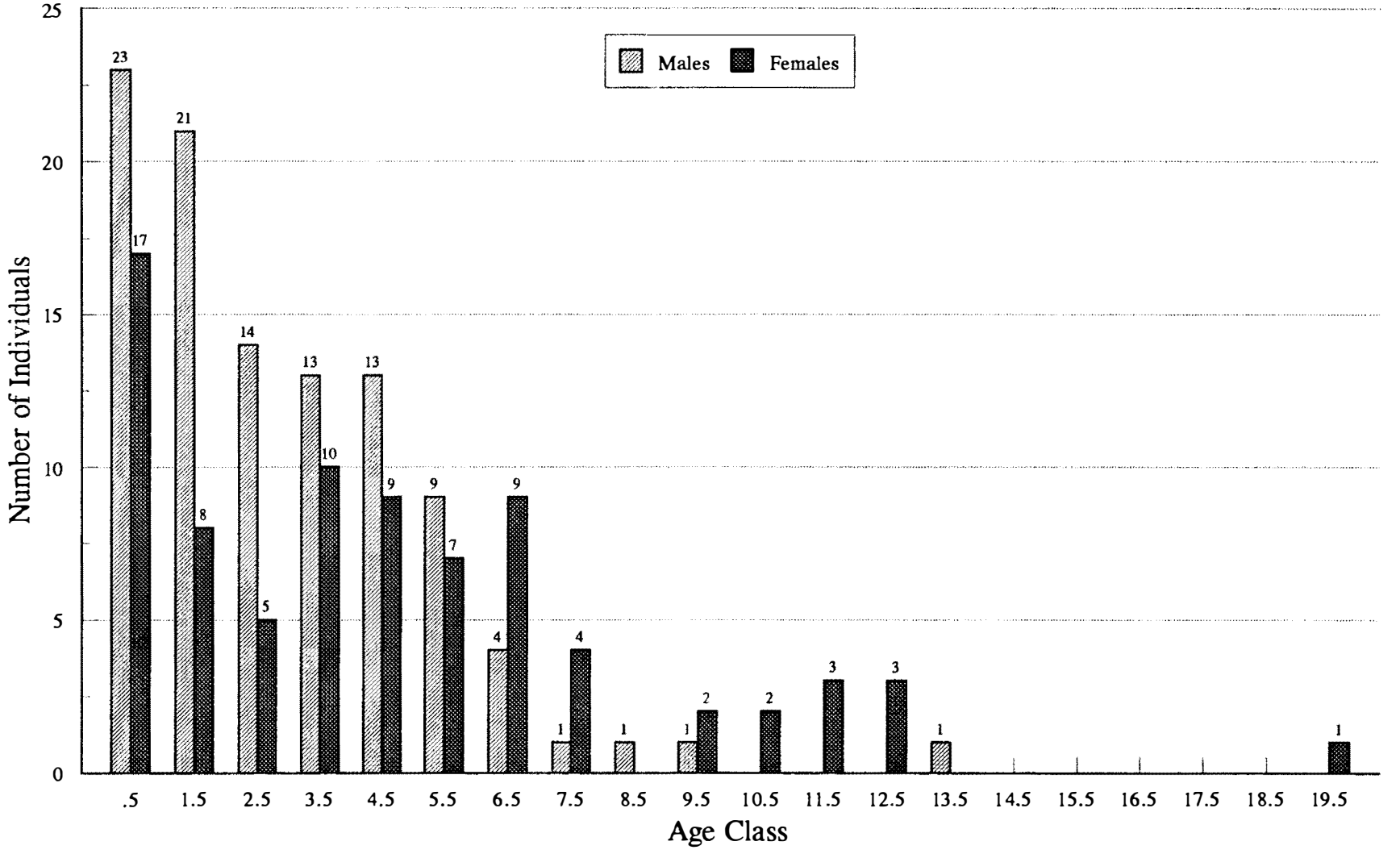


Figure F.15. Sex and age distribution of black bears known to be alive during the summer of 1986.

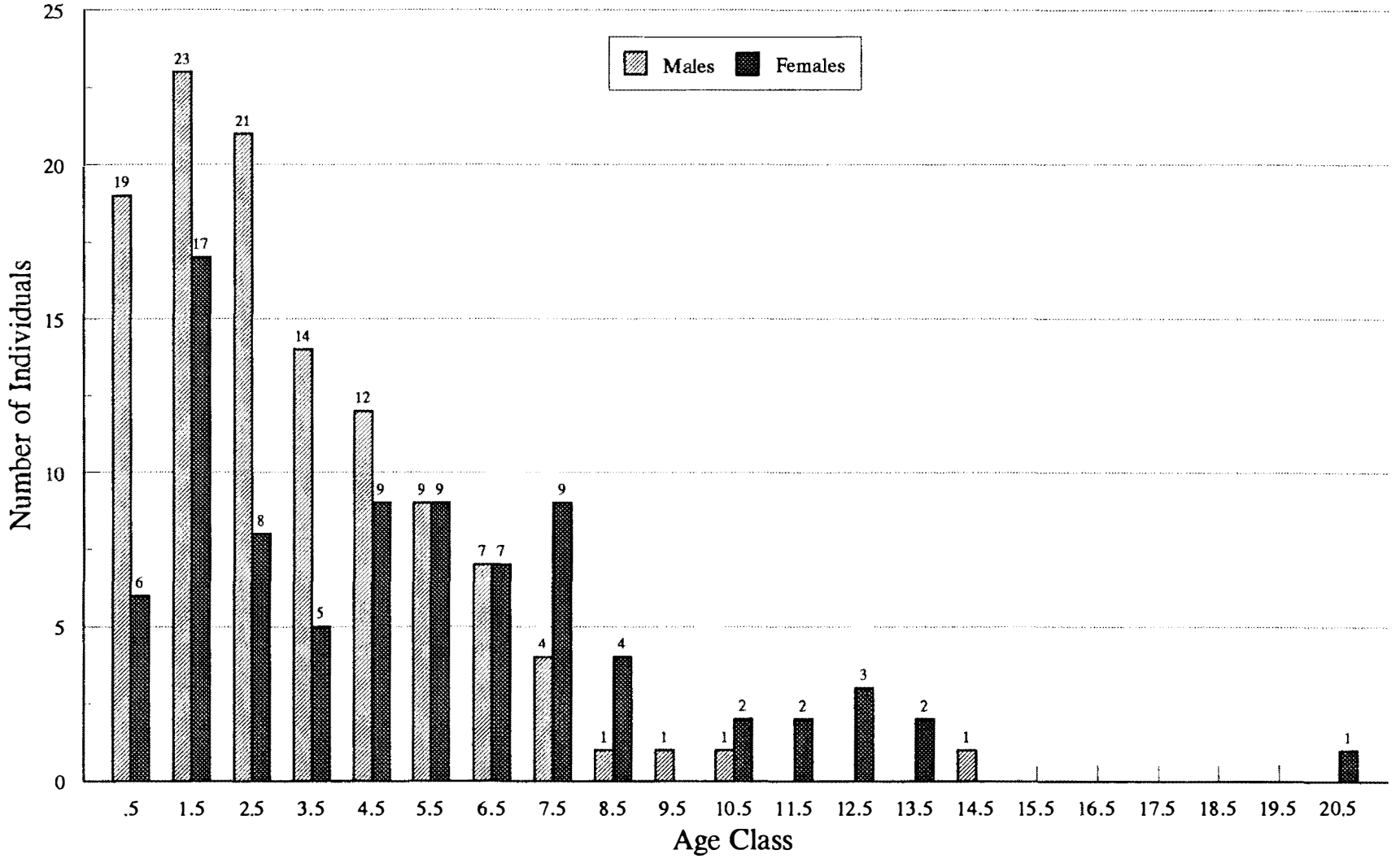


Figure F.16. Sex and age distribution of black bears known to be alive during the summer of 1987.

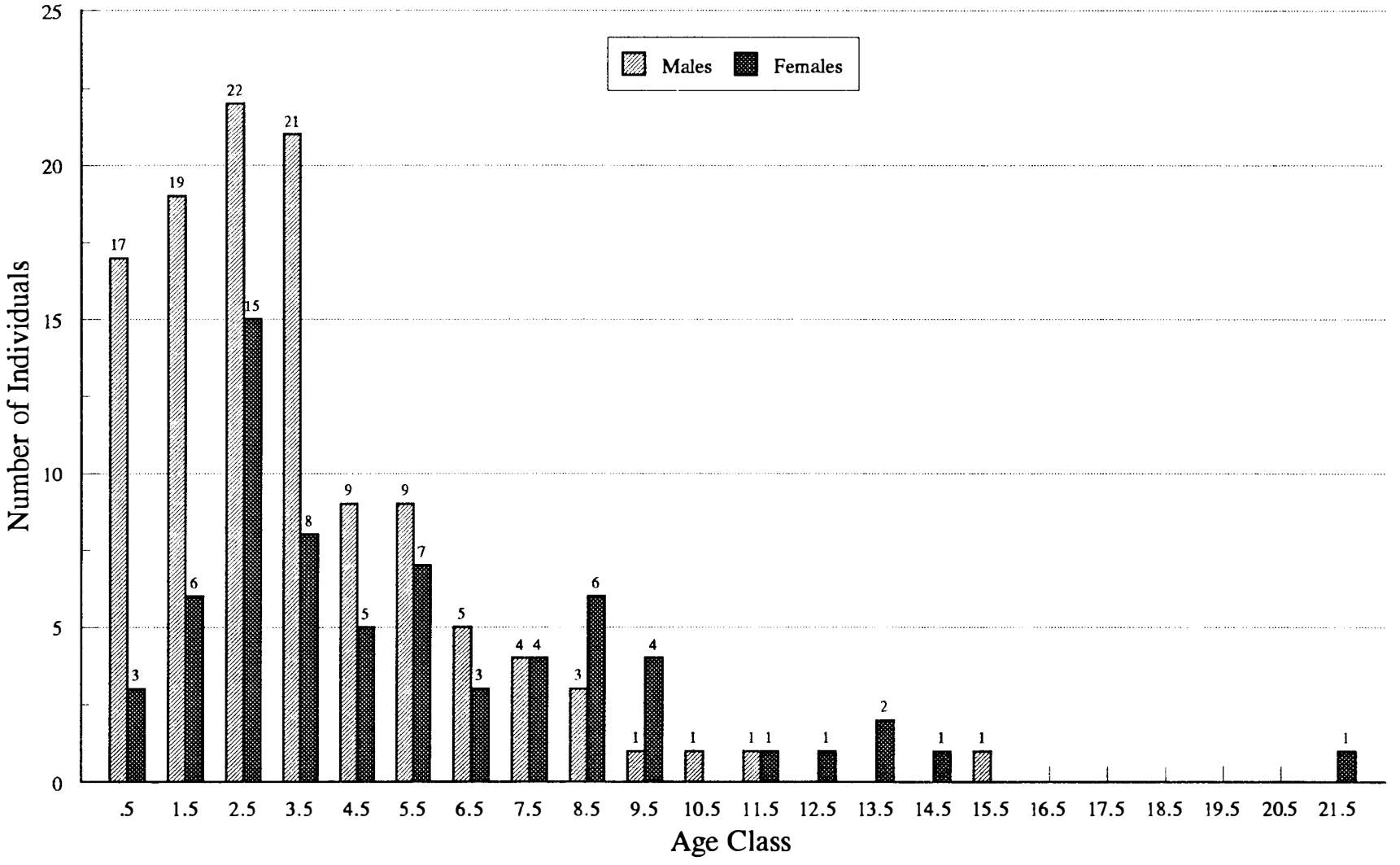


Figure F.17. Sex and age distribution of black bears known to be alive during the summer of 1988.

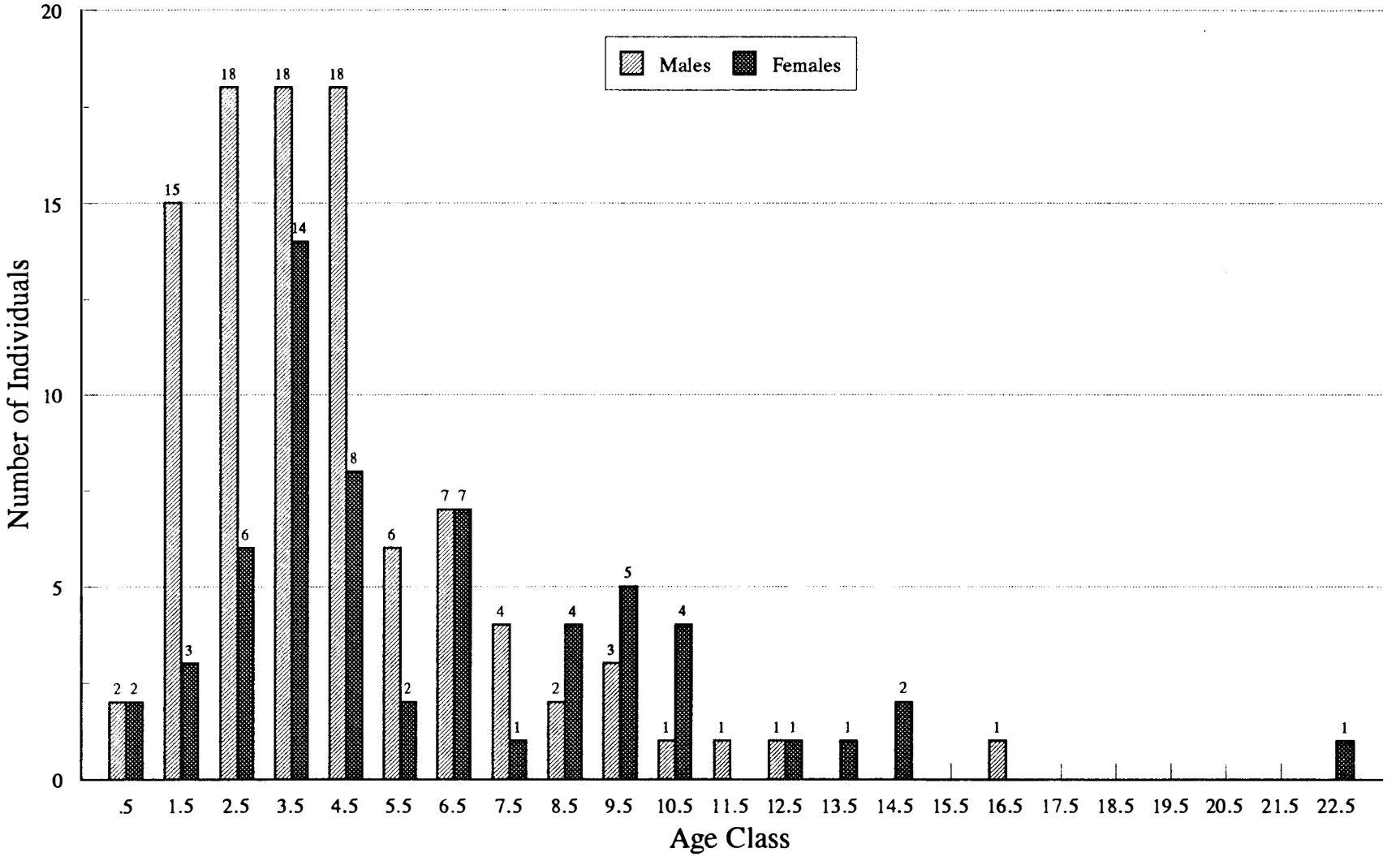


Figure F.18. Sex and age distribution of black bears known to be alive during the summer of 1989.

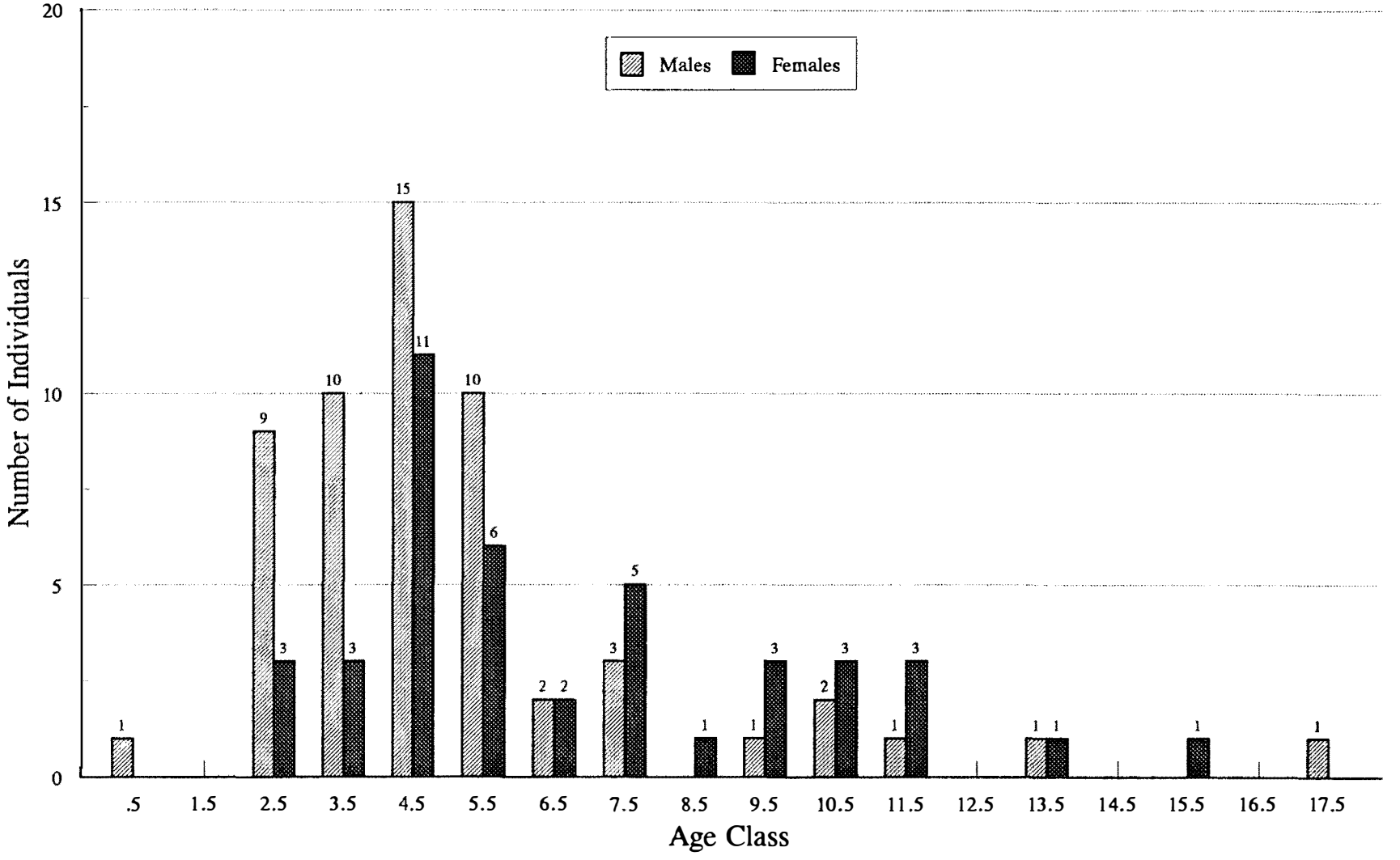


Figure F.19. Sex and age distribution of black bears known to be alive during the summer of 1990.

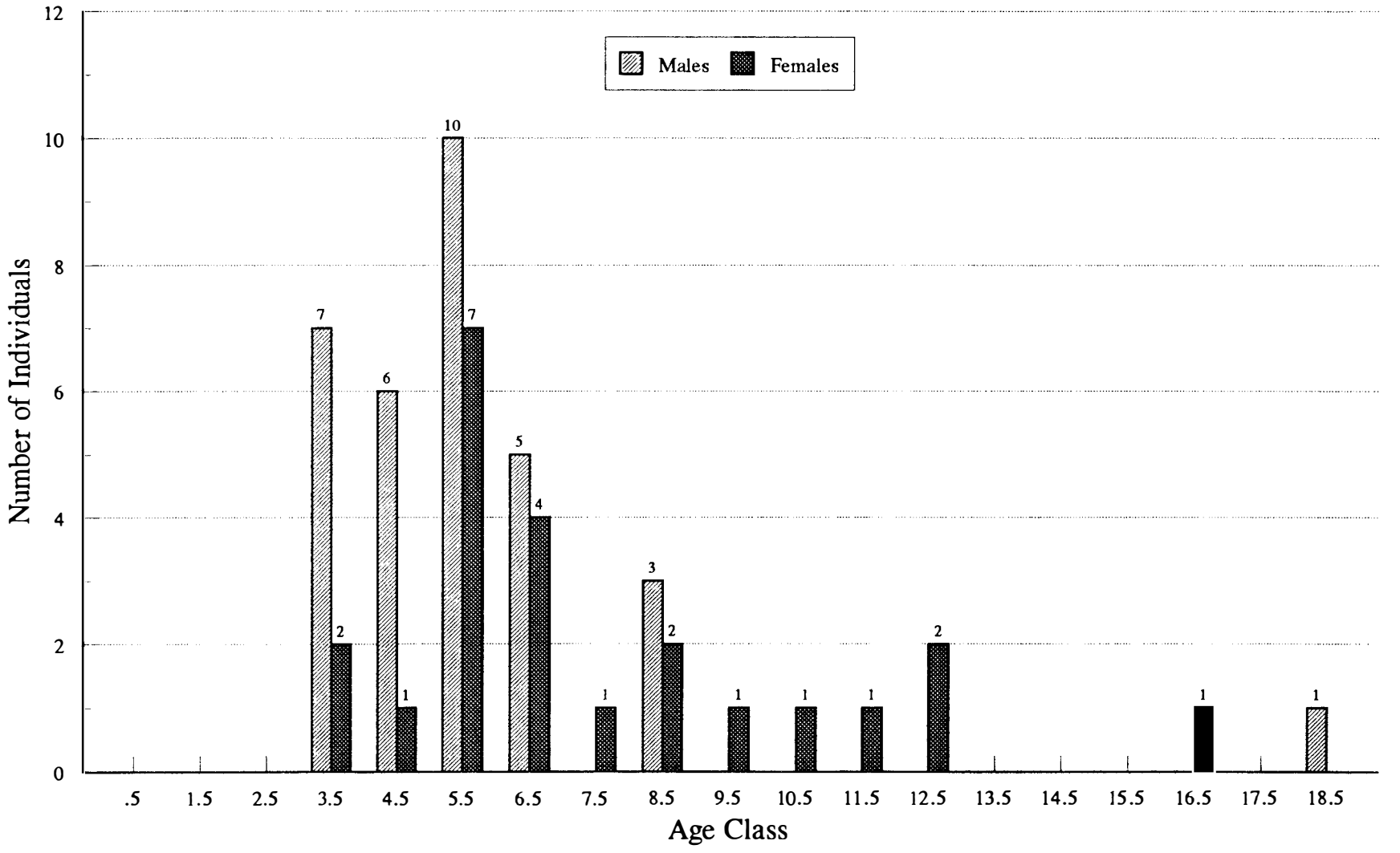


Figure F.20. Sex and age distribution of black bears known to be alive during the summer of 1991.

APPENDIX G

HARD MAST RESULTS

Table G.1. Whitehead hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1977-1991.

Year	White oaks	Red oaks	All oaks
1977	3.25 (20)	3.68 (16)	3.44 (36)
1978	- - -	- - -	- - -
1979	3.84 (24)	3.19 (20)	3.50 (44)
1980	2.43 (23)	4.45 (21)	3.31 (44)
1981	4.05 (20)	3.57 (16)	3.81 (36)
1982	2.56 (16)	2.82 (30)	2.73 (46)
1983	3.47 (9)	3.01 (7)	3.27 (16)
1984	- - -	- - -	- - -
1985	2.93 (27)	2.93 (29)	2.93 (56)
1986	3.19 (30)	3.57 (31)	3.38 (61)
1987	3.15 (33)	3.40 (47)	3.30 (80)
1988	3.50 (16)	3.52 (64)	3.52 (80)
1989	3.04 (15)	3.54 (62)	3.44 (77)
1990	3.01 (38)	3.00 (30)	3.02 (68)
1991	3.00 (38)	3.18 (38)	3.09 (76)

Table G.2. MPPI hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1977-1991.

Year	White oaks	Red oaks	All oaks
1977	2.41 (14)	8.08 (14)	5.25 (28)
1978	- - -	- - -	- - -
1979	16.64 (21)	6.02 (12)	12.78 (33)
1980	- - -	37.40 (18)	37.40 (18)
1981	33.49 (19)	23.46 (12)	29.61 (31)
1982	0.01 (4)	2.06 (12)	1.55 (16)
1983	8.43 (9)	1.65 (5)	6.01 (14)
1984	- - -	- - -	- - -
1985	2.60 (16)	0.82 (16)	1.71 (32)
1986	2.61 (26)	5.40 (29)	4.08 (55)
1987	0.85 (27)	4.93 (41)	3.31 (68)
1988	3.90 (15)	5.51 (53)	5.15 (68)
1989	0.76 (10)	2.66 (56)	2.37 (66)
1990	1.56 (24)	1.36 (18)	1.47 (42)
1991	3.56 (21)	1.34 (24)	2.38 (45)

Table G.3. Whitehead hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1980-1983.

Year	White oaks	Red oaks	All oaks
1980	2.43 (23)	4.45 (21)	3.31 (44)
1981	4.05 (20)	3.57 (16)	3.81 (36)
1982	2.56 (16)	2.82 (30)	2.73 (46)
1983	3.47 (9)	3.01 (7)	3.27 (16)

Table G.4. MPPI hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1980-1983.

Year	White oaks	Red oaks	All oaks
1980	- - -	37.40 (18)	37.40 (18)
1981	33.49 (19)	23.46 (12)	29.61 (31)
1982	0.01 (4)	2.06 (12)	1.55 (16)
1983	8.43 (9)	1.65 (5)	6.01 (14)

Table G.5. Whitehead hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1984-1991.

Year	White oaks	Red oaks	All oaks
1984	- - -	- - -	- - -
1985	3.00 (39)	2.98 (33)	2.99 (72)
1986	3.26 (43)	3.55 (34)	3.39 (77)
1987	3.23 (44)	3.41 (52)	3.33 (96)
1988	3.52 (26)	3.51 (70)	3.51 (96)
1989	3.07 (25)	3.51 (68)	3.39 (93)
1990	3.09 (49)	3.00 (31)	3.07 (80)
1991	2.91 (49)	3.12 (41)	3.01 (90)

Table G.6. MPPI hard mast survey results from Great Smoky Mountains National Park for the sampling interval 1984-1991.

Year	White oaks	Red oaks	All oaks
1984	- - -	- - -	- - -
1985	4.87 (23)	2.95 (18)	4.03 (41)
1986	4.92 (38)	5.65 (31)	5.25 (69)
1987	1.63 (38)	4.62 (46)	3.27 (84)
1988	4.05 (24)	5.02 (59)	4.74 (83)
1989	1.82 (18)	2.49 (61)	2.34 (79)
1990	4.95 (33)	1.29 (19)	3.61 (52)
1991	3.12 (24)	1.34 (24)	2.23 (48)

Table G.7. Whitehead hard mast survey results from Great Smoky Mountains National Park for the sampling intervals 1987-1991, 1988-1991, and 1989-1991.

Year	White oaks	Red oaks	All oaks
1987	3.23 (44)	3.41 (52)	3.33 (96)
1988	3.52 (26)	3.51 (70)	3.51 (96)
1989	3.07 (25)	3.51 (68)	3.39 (93)
1990	3.09 (49)	3.00 (31)	3.07 (80)
1991	2.91 (49)	3.12 (41)	3.01 (90)

Table G.8. MPPI hard mast survey results from Great Smoky Mountains National Park for the sampling intervals 1987-1991, 1988-1991, and 1989-1991.

Year	White oaks	Red oaks	All oaks
1987	1.63 (38)	4.62 (46)	3.27 (84)
1988	4.05 (24)	5.02 (59)	4.74 (83)
1989	1.82 (18)	2.49 (61)	2.34 (79)
1990	4.95 (33)	1.29 (19)	3.61 (52)
1991	3.12 (24)	1.34 (24)	2.23 (48)

APPENDIX H

SAS PROGRAMS FOR AGE PREDICTION

```
OPTIONS LS=80;
PROC IML;
SIGMA={125.8 40.86 19.82,
      40.86 41.06 1.732,
      19.82 1.732 51.57};  /* COVARIANCE MATRIX OF RESIDUALS*/
A={104.747, 53.126, 50.71}; /* INTERCEPTS */
B={28.95, 13.87, 16.953};   /* SLOPES */
P={1,1,1,1,1,1};            /* PRIOR PROBABILITIES FOR DIFFERENT AGE GROUPS */
N=118;                      /* SAMPLE SIZE */
D=3;                        /* DIMENSION OF MEASUREMENT VECTOR*/
DF=N-2;                     /* DEGREES OF FREEDOM */
M={120.,60.,60.};           /* TOT_LGT, SHOULDER, CHEST MEASUREMENTS FOR BEAR */
MEAN_AGE=1.0614;            /* MEAN OF LOG(AGE) FOR SAMPLE DATA */
SS_AGE=94.7885;             /* SUM OF SQUARES FOR LOG(AGE) */
INVSIGMA=INV(SIGMA);
FP={0 0 0 0 0 0};
GP={0 0 0 0 0 0};
SUMF=0;
SUMG=0;
DO I=1 TO 6;
AGE=I-.5;
MU=A+B*LOG(AGE);
V_MU=1+1/N+(LOG(AGE)-MEAN_AGE)**2/SS_AGE;
Q=(M-MU)'*INVSIGMA*(M-MU);
F=V_MU**(D/2)*(1+Q/(DF*V_MU))**(.5*(N-1));
FP[I]=P[I]/F;               /* BASED ON D MEASUREMENTS */
MU1=A[1]+B[1]*LOG(AGE);
Q=(M[1]-MU[1])**2/SIGMA[1,1];
G=SQRT(V_MU)*(1+Q/(DF*V_MU))**(.5*(N-1));
GP[I]=P[I]/G;               /* BASED ON 1ST MEASUREMENT ONLY*/
SUMF=SUMF+FP[I];
SUMG=SUMG+GP[I];
END;
DO I=1 TO 6;
FP[I]=FP[I]/SUMF;
GP[I]=GP[I]/SUMG;
END;
PRINT FP GP;                /* PREDICTIVE PROBABILITIES BASED ON D & 1 MEASUREMENTS*/
```

Figure H.1. SAS program for predicting black bear ages in Great Smoky Mountains National Park using morphometrics.

VITA

Alex Blandon Coley, son of Jim and . ly Coley, was born in Johnson City, Tennessee, on 14 February 1968. He attende Gate City High School in Gate City, Virginia, and graduated in 1986. He then atten d Virginia Tech and received his B.S. in Forestry - Wildlife Management option with minor in biology in May 1990. That same month he began trapping black bears in the Great Smoky Mountains National Park as part of his appointment as a teaching/research .ssistant at the University of Tennessee. He was married to Tracy Riddle in May of 1989 and their first child, Brennan McGee, was born in October of 1992. He graduated with a Master of Science degree in Wildlife and Fisheries Science from the University of Tennessee, Knoxville, in May 1995.