To the Graduate Council:

I am submitting herewith a thesis written by Jaime Suzanne McNutt entitled "The Effects of Variation in Acorn Production on Black Bear Population Trends and Survivorship of Female Black Bears in Great Smoky Mountains National Park." I have examined the final paper copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Dr. Frank van Manen, Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

Vice Provost and Dean of Graduate Studies

THE EFFECTS OF VARIATION IN ACORN PRODUCTION ON BLACK BEAR POPULATION TRENDS AND SURVIVORSHIP OF FEMALE BLACK BEARS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

A Thesis

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ABSTRACT

Acorn Production and Black Bear Abundance

I investigated the relationship between black bear population abundance and acorn production based on two different mast indices (Whitehead index and a mast regression index) in the Great Smoky Mountains National Park. I used hard mast data on northern red oak trees and white oak trees obtained from the National Park Service annual mast surveys (1979–2000). Estimates of bear population abundance were obtained from a mark-recapture study in the northwestern quadrant of Great Smoky Mountains National Park, and were divided into two time periods: 1981–1999, and 1990–2000. Black bear population abundance was calculated using the Jolly-Seber model.

Mast data and black bear population estimates used in this study were time-series, so relationships were examined using autoregressions. I explored all possible variable combinations of northern red oak and white oak using lag times in the data for up to 3 years. For the period 1981–1999, the best model for both mast production methods included the white oak mast index from the current year. The mast regression index best predicted black bear population estimates for this time period ($R^2 = 0.53$). Autoregressions using population estimates from 1990–2000 indicated that white oak mast from 2 years before was an important variable. The Whitehead index best predicted black bear population estimates for this time period ($R^2 = 0.49$).

My study suggests that white oak mast may correspond more to population dynamics of black bears than northern red oak. White oak from previous years occurred more often than red oak in the more significant regression models. White oak mast from

the current year also consistently showed significance; because population estimates for a given year were derived before the mast surveys were conducted; this variable likely is a surrogate for soft mast production. Northern red oak from the previous year also was an important variable.

For the time period 1981–1999 the mast regression index predicted black bear population estimates better than the Whitehead index. For the time period 1990–2000 the Whitehead index better predicted the black bear population estimates than the mast regression index. Population estimates for the period 1990–2000 may have been more accurate, which may have caused this difference in results compared with the 1981–1999 period. Because bears can easily switch to alternate food sources, problems may arise in detecting relationships between the black bear population and only one food source. In this study much of the variation cannot be explained, and future studies including other species of oaks along with other food sources may need to be examined. Information from this study may help wildlife managers better anticipate how the black bear population in Great Smoky Mountains National Park will respond to certain changes in mast production.

Survival of Female Black Bears

From 1999 through 2001, adult female black bears trapped during the summer mark-recapture study conducted in the northwestern quadrant of Great Smoky Mountains National Park were fitted with radio collars. From October 1999 through April 2001, I located 32 radio-collared female bears once every month. To estimate survival, I used a modified Kaplan-Meier staggered entry procedure, which corrects for the number of

animals at risk (number of animals detected) due to uncertain relocation of individuals (Bunck et al. 1995). During the study 6 bears were censored, and signals of 9 radio collars switched to mortality mode; of these 3 could not be retrieved and 6 were prematurely dropped. No mortalities were observed throughout the study, and the survival rate of female black bears was 1.0.

The results of my study suggest that survival among adult female bears within a protected area is high. Expanding the use of aerial telemetry during future monitoring may reduce the number of censored bears and improve the ability to detect mortalities. Due to the longevity of bears, longer-term research will be needed to better document trends in female black bear survival in Great Smoky Mountains National Park.

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PART I

INRODUCTION

CHAPTER I

ACORN PRODUCTION AND BLACK BEAR ABUNDANCE

I investigated the relationship between black bear population abundance and acorn production based on two different mast indices: the Whitehead index and a mast regression index. I chose Great Smoky Mountains National Park as the study area because of the availability of long-term mast and bear abundance data. Hard mast data used in this study were obtained from the National Park Service annual mast surveys collected from 1979–2000 and included 1,702 observations on northern red oak trees and 820 observations on white oak trees. Estimates of bear population abundance were obtained from a mark-recapture study in the northwestern quadrant of Great Smoky Mountains National Park, and were divided into two time periods: 1981–1999, and 1990–2000. Sampling during the latter period was more consistent than the first period, resulting in a larger and more continuous study area compared with the 1981–1999 period. Black bear population abundance was calculated using the Jolly-Seber model.

Mast data and black bear population estimates used in this study were time-series, so relationships were examined using autoregressions. I explored all possible variable combinations of northern red oak and white oak using lag times in the data for up to 3 years. The most significant model was selected for each mast production method within each time period. The best models for each method were then compared to determine which method of mast calculation produced the most accurate model.

For the period 1981–1999, the best model for both mast production methods included the white oak mast index from the current year. The mast regression index best

predicted black bear population estimates for this time period ($R^2 = 0.53$). Autoregressions using population estimates from 1990–2000 and all combinations of northern red and white oak for each of the two mast indices indicated that white oak mast from 2 years before was an important variable. The Whitehead index best predicted black bear population estimates for this time period ($R^2 = 0.49$).

My study suggests that black bear abundance may be influenced by white oak mast from two years previous. This study also suggests that white oak mast may correspond more to population dynamics of black bears than northern red oak. White oak from previous years occurred more often than red oak in the more significant regression models. White oak mast from the current year also consistently showed significance; because population estimates for a given year were derived before the mast surveys were conducted; this variable likely is a surrogate for soft mast production. Northern red oak from the previous year also was an important variable. In poor mast years black bears may exhibit wide-ranging movements in search of food outside the national park. These movements may increase the chance of mortality, possibly reducing population abundance during the subsequent year.

For the time period 1981–1999 the mast regression index predicted black bear population estimates better than the Whitehead index. For the time period 1990–2000 the Whitehead index better predicted the black bear population estimates than the mast regression index. Population estimates for the period 1990–2000 may have been more accurate, which may have caused this difference in results compared with the 1981–1999 period. Many other variables not examined in this study play a role in black bear population dynamics. Because bears can easily switch to alternate food sources,

problems may arise in detecting relationships between the black bear population and only one food source. In this study much of the variation cannot be explained, and future studies including other species of oaks along with other food sources may need to be examined to gain a better understanding of how the black bear population is responding to fluctuations in food. Information from this study may help wildlife managers better anticipate how the black bear population in Great Smoky Mountains National Park will respond to certain changes in mast production.

CHAPTER II

SURVIVAL OF FEMALE BLACK BEARS

From 1999 through 2001, adult female black bears trapped during the summer mark-recapture study conducted in the northwestern quadrant of Great Smoky Mountains National Park were fitted with radio collars. From October 1999 through April 2001, I located 32 radio-collared female bears once every month. I used a modified Kaplan-Meier staggered entry procedure, to correct for the number of animals at risk (number of animals detected) due to uncertain relocation of individuals (Bunck et al. 1995).

Of the 32 female bears with radio-collars entered into this study, six bears were censored and an average of 14 bears were heard each month. Signals of 9 radio collars switched to mortality mode; of these 3 could not be retrieved and 6 were prematurely dropped. No mortalities were observed throughout the study, and the survival rate of female black bears was 1.0.

The results of my study suggest that survival among adult female bears within a protected area is high. Hunting is the primary source of mortality for black bears (Elowe et al. 1991). However, hunting is not allowed in Great Smoky Mountains National Park; therefore the black bear population is relatively unexploited. Expanding the use of aerial telemetry during future monitoring may reduce the number of censored bears and improve the ability to detect mortalities. Due to the longevity of bears, longer-term research will be needed to better document trends in female black bear survival in Great Smoky Mountains National Park.

CHAPTER I

INTRODUCTION

Although the American black bear (*Ursus americanus*) is taxonomically classified as a carnivore, feeding behaviors throughout the range of the species are mostly omnivorous (Pelton 1982). In many areas black bears subsist primarily on berry and nut crops (Pelton 1989). Bears are well adapted for locating and acquiring these relatively small food items that are high in nutrients, low in cellulose, and available only seasonally. Black bears locate areas where good acorn crops are produced, and can move long distances to return to these areas (Garshelis and Pelton 1981, Pelton 1982). Black bears are adapted for climbing, tearing apart logs, and bending branches. These animals have bunodont teeth, which are well suited for crushing hard-shelled nuts, and their digestive systems are adapted for digesting fruit, nuts, insects, and succulent vegetation (Rogers 1987).

Mast crops from oaks serve as important determinants of community function within Appalachian forests (McShea 2000). McShea (2000) found that white-tailed deer (*Odocoileus virginianus*), white-footed mouse (*Peromyscus leucopus*), eastern chipmunk (*Tamias striatus*), and gray squirrel (*Sciurus carolinensis*) population trends were significantly correlated with annual fluctuations in the acorn crop. In the southern Appalachians, the population dynamics of black bears are also strongly influenced by the availability of fall foods (Pelton 1989, Inman 1997). Oak mast is one of the primary fall foods black bears consume to build fat reserves in preparation for winter denning (Beeman and Pelton 1980). On average, northern red oak and white oak are superior

acorn producers (Beck 1989, Greenberg 2000). Greenberg and Parresol (2002) found that northern red oak and white oak produced significantly greater green weight and dry biomass than chestnut, black, or scarlet oak. The distribution of oak mast, primarily white oak and northern red oak, has a significant impact on bear populations (Pelton 1989).

Habitats where oak species are plentiful are used extensively by black bears (Quigley 1982, Carr 1983, Clevenger 1986) and provide a diet essential for survival and reproduction (Eagle and Pelton 1983, Eiler et al. 1989, Pozzanghera 1990, McLean 1991). Results from many studies have consistently shown large variation in acorn production between locations, years, species, and among individual oak trees (Downs and McQuilken 1944, Burns et al. 1954, Gysel 1956, Sharp and Sprague 1967, Christisen and Kearby 1984, Beck 1989, McGee 1989, Koenig et al. 1994, Sork et al. 1993, Greenberg 2000). This variation can have substantial consequences for black bears in terms of natality, mortality, and movements (Beeman 1975, Garshelis 1978, Eiler et al. 1989).

To understand the relationship between oak mast production and black bear populations, it is important to first examine the biology and reproduction of oak species. Oak reproduction begins with pistillate flower development during spring. Male flowers form in ephemeral catkins and female flowers develop in the axils of leaves. Female flowers appear 5–10 days after the emergence of the male catkins and are found on shoots from the current year. After pollen transfer occurs, the development of a stalk begins. The stalk provides organic material to the endosperm, which then develops into the acorn (Sharp and Sprague 1967).

White and red oaks differ in the length of time between flowering and fertilization (Romashov 1957 in Sharp and Sprague 1967). White oaks produce flowers during spring, which, when fertilized, develop into mature acorns during autumn of the same year. Red oaks produce flowers in the spring of one year, but fertilization and maturation does not take place until the following year. All oak species initiate staminate floral buds during the spring of the year prior to flowering, and initiate pistillate floral buds in late summer in the year prior to flowering. Therefore, full development of flowers to mature acorns spans 2 years in white oaks and 3 years in red oaks (Minima 1954 in Sork et al. 1993, Romashov 1957 in Sharp and Sprague 1967, Merkle et al. 1980).

Acorn production is influenced by weather conditions. Oak trees produce more seeds when weather conditions promote greater photosynthate production (Norton and Kelly 1988). Killing freezes, drought, and prolonged rainy periods can put excessive stress on trees resulting in poor acorn crops (Toumey and Korstian 1937, Baldwin 1942, Baker 1950). Temperature directly affects relative humidity, wind, and drought and is the primary cause of annual variation in white oak acorn crops (Sharp and Sprague 1967). Sharp and Sprague (1967) found that precipitation by itself showed no direct relationship with acorn crop production. Even during a severe drought, acorn yields can be excellent. Oaks are wind-pollinated species, but strong winds can desiccate catkins and dehisce pollen prematurely. Poor acorn crop production by white oak has been associated with low April temperatures, whereas good acorn production has been linked to warmer April temperatures followed by cool temperatures in May. According to Sharp and Sprague (1967), good acorn crops often are produced following this temperature regime because warm April temperatures advance catkin emergence and shoot and leaf development,

whereas cool periods in May delay pollen dispersal to coincide with pistillate flower development. The impact of temperature is seen through flower to fruit survival rather than flower initiation. Sork et al. (1993) found that spring temperature during the season of fruit maturation was correlated with acorn crop size for both white and red oak. Killing frosts also may be a major factor affecting acorn production. However, when killing freezes occur, they often are confined to frost-pocket areas, and may not cause complete acorn failures. In a 14-year study, Sharp and Sprague (1967) found most killing freezes occurred during years in which late April was unseasonably warm followed by a freeze in May.

Oaks may have an inherent cycle of reproduction that can be modified by the impacts of weather conditions. Sork et al. (1993) suggest that patterns of acorn production are not simply responses to weather events but also a function of prior reproductive events: individuals within a species tend to produce large acorn crops in the same year, but each species may differ in which years they produce large crops. Sork et al. (1993) found that flower abundance and survival of flowers to fruit determined the overall size of a given acorn crop. Although weather conditions influenced acorn production, each oak species exhibited its own tendency to produce large acorn crops at certain intervals. This tendency may be a result of the interval of time it takes for a particular tree to store or restore the resources needed for acorn production (Sork et al. 1993). Koenig et al. (1994) observed that individual trees tend to mast at species-specific intervals, but these patterns did not result in regular masting cycles at the population level.

Because of the various factors discussed previously, acorn production can vary widely by year, location, species, and individual tree (Beck 1989, McGee 1989, Greenberg 2000). Greenberg (2000) studied acorn production in the southern Appalachians during 1993–1997, and found that the average number of acorns produced per m^2 basal area differed significantly among oak species. She also found that fruiting frequency varied among individual trees within species, and good acorn producers, although often representing a small portion of the population, outperformed poor and moderate producers by a wide margin of production. Although oaks are capable of producing good acorn crops every two to three years, local mast failures frequently occur in the southern Appalachians. At least five major hard mast failures have occurred in Great Smoky Mountains National Park during the past 32 years; two of these failures were within the last ten years (1992 and 1997; F. T. van Manen, U. S. Geological Survey, personal communication). This variation in acorn production over time can influence demographic responses of mast-dependent species. In the southern Appalachians, the black bear is one such species whose survival and reproduction is tightly linked to masting events. Thus, it is important to determine how variation in acorn production affects black bear populations over time.

Understanding the biology of black bears also is important to determine the relationships that may exist between black bear populations and hard mast production. The abundance and quality of food available to an animal influences its movements and activities, general condition and health, and ability to reproduce (Christisen and Korschgen 1955). Black bear home ranges and movements are shifted to accommodate fluctuations in mast production (Garshelis and Pelton 1981). Black bear ranges during

fall tend to vary more from year to year than spring or summer ranges because of this variability in hard mast production (Carr 1983). Shifts in movements occur when productive foods become patchily distributed, which often takes place when bears switch from consuming predominantly soft mast during summer and early fall to mostly hard mast in late fall (Garshelis and Pelton 1981, Hellgren and Vaughan 1990).

Reproduction in black bears is mainly controlled in a density-independent manner by fruit and mast supplies that fluctuate in abundance from year to year (Rogers 1987). The availability of hard mast during fall affects the minimum reproductive age and productivity of female black bears and cub survival (Eiler et al. 1989, Pozzanghera 1990, McLean 1991). Black bears mate mostly in July, and the fertilized eggs undergo a period of arrested development for 5–6 months (delayed implantation; Eiler et al. 1989). The blastocysts implant into the uterine wall and development continues around the time that female bears enter their winter dens. Altricial cubs are born in late January or early February. Females bears nurse the cubs throughout the summer and usually den with the cubs the following winter (Pelton 1982). Because it is unusual for females with cubs to mate, a full reproductive cycle takes 2 years. Consequently, this 2-year reproductive cycle may cause lag times between hard mast production and any population response. The effects from the variability of hard mast in one year may not be seen until later years (Pelton 1989).

The normal reproductive pattern of black bears may be modified due to the effects of variation in food availability on the nutritional condition of female bears. For example, Elowe and Dodge (1989) found that 26 of 28 females with access to high fat and carbohydrate diets produced cubs, but all of 10 females with low carbohydrate fall

diets failed to produce cubs. Furthermore, Samson and Huot (1995) found that body mass of female black bears in early winter also influenced litter size. In the southern Appalachians, Eiler et al. (1989) found that females exhibited skips in the 2-year reproductive cycle following poor mast years and that minimum reproductive age also may be delayed. Lactating females have increased nutritional demands and are more active than other bears (Garshelis and Pelton 1981, Villarrubia 1982); a mast failure during fall could prevent female bears from attaining a body weight necessary to support a litter of cubs throughout the winter. McLean and Pelton (1994) created a model based on the proportion of lactating females following good, bad, and average years of hard mast production. Although the frequency of lactation was correlated with hard mast production, periodic fluctuations in mast production and the longevity of black bears confounded the ability to clearly elucidate these relationships (McLean and Pelton 1994).

Mast availability can also affect cub survival (LeCount 1987), which may have a greater influence on population growth than birth rate (Cole 1954). Eiler et al. (1989) found that cub survival was related to differences in mast yields and female bears may lose an entire litter in years following poor mast production. Fall mast availability may influence bear densities through the number of female cubs born (Elowe and Dodge 1989). In Massachusetts, Elowe and Dodge (1989) found that most cub mortality occurred between 1.5 and 5 months of age, but at a much greater rate for male than for female cubs.

Availability of hard mast also influences adult mortality during the fall; poor acorn crops often cause wide-ranging movements among bears, increasing the likelihood of harvest mortality and vehicle collisions (Pelton 1989). Samson and Huot (1998)

examined the influence of the distribution of vegetation types at the landscape level on movements of female bears in and around a national park in Quebec, Canada. These researchers found that lack of preferred foods within the protected area increased the vulnerability of female black bears to human-related mortality due to movements outside the national park in search of food. Hellgren and Vaughan (1989) also found that mortality was influenced by food availability in the Great Dismal Swamp of Virginia and North Carolina.

Considering the influence of mast crops on black bears, it is important to understand how the availability of hard mast affects their populations. Biologists could use this information to make better management decisions related to population harvesting, nuisance management, and habitat management. If relationships between mast production and black bear abundance are recognized, wildlife managers can better anticipate how the bear population may respond to certain mast events and adjust management accordingly.

A consistent and long-term database of black bear captures is important to document population trends. Black bears have been studied in the northwestern quadrant of Great Smoky Mountains National Park since 1968, providing a unique opportunity to determine the long-term relationships between acorn production and bear population dynamics.

Mast production has been monitored annually in Great Smoky Mountains National Park since the late 1970s using visual surveys (the Whitehead index method; Whitehead 1969). However, the Whitehead index is vulnerable to inconsistencies in data collection and problems with technical application (Pozzanghera 1990). Recent studies

in North Carolina and Tennessee have documented the temporal and spatial variation in mast abundance, possibly providing better measures of mast production (Greenberg 2000, Greenberg and Parresol 2000). The study by Greenberg (2000) was based on acorn trap data, which are less subjective than visual assessments. Greenberg and Parresol (2000) found that the proportion of acorn-bearing trees could be used as a strong predictor of acorn yield. Data from visual mast assessments can be used to calculate the proportion of acorn-bearing trees and thus to apply the regression equations developed by Greenberg and Parresol (2000) to predict acorn yield.

The primary objective of this study was to determine relationships between acorn production and black bear population trends. Specific study objectives were to:

1) compare the mast production method of the Whitehead Index with the method described by Greenberg and Parresol (2000), and
2) determine relationships between black bear population abundance and acorn production.

CHAPTER II

STUDY AREA

Location

Great Smoky Mountains National Park is located on the border of Tennessee and North Carolina and is surrounded by 3 national forests: Nantahala National Forest and Pisgah National Forest in North Carolina, and Cherokee National Forest in Tennessee. The national park encompasses approximately 2,000 km^2 from 35°29' to 35°47' N latitude and 83°05' to 83°55' W longitude. The national park covers portions of Blount, Cocke, and Sevier counties in Tennessee, and Haywood and Swain counties in North Carolina (Figure 2.1). Black bears have been studied since 1968 in the northwestern quadrant of Great Smoky Mountains National Park (Pelton and van Manen 1996). Mark-recapture studies for population estimation have focused on a 328-km^2 portion of this study area.

Physiography, Geography, and Soils

The Great Smoky Mountains are part of the Unaka Mountain Range of the Blue Ridge Province and lie in the Southern Appalachian Highlands (Fennemans 1938). The main ridge crest runs in a northeast–southwest direction and forms the boundary between Tennessee and North Carolina. The area consists of steep ridges extending out from the main ridge, and narrow valleys created by fast-flowing streams (King and Stupka 1950).

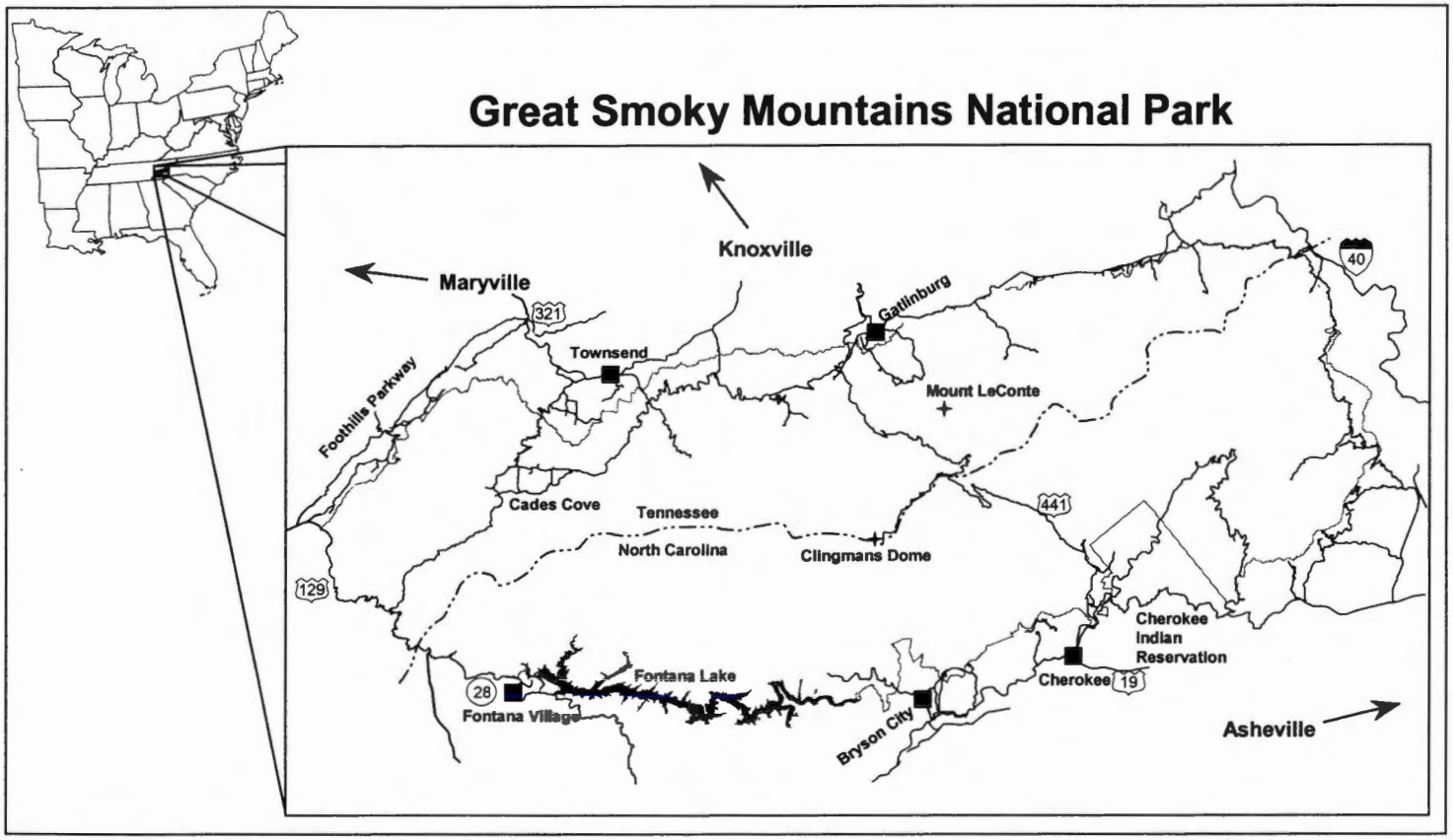


Figure 2.1. Great Smoky Mountains National Park, Tennessee and western North Carolina

Elevation ranges from 267 m at Chilhowee Lake to 2,024 m at Clingmans Dome (King et al. 1968).

Precambrian sedimentary rocks of the Ocoee series make up the bedrock found in the Great Smoky Mountains (King et al. 1968). Sandstone dominates the Ocoee series along with limestones and shales. Parent materials include quartz, feldspar, shale, slate and phyllites with a small amount of schist and limestone (King et al. 1968).

Great Smoky Mountains National Park is primarily covered with colluvial and residual soils (Golden 1974). Soils of the Ramsey association predominate, characterized by low to moderate fertility, low water storage capacity, medium to high acidity, and susceptiblity to erosion. Higher elevations consist of soils in the Ramsey Series and lower elevations in the Jefferson Series (Soil Survey 1945, 1953). Deep alluvial soil deposits can be found at the base of slopes and along riparian zones (Cain 1930), whereas shallow soils are consistently found along ridges and steep slopes.

Climate

Average annual temperatures vary from 14 °C at low elevations, to 8 °C at high elevations. Temperatures in January range from an average of 4.4°C at 445 m to -1.8°C at 1,919 m and in July from an average of 22.1°C at 445 m to 13.6°C at 1,919 m (Stephens 1969). The lowest temperatures have been recorded in February, and highest temperatures in July. The Great Smoky Mountains are considered a warm-temperate rain forest with an annual precipitation of 140 cm at low elevations and 230 cm at high elevations. Precipitation is greatest in late winter and mid summer, and lowest in October (Dickson 1960). Cloud cover increases with elevation and during the winter. Annual

average snow accumulation is low with only 16 days receiving snowfall. A large variety of microclimates exist within the national park due to large variation in elevation, aspect, rainfall amount, and temperature (Whittaker 1956).

Vegetation

The variety of microclimates supports a wide diversity of plant communities. Over 1,300 species of flowering plants, including 131 species of trees, can be found in the Park (Stupka 1960). Stupka (1960) also reported over 350 mosses and liverworts, 230 lichens, 50 ferns and fern allies, and 2,000 species of fungi. Much of the vegetation of the area is considered topographical climax or secondary succession (Whittaker 1956). Forests comprise approximately 95% of the national park and consist of a complex mixture of deciduous and coniferous types (Stupka 1960). Grass and heath balds and open fields make up the remaining area. Vegetation types have been classified by Cain (1930), Shanks (1954), Whittaker (1956), Golden (1974), Pyle (1988), and MacKenzie (1993). The vegetation classification by MacKenzie (1993) is the most recent (Table 2.1).

Wildlife

Great Smoky Mountains National Park is home to a large diversity of wildlife. Sixty-five species of mammals have been documented within the national park, of which 6 mammalian species have been extirpated (Linzey and Linzey 1971). Nearly half of the existing species are classified in the order Rodentia. Large mammals present within the

Table 2.1. Area and percentage of forest types with dominant tree species (ordered according to dominance), Great Smoky Mountains National Park (adapted from Mackenzie 1993).

	Dominant tree species			
Forest Type	**Common name**	**Scientific name**	**Hectares**	**Percentage**
Cove hardwood	Eastern hemlock	*Tsuga canadensis*	69,369	33%
	Sweet birch	*Betula lenta*		
	Red maple	*Acer rubrum*		
	Carolina silverbell	*Halesia carolina*		
	Tulip poplar	*Liriodendron tulipifera*		
	Northern red oak	*Quercus rubra*		
	American basswood	*Tilia heterophylla*		
	Yellow birch	*Betula lutea*		
Mixed mesic hardwood	Tulip poplar	*Liriodendron tulipifera*	33,096	16%
	Red maple	*Acer rubrum*		
	Eastern hemlock	*Tsuga canadensis*		
	Chestnut oak	*Quercus prinus*		
Pine	Table mountain pine	*Pinus pungens*	23,167	11%
	Pitch pine	*Pinus rigida*		
	Virginia pine	*Pinus virginiana*		
	Scarlet oak	*Quercus coccinea*		
Mesic oak	Northern red oak	*Quercus rubra*	21,327	10%
	Red maple	*Acer rubrum*		
	Chestnut oak	*Quercus prinus*		
Xeric oak	Chestnut oak	*Quercus prinus*	20,793	10%
	Red maple	*Acer rubrum*		
	Tulip poplar	*Liriodendron tulipifera*		
	Sourwood	*Oxydendrum arboreum*		
	Scarlet oak	*Quercus coccinea*		

Table 2.1 (continued)

	Dominant tree species			
Forest Type	**Common name**	**Scientific name**	**Hectares**	**Percentage**
Northern hardwood	Yellow birch	*Betula lutea*	19,329	9%
	American beech	*Fagus grandifolia*		
	Sweet birch	*Betula lenta*		
	Eastern hemlock	*Tsuga canadensis*		
	Red maple	*Acer rubrum*		
	Northern red oak	*Quercus rubra*		
	Red spruce	*Picea rubens*		
Tulip poplar	Tulip poplar	*Liriodendron tulipifera*	5,514	3%
	Red maple	*Acer rubrum*		
	Carolina silverbell	*Halesia carolina*		
Pine - oak	Scarlet oak	*Quercus coccinea*	5,067	2%
	Table mountain pine	*Pinus pungens*		
	Black gum	*Nyssa sylvatica*		
	Red maple	*Acer rubrum*		
	Chestnut oak	*Quercus prinus*		
Spruce - fir	Yellow birch	*Betula lutea*	5,002	2%
	Red spruce	*Picea rubens*		
	Red maple	*Acer rubrum*		

Park include black bear, white-tailed deer, and European wild boar (*Sus scrofa*), an exotic species. River otter (*Lutra canadensis*) populations have been restored through reintroductions, and although attempts to reintroduce the red wolf (*Canis rufus*) have failed, the reintroduction of elk (*Cervus canadensis*) currently is underway and looks promising. Over 200 bird species, 130 reptiles, 39 amphibians, 70 fish species, and a large diversity of invertebrates also have been reported within the national park (King and Stupka 1950). Currently, an all taxa biodiversity inventory is underway to document all species occurring within the Great Smoky Mountains National Park.

Park History and Land Use

The area that now makes up Great Smoky Mountains National Park has long been influenced by humans. European settlers used the land for farming, small and large-scale logging, livestock ranging, and burning (Pyle 1988). Farming occurred throughout this area, primarily on small farms located in coves and valleys. Open range pasturing was legal until 1913, when the fence law was enacted (Pyle 1988). These activities shaped the land in many different ways, particularly in the lower, more accessible areas. By the beginning of the twentieth century, approximately 85% of the Great Smoky Mountains were owned by timber and pulpwood companies. Large commercial timber companies dominated the ownership, bringing in steam engines, railroads, cable logging, and clear cutting techniques. These more advanced techniques allowed them to log in previously inaccessible areas (Pyle 1988).

Dr. Chase Ambler began the Appalachian National Park Association in 1899, with the purpose of establishing a national park in the area (Frome 1985). Dr. Ambler

and others, such as Carlos C. Cambpell and Mr. and Mrs. Willis Davis, played crucial roles in creating the national park (Campbell 1964). The Great Smoky Mountains were chosen as the best location, and land acquisition was completed in 1934, when Great Smoky Mountains National Park was dedicated (Lambert 1961). Great Smoky Mountains National Park is managed by the U.S. Department of the Interior, National Park Service and is currently one of the most visited parks in the country with >10 million visits per year.

CHAPTER III

MATERIALS AND METHODS

Hard Mast Data

Mast data for Great Smoky Mountains National Park were obtained from annual mast surveys conducted by the National Park Service from 1979 to 2000 (unpublished data, National Park Service, Gatlinburg, Tennessee, USA). These surveys were based on what has become known as the Whitehead index (Whitehead 1969). This technique involves random sampling of trees at 0.8-km intervals along established routes. Along each route, one vigorous tree with a 30-cm to 80-cm diameter at breast height (DBH) is chosen at each of 8 stops and the percentage of crown-bearing acorns is estimated. Five branches approximately 90-cm in length are chosen at random in the live crown of each sampled tree. The number of twigs on each branch, number of twigs with acorns, and the total number of acorns are recorded for each branch. Category totals are made for each tree from summed branch observations (Whitehead 1969). The Whitehead index (I) is calculated by:

$$I = ((D + B\backslash A) \times 0.0124) + (C\backslash B \times 0.4178) + 2.4281,$$

where, A is the total number of twigs, B is the total number of twigs with acorns or nuts, C is the total number of acorns or nuts, and D is the estimated percentage of crown producing acorns or nuts. The effectiveness of this survey method has been questioned due to unstandardized routes and surveying times and inconsistent application of the technique among personnel (Pozzanghera 1990). Nicholas and White (1984) also

criticized this method stating there was no biological rationale for calculating the percentage of the crown's twigs with acorns.

Recent research suggests alternative methods may be developed that are less subjective and based on quantitative relationships (Greenberg 2000). Greenberg (2000) placed acorn traps under the crowns of 765 individual oak trees from five oak species sampled throughout the southern Appalachians in Tennessee, North Carolina, and northern Georgia from 1993–1997. Oak species included northern red oak (n = 148), scarlet oak (*Q. coccinea*) (n = 142), black oak (*Q. velutina*) (n = 91), chestnut oak (*Q. prinus*) (n = 201), and white oak (n = 183). Greenberg (2000) calculated acorn production for individual trees by multiplying the number of mature acorns collected per m^2 trap area by tree crown area. She standardized comparisons among different-sized trees by taking the number of acorns per tree and converting it to the number of acorns per m^2 basal area per tree. Acorn production of each tree was ranked as 'poor', 'moderate', or 'good' by comparing its 5-year mean number of acorns/m^2 basal area to the 5-year mean of its species. Using these data, Greenberg and Parresol (2000) developed linear regression models of acorn yield (mean number of acorns per m^2 basal area) for the 5 oak species. They found that the proportion of sampled trees bearing acorns was a significant and strong predictor of acorn yield in any given year. Field data from visual mast surveys, such as the Whitehead index, can be used with these equations to quantitatively estimate within-year acorn yields for each species (Greenberg and Parresol 2000).

Pelton (1989) suggested the distribution of white oak and northern red oak mast substantially influences black bear population in the southern Appalachians. Indeed,

northern red and white oaks have been found to be the best producers of acorns in the areas around Great Smoky Mountains National Park (Greenberg and Parresol 2002), and therefore, were the focus of my study. To apply the National Park Service mast data to the equation outlined by Greenberg and Parresol (2000), the proportion of acorn-bearing trees must be known. Mast data collected by National Park Service personnel included the number of trees of each species with and without acorns for each year. Thus, I compiled the northern red and white oak mast data by year, and recorded how many trees within each year produced acorns. For each species, I then calculated the proportion of sampled trees bearing acorns for each year. Once the proportion of acorn-bearing trees was estimated, I calculated the natural logarithm of acorn crop yield as follows:

$$\hat{y} = b_0 + b_1 x, \qquad \text{eq. 1}$$

where, $\hat{y}$ is the predicted logarithm of acorn crop yield, b_0 is the intercept, b_1 is the regression coefficient, and x is an estimate of the proportion of acorn-bearing trees within the sample. Equation 1 is based on basal area measurements (m^2), thus the predicted acorn crop yield can only be derived by incorporating the basal area of each tree species within a given year and area (Greenberg and Parresol 2000). However, mast data collected by the National Park Service did not include basal area measurements. Therefore, applying equation 1 to the mast data from the National Park Service (1981-1999) would require the assumption that there is no change in basal area over this time period, which is unlikely. Basal area can be derived from diameter at breast height (DBH) measurements, which was collected for all sampled trees during 1990-1999. However, only trees within a specific DBH range (30–80 cm) were sampled. Typically, basal area is measured in vegetation plots instead of selecting random trees over a large

area, with only a minimum DBH (e.g., 10 cm) for sampling. Therefore, basal area measurements derived from these DBH measurements may not be very accurate. In order to use the regression equation described by Greenberg and Parresol (2000), I used a modification of equation 1 by omitting the basal area conversions. However, leaving out this portion of the equation changes the interpretation of the results to reflect an index of acorn production (hereafter referred to as the mast regression index) rather than an estimate of acorn yield.

Black Bear Population Estimates

Estimates of black bear population abundance were obtained from a long-term black bear study in the northwestern quadrant of Great Smoky Mountains National Park. Black bears have been captured and tagged on this study area since 1969 with barrel or culvert traps and Aldrich spring-activated foot snares (Aldrich Animal Trap Company, Clallam Bay, Washington, USA). Spring-activated snares were used exclusively after 1982 for the mark-recapture study. Since 1989, livetrapping has been conducted on 8 traplines with 6–9 trap sites each. Beginning in May and concluding in August of each year, two teams of field researchers simultaneously trapped 2 traplines for 14 trapnights each, resulting in 4 trapping periods of 2 traplines each summer. Trapsites averaged 774 m in elevation and were set an average of 587 m apart (Eason 2002). Trapsites were placed away from trails so hikers could not easily see or hear captured bears.

Black bears were immobilized with M99 (Etorphine hydrochloride, D-M Pharmaceuticals, Rockville, Maryland, USA) at a dosage of 1 ml per 45.5 kg body weight, Sernylan (Phencyclidine hydrochloride, Parke Davis and Co., Morris Plains, New

Jersey, USA) at a dosage of 1 ml per 1 kg body weight (Cook and Pelton 1982), or, since the mid 1980s, a mixture of ketamine hydrochloride (200 mg/ml); (Aveco Co., Inc., Fort Dodge Iowa, USA), and xylazine hydrochloride (100 mg/ml) (Rugby Laboratories, Inc., Rockville Center, New York, USA), at a dosage of 1 ml per 2.5 kg body weight. Upon immobilization, an ophthalmic ointment was used to moisturize the bear's eyes and triple antibiotic was used to treat any cuts or minor wounds. Bears with more serious injuries were intramuscularly injected with antibiotic (Liquamycin) at a dosage of 8.8 mg/kg body weight. All bears were ear tagged, lip tattoed, measured, and weighed. A premolar tooth was extracted for aging purposes by counting cementum annuli (Willey 1974). Radio collars (Telonics, Mesa, Arizona, USA) with motion-sensitive activity monitors were fitted on adult females. Any female bear that was lactating was given a 1-ml intramuscular injection of oxytocin (Burns Veterinary Supply, Oakland, California, USA) to stimulate milk production. Since 1989, yohimbine hydrochloride (Sigma Chemical Co., St. Louis, Missouri, USA) was injected intravenously at a dosage of 1 ml per 45.5 kg body weight as an antagonist to xylazine hydrochloride.

I used the mark-recapture data based on livetrapping to calculate annual Jolly-Seber population estimates. Jolly-Seber is an open model of population estimation produced by program JOLLY (Pollock et al. 1990), which allows additions (birth or immigration) and deletions (death or emigration) to the population during the sampling period. The Jolly-Seber model requires a minimum of 3 sampling periods, and is based on the following assumptions:

1) the probability of survival and capture is equal among individuals,
2) marks are not lost, and

3) animals are returned to the population immediately after marking.

Population size is estimated by:

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

where $\hat{N}_i$ represents the total number of animals in the population just before the i^{th} sample, n_i is the number of animals captured in the i^{th} sample, m_i is the number of marked animals captured in the i^{th} sample, and $\hat{M}_i$ is the total number of marked animals in the population just before the i^{th} sample;

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

where z_i is the number of animals captured before the i^{th} sample that were not captured in the i^{th} sample, but are captured in a later sample, r_i is the number of animals released from the i^{th} sample that are subsequently recaptured, and R_i is the number of animals released with marks from the i^{th} sample. Population estimates can be derived using several Jolly-Seber models. Model A is the standard Jolly-Seber model for open populations and allows capture and survival probabilities to vary over time. Model A', sometimes referred to as the "deaths only" model, allows deletions to the population through death and emigration, but assumes negligible additions due to births and immigration. Model B, the constant survival model, requires survival probabilities to remain constant throughout the study. Model D requires both survival and capture probabilities to remain constant during the study.

I used program JOLLY (Pollock et al. 1990) to calculate all Jolly-Seber population estimates. I selected the best model by using goodness-of-fit tests produced by program JOLLY. However, Pollock et al. (1990) noted that non-significant goodness-of-fit tests do not guarantee that all model assumptions are met. It is important to look at the characteristics of the data upon which the model is based, along with the goodness-of-fit tests, to determine which model best fits the data.

Data Analysis

My analysis focused on comparing relationships between population data and mast data from 2 time periods: 1981–1999 and 1990–2000. Trapping was performed more consistently during 1990–2000 than 1981–1999, which resulted in a more contiguous and larger sampling area (Figure 3.1).

A correlation analysis was first performed on the proportion of sampled trees bearing acorns for northern red oak and white oak to determine if differences in acorn production existed. I then performed a correlation analysis between the two methods of mast calculation, the Whitehead Index and mast regression index, to determine if similarities existed. These correlations were based on mast indices from white oak alone, northern red oak alone, and the two species combined.

Estimates of the black bear population and National Park Service mast indices were derived annually from 1981–1999. Black bear population estimates and mast data were characterized as time series data. Time series are sets of time-ordered observations in which the interval of time that separates each observation is constant. Data in a time series may not be independent of each other as required by normal regression analysis.

For example, black bear population abundance is influenced by population trends of previous years. Data must be comparable in location and time to ensure reliable results (Pinola and Rahgozar 1997). A time series analysis can be used to identify periodicities in data, determine what portion of the fluctuations in the data is due to random error (noise) versus more systematic sources, and identify trends in data. Results from a time series analysis can be used for predictive purposes or to determine why the data behave in a certain way (Bart and Garton 1996).

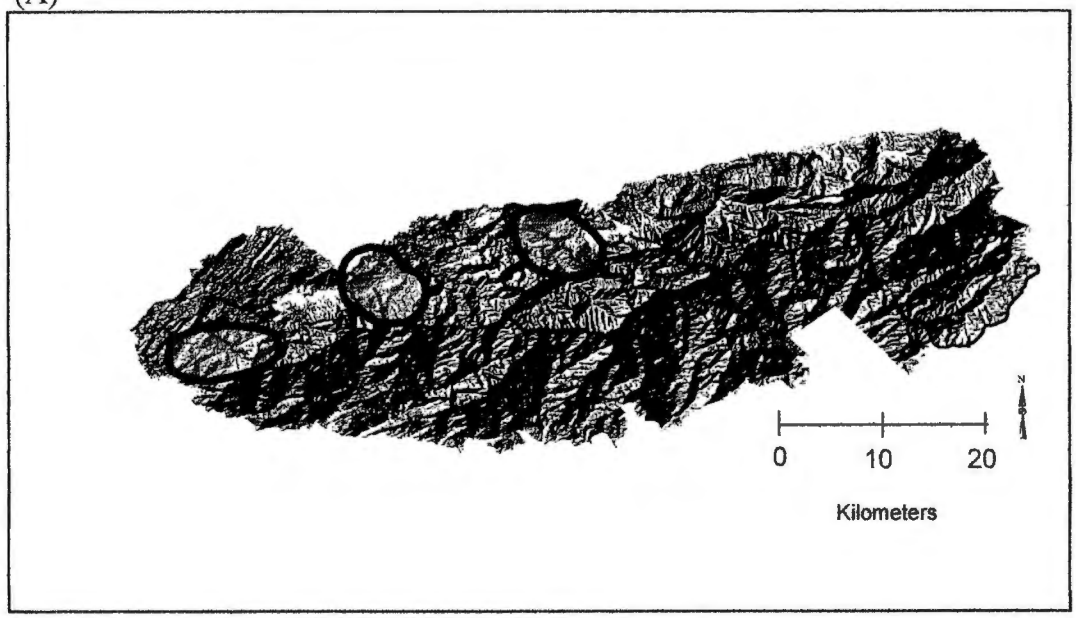
Ordinary regression analysis is based on the assumption that errors are independent of each other. The assumption of uncorrelated or independent error terms often is violated in time series data (Neter et al. 1996). In ordinary regression this violation causes the statistical tests of the significance of parameters and confidence limits for the predicted values to be incorrect. Furthermore, the function of regression coefficients also may be lost. An example of an appropriate regression model for time series analysis is:

$$y_t = \beta_o + \beta_1 x_1 + \epsilon_t \qquad t = 1, \ldots, n$$

where, y_t is the dependent variable, β_o is the intercept, β_1 is the regression coefficient, x_1 is the independent variable, and ϵ_t represents the autocorrelation assumption.

I used autoregression analyses (PROC AUTOREG; SAS Institute 1999) to determine whether hard mast production was associated with population trends of black bears. Autoregression analyses have been used with time series population data of other animal species (e.g., snowshoe hare (*Lepus americanus*) (Stenseth et al. 1997) and lynx (*Lynx Canadensis*) (Stenseth et al. 1998)). The AUTOREG procedure estimates and forecasts linear regression models for

(A)



(B)

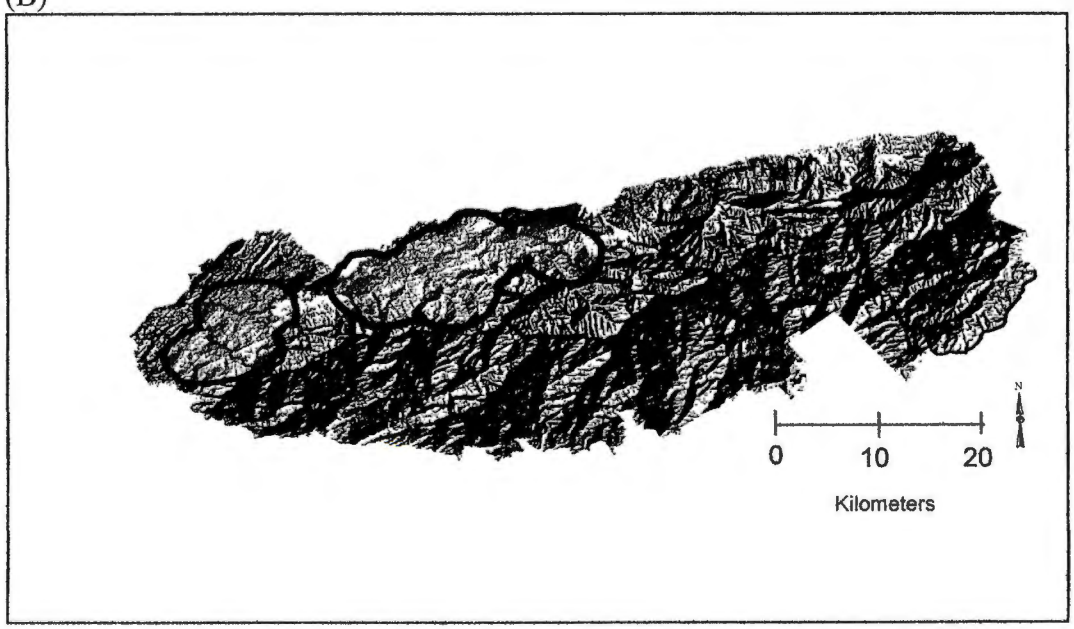


Figure 3.1. Great Smoky Mountains National Park and the black bear study area based on mark-recapture period (A) 1989–1999 and (B) 1990–2000.

time series data when the errors are autocorrelated or heteroscedastic. PROC AUTOREG is a useful tool for forecasting because it uses the time series component of the model as well as the systematic component in generating predicted values. The autoregressive error model takes into account recent departures from the trend in producing forecasts. The AUTOREG procedure produces generalized Durbin-Watson (DW) statistics and their marginal probabilities to diagnose autocorrelation. Exact *P*-values are reported for generalized Durbin-Watson tests to any specified order. Adjustments for autocorrelation can be made to the data by including autoregressive terms in the model. These autoregressive terms produce autocorrelation parameters to a specified order. The AUTOREG procedure uses a hierarchy principal when using autoregressive terms. For example, if one specifies a second-order autoregressive term, the program will automatically give results for the first- and second-order autoregressive terms.

In addition to time series effects, lag times in the data may play a part in relationships between mast production and the black bear population. Population estimates are based on the mark-recapture study during the summer months, whereas mast production occurs during fall. Mast production from one year clearly could not affect the black bear population estimate from the same year because it occurs after the population estimate for that year is determined. However, mast production may have considerable effects on the population in subsequent years. Female black bears may first produce offspring as early as 3 years, but more commonly at 4–5 years. Once maturity is reached, female black bears usually reproduce once every 2 years. Offspring are born in late January or early February and stay with their mother through the next winter den season (Pelton 1982). The nutritional condition of black bears during hibernation can be

affected by food production during fall. The physical condition of a pregnant female when entering the den may influence the number of cubs born, their health, and, ultimately, their survival (Eiler et al. 1989). Consequently, severe mast failures may result in no or low reproductive success. If abundant mast crops follow a mast failure in subsequent years, breeding synchrony may occur, resulting in marked population responses. Eason (2002) showed an example of breeding synchrony in Great Smoky Mountains National Park with marked hard and soft mast failures in 1992 causing a loss of cubs in 1993. The fall food shortage in 1992 synchronized breeding in 1993, causing birth pulses during 1994, 1996, and 1998. The year following a poor mast season also may show an increase in bear mortality in the younger age classes. Competition for food with dominant bears may cause subordinate bears to move out of the Park, where they are at greater risk of mortality. Because events such as these may create a delayed response of 1–3 years, I examined lags of 1, 2, and 3 years between the population estimates and the mast data. For example, population estimates from 1990, were compared with mast data from 1989 (1-year lag), 1988 (2-year lag), or 1987 (3-year lag).

I used the black bear population estimates as the dependent variable and the northern red oak, white oak, and combined mast indices as the independent variables. All possible variable combinations, including lag times up to 3 years, were explored. Autocorrelation was assessed using Durbin-Watson statistics. First- and second-order autoregression terms were used in some of the regressions to account for serial correlation. Results were based on significance of the model (*P*-values), the amount of variation explained (R^2), the model fit based on Akaike's Information Criterion (AIC), and the predictive qualities (mean difference between population estimates and predicted

population estimates, Root MSE). In comparing models, the lowest *P*-values, AIC values, and Root MSE values along with the largest R^2 values were used to select the best models. I selected the best model for each method within each of the 2 time periods, and compared these models to determine which method of mast calculation produced the best predictions.

CHAPTER IV

RESULTS

Hard Mast Data

Hard mast data used in this study were collected by the National Park Service from 1979–1982 and 1985–2000, and included 1,702 observations on northern red oak trees and 820 observations on white oak trees. The National Park Service used these data to calculate the Whitehead index (Table 4.1). To calculate the mast regression index from these mast data, I calculated the proportion of sampled trees bearing acorns for each year (Table 4.2). I then incorporated those values into the regression equations given by Greenberg and Parresol (2000) to calculate the mast regression index (Table 4.3).

Correlations

The proportion of sampled northern red oak and white oak trees bearing acorns showed some similarity, but was not strongly correlated ($R^2 = 0.41$, $P = 0.077$). White oak acorn production exhibited more variability than northern red oak (Figure 4.1). The mast regression index was correlated with the Whitehead index for northern red oak ($R^2 = 0.80$, $P < 0.001$), white oak ($R^2 = 0.86$, $P < 0.001$), and a combination of the two oaks ($R^2 = 0.76$, $P < 0.001$).

Table 4.1. Annual acorn production estimates based on the Whitehead index, Great Smoky Mountains National Park, 1979–2000 (Unpublished data, National Park Service, Gatlinburg, Tennessee, USA).

Year	Northern red oak	White oak	Combined oak[a]
1979	3.48	3.84	3.66
1980	4.77	0.50	2.99
1981	2.66	4.13	3.29
1982	2.14	0.65	1.62
1983			
1984			
1985	2.60	3.08	2.83
1986	3.46	2.82	3.17
1987	3.34	3.39	3.36
1988	3.33	3.22	3.30
1989	3.62	1.77	3.03
1990	2.74	2.28	2.52
1991	1.46	1.54	1.49
1992	2.05	1.65	1.88
1993	3.31	0.27	2.19
1994	2.62	1.34	2.04
1995	4.60	1.99	3.63
1996	2.22	4.05	2.94
1997	2.88	0.46	1.98
1998	3.84	1.81	3.19
1999	1.84	1.55	1.72
2000	1.80	0.80	1.46

[a] Northern red oak and white oak combined

Table 4.2. Number and proportion of northern red oak and white oak trees producing acorns within each year, Great Smoky Mountains National Park, 1979–2000.

	White oak				Northern Red Oak			
Year	No Acorns	Acorns	Total	Proportion with Acorns	No Acorns	Acorns	Total	Proportion with Acorns
1979	6	17	23	0.739	11	24	35	0.686
1980	14	7	21	0.333	6	35	41	0.854
1981	6	29	35	0.829	23	22	45	0.489
1982	18	7	25	0.280	32	21	53	0.396
1983								
1984								
1985	5	26	31	0.839	6	25	31	0.806
1986	6	36	42	0.857	3	69	72	0.958
1987	1	49	50	0.980	12	75	87	0.862
1988	7	46	53	0.868	19	111	130	0.854
1989	24	44	68	0.647	12	127	139	0.914
1990	7	38	45	0.844	10	68	78	0.872
1991	19	23	42	0.548	61	51	112	0.455
1992	29	12	41	0.293	65	70	135	0.519
1993	26	5	31	0.161	23	83	106	0.783
1994	13	38	51	0.745	31	74	105	0.705
1995	14	33	47	0.702	7	93	100	0.930
1996	2	43	45	0.956	31	59	90	0.656
1997	28	11	39	0.282	28	51	79	0.646
1998	14	25	39	0.641	13	94	107	0.879
1999	23	31	54	0.574	33	43	76	0.566
2000	21	17	38	0.447	47	34	81	0.420

Table 4.3. Acorn production estimates for white oak and northern red oak based on the mast regression index, Great Smoky Mountains National Park (1979–2000).

Year	Northern Red Oak	White Oak
1979	7.826	8.556
1980	8.846	5.275
1981	6.631	9.279
1982	6.068	4.844
1983		
1984		
1985	8.560	9.361
1986	9.482	9.510
1987	8.898	10.503
1988	8.848	9.597
1989	9.211	7.811
1990	8.957	9.407
1991	6.427	7.007
1992	6.811	4.946
1993	8.417	3.884
1994	7.942	8.604
1995	9.310	8.256
1996	7.643	10.305
1997	7.582	4.860
1998	8.997	7.762
1999	7.098	7.221
2000	6.211	6.197

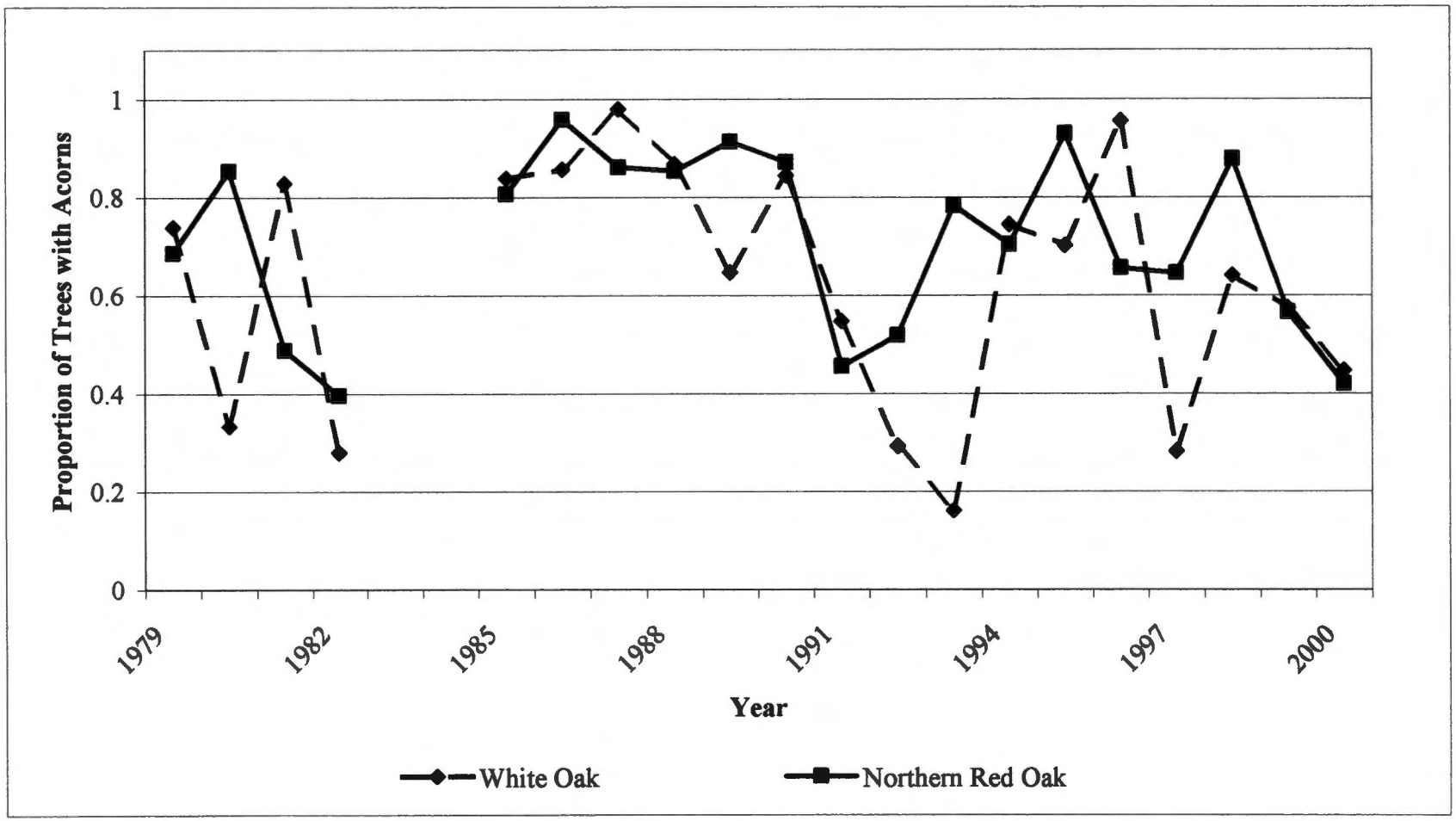
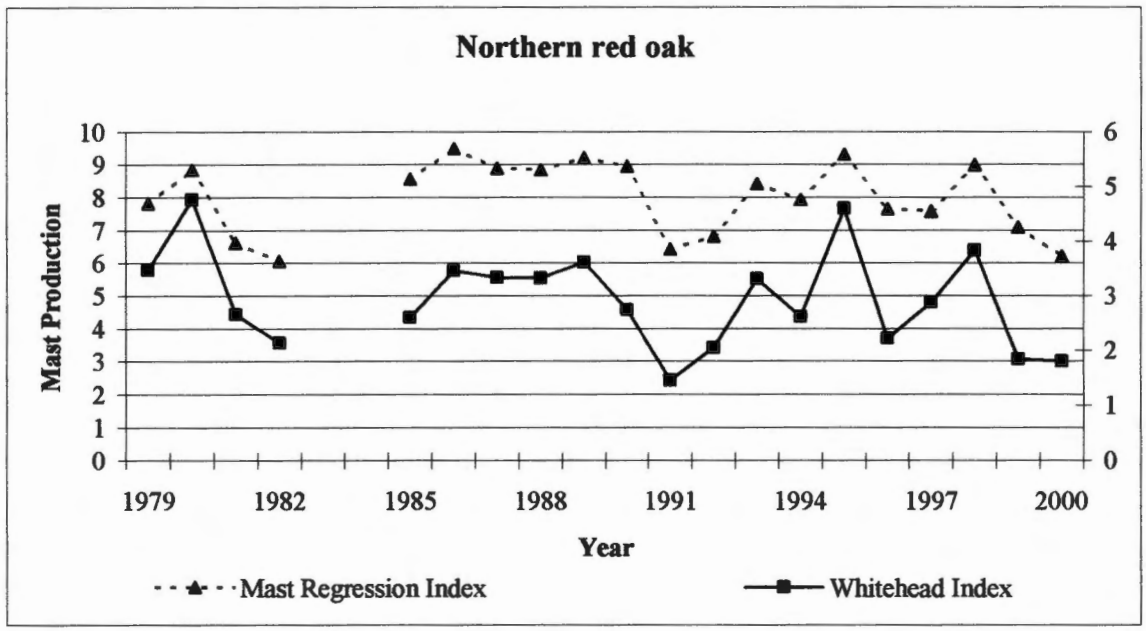


Figure 4.1. Proportion of sampled white oak and northern red oak trees with acorns, Great Smoky Mountains National Park, 1979–2000.

(A)



(B)

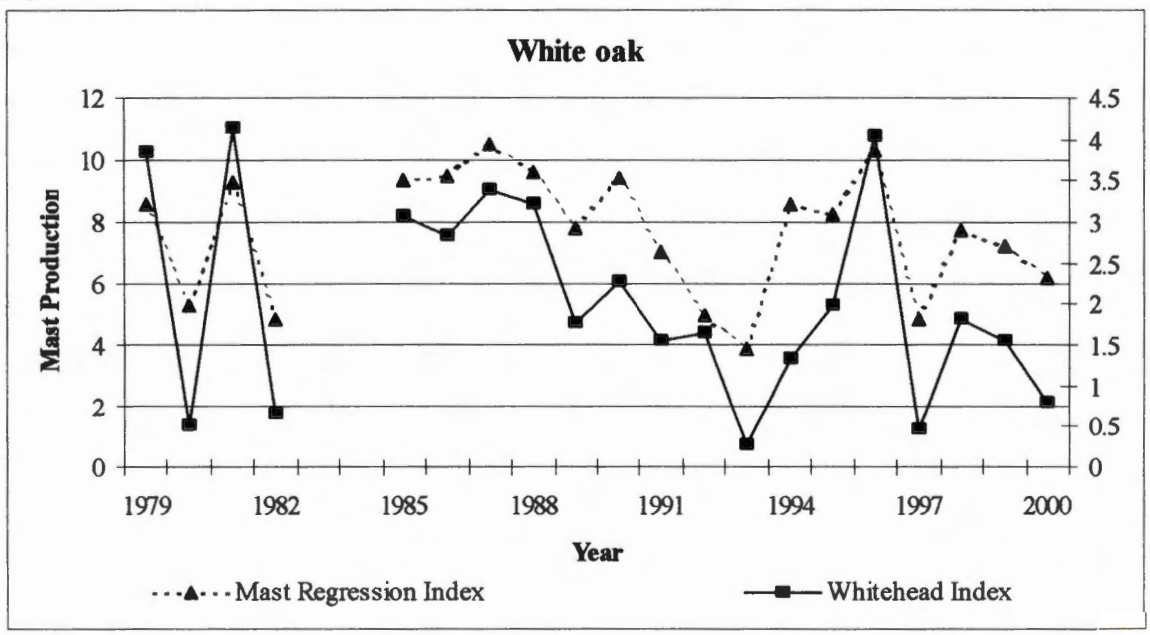


Figure 4.2. Mast indices calculated based on the mast regression index and whitehead index for (A) northern red oak, (B) white oak, and (C) northern red oak and white oak combined, Great Smoky Mountains National Park, 1979–2000.

(C)

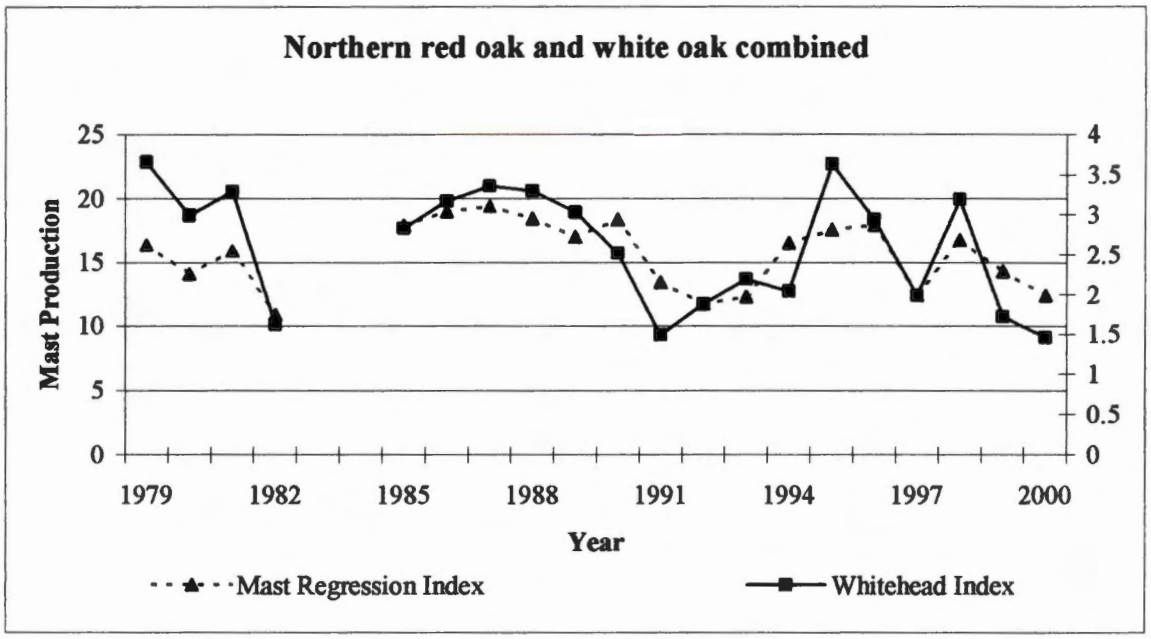


Figure 4.2. (continued)

Black Bear Population Estimates

Jolly-Seber models A (1981–1999) and B (1990–2000) best fit the data according to the goodness-of-fit tests produced by Program JOLLY. Model A is the standard Jolly-Seber model that allows capture and survival probabilities to vary over time. Model A was to estimate population abundance for 1981–1999 (Table 4.4); this seemed reasonable because capture and survival probabilities likely vary over such a long period of time. Jolly-Seber model B is based on constant survival and was used to estimate bear abundance for the period 1990–2000 (Table 4.5). This model was appropriate because survival within a protected black bear population tends to be high and exhibit little variation, particularly over a relatively short time period.

Autoregression Analysis

Period 1981–1999. All models during the 1981–1999 time period exhibited common trends. Models including white oak mast from the current year showed more significant results compared with all other models (Appendix A). Models based on the mast regression index showed that white oak combined with two autoregression parameters was the best model (Model 11, Tables 4.6 and A.2). The second autoregression term corrected for autocorrelation ($P = 0.056$) within the white oak variable and increased the model's significance ($P = 0.001$ and $R^2 = 0.53$). Predicted values based on this regression model (Model 11) were similar to actual population estimates with an average difference of 49 bears (Root MSE) between the observed population estimate and the predicted values (Figure 4.3).

Table 4.4. Black bear population estimates (*N*) and standard error (SE) based on Jolly-Seber Model A, Great Smoky Mountains National Park, 1981–1999.

Year	*N*	SE
1981	105	38
1982	43	18
1983	107	43
1984	66	26
1985	134	62
1986	166	81
1987	203	98
1988	148	75
1989	186	89
1990	123	65
1991	92	36
1992	139	55
1993	63	23
1994	132	42
1995	124	30
1996	324	130
1997	113	27
1998	102	28
1999	74	27

Table 4.5. Black bear population estimates (*N*) and standard error (SE) based on Jolly-Seber Model B, Great Smoky Mountains National Park, 1990–2000

Year	*N*	SE
1990	314	93
1991	294	68
1992	311	67
1993	216	43
1994	261	44
1995	281	33
1996	325	41
1997	292	29
1998	389	53
1999	304	34
2000	264	35

Table 4.6. Autoregression results for the mast regression index and Whitehead index with population estimates based on Jolly-Seber Model A, Great Smoky Mountains National Park, 1981–2000.

Model	Method	Variable	Parameter Estimate	*P*	R^2	AIC	Durbin Watson	Root MSE
1	Mast Regression Index	Intercept	-35.27	0.400	0.53	184.99	$P > 0.05$	48.81
		White Oak	22.54	0.001				
		Autoregression Term 1	0.05	0.853				
		Autoregression Term 2	0.52	0.056				
2	Whitehead Index	Intercept	58.35	0.040	0.42	183.53	$P > 0.05$	50.60
		White Oak	35.50	0.005				

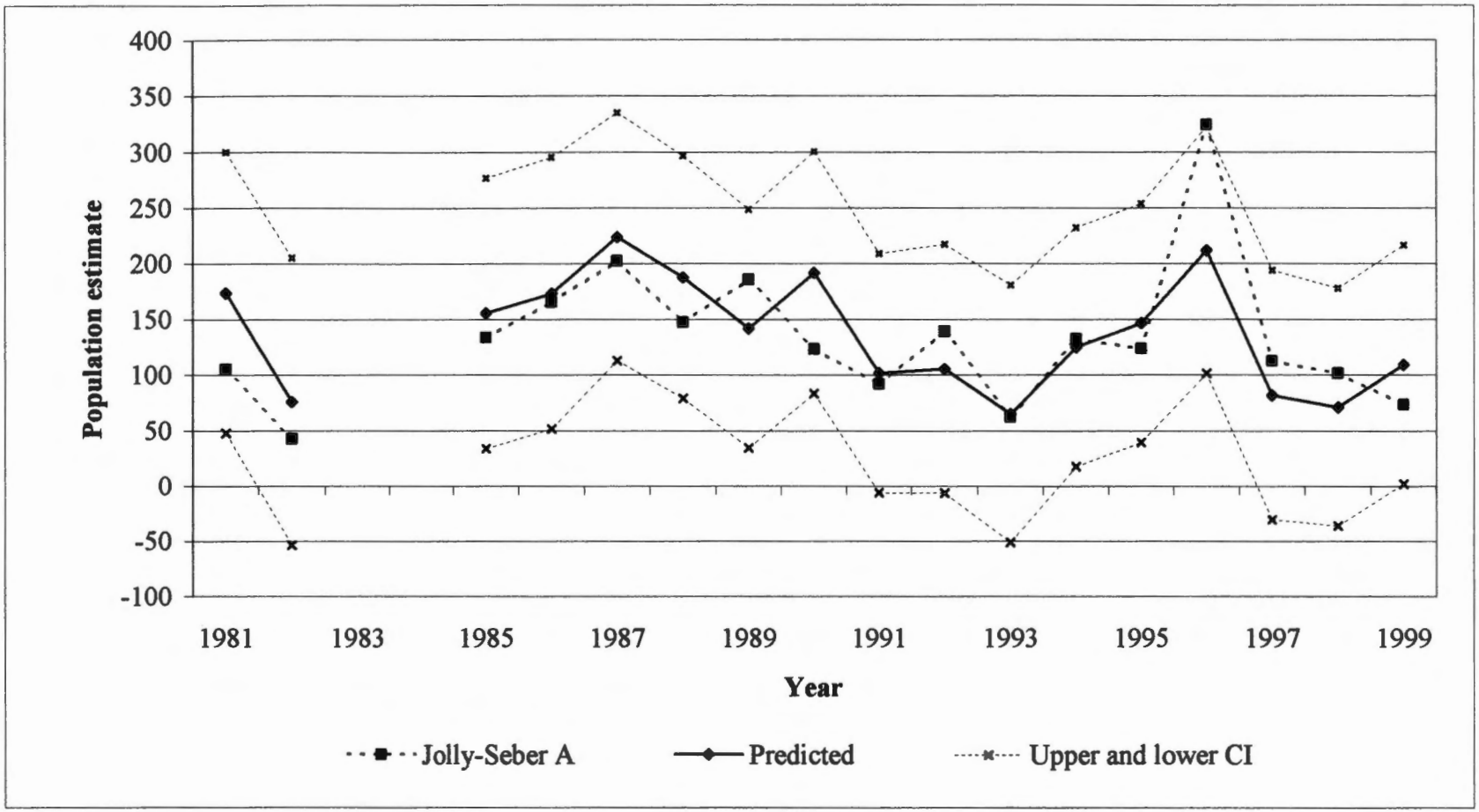


Figure 4.3. Predicted black bear population estimates with 95% confidence intervals (CI) based on regression with the mast regression index (Model 11), Great Smoky Mountains National Park, 1981–1999. Observed Jolly-Seber (Model A) population estimates are shown for reference.

White oak mast of the current year also was the best model based on mast data from the Whitehead index (Model 7, Tables 4.6 and A.1). There was an average difference of 51 bears between predicted and observed population estimates (Figure 4.4). Comparisons of these 2 models indicated that their predictive capabilities were similar.

Period 1990–2000. Autoregressions based on population estimates from 1990–2000 and all combinations of northern red and white oak for the two mast indices (Appendix B) indicated that white oak with a 2-year lag was an important variable. This variable provided the best model using the mast regression index (Model 9, Tables 4.7 and B.2), and was included in the best model using the Whitehead index (Model 16, Tables 4.7 and B.1).

White oak mast from 2 years previous provided the best model based on the mast regression index (Model 9, Tables 4.7 and B.2). Predicted population estimates based on this model closely matched actual population estimates (Figure 4.5, Root MSE = 38.40). For the Whitehead index, the white oak mast from 2 years before also was significant, and adding the northern red oak mast from the previous year further improved this model (Model 16, Tables 4.7 and B.1). Application of this model indicated an average difference of 35 bears (Root MSE) between the predicted and observed population estimates (Figure 4.6). Comparisons of the two mast indices showed that the model for the Whitehead index was slightly more significant ($P = 0.041$) than the mast regression index ($P = 0.079$) and explained more of the variation in the data ($R^2 = 0.30$ and 0.49, respectively; Table 4.7).

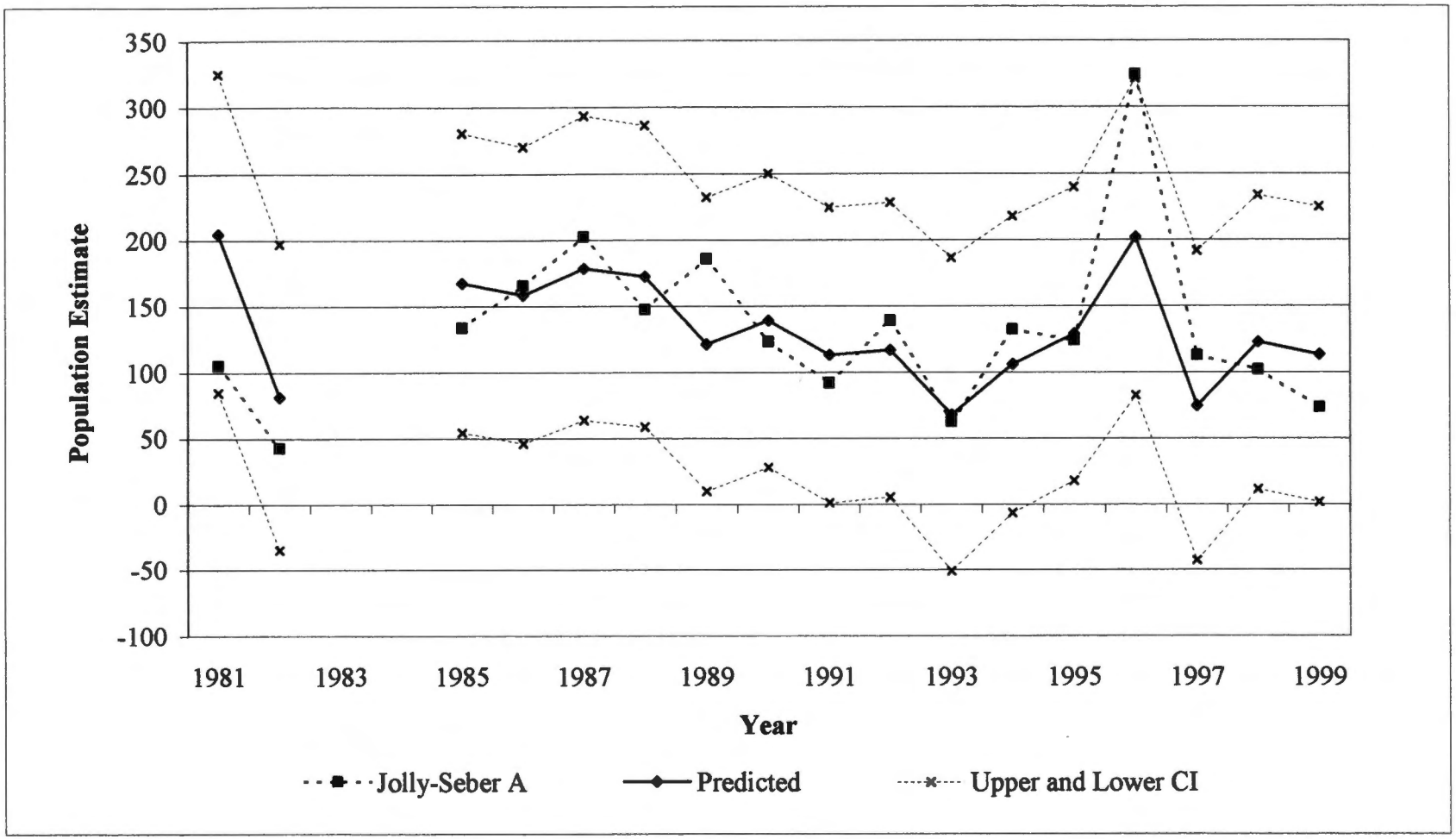


Figure 4.4. Predicted black bear population estimates with 95% confidence intervals (CI) based on regression with the Whitehead index (Model 7), Great Smoky Mountains National Park, 1981–1999. Observed Jolly-Seber (Model A) population estimates are shown for reference.

Table 4.7. Autoregression results for the mast regression index and Whitehead index with population estimates based on Jolly-Seber Model B, Great Smoky Mountains National Park, 1990–2000.

Model	Method	Variable	Parameter Estimate	*P*	R^2	AIC	Durbin Watson	Root MSE
9	Mast regression index	Intercept	210.20	0.001	0.30	113.27	$P > 0.05$	38.40
		White oak, 2-year lag	11.40	0.079				
16	Whitehead Index	Intercept	194.72	0.002	0.49	111.82	$P > 0.05$	34.82
		Northern red oak, 1-year lag	19.37	0.138				
		White oak, 2-year lag	24.84	0.041				

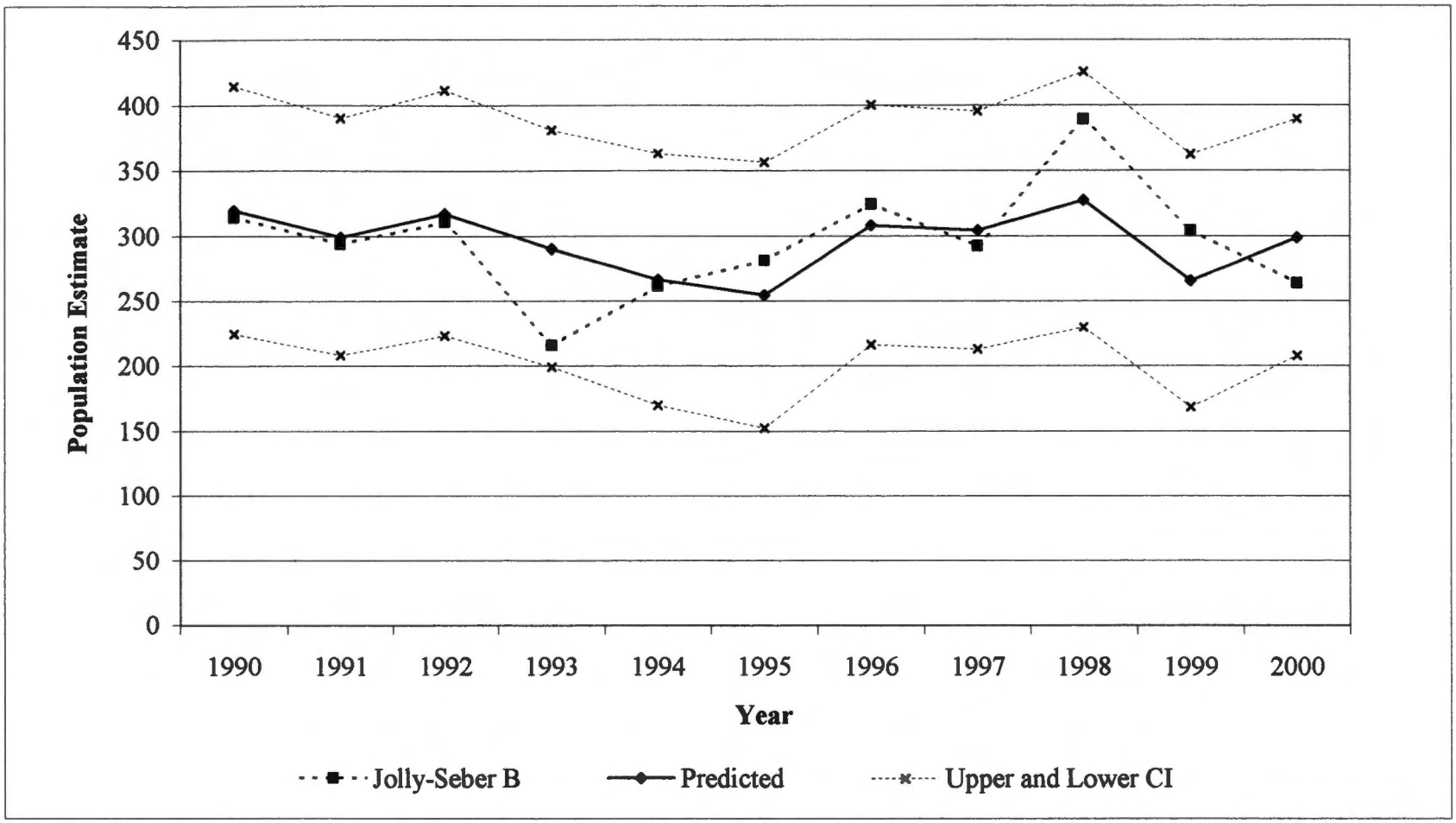


Figure 4.5. Predicted black bear population estimates with 95% confidence intervals (CI) based on regression with the mast regression index (Model 9), Great Smoky Mountains National Park, 1990–2000. Observed Jolly-Seber (Model B) population estimates are shown for reference.

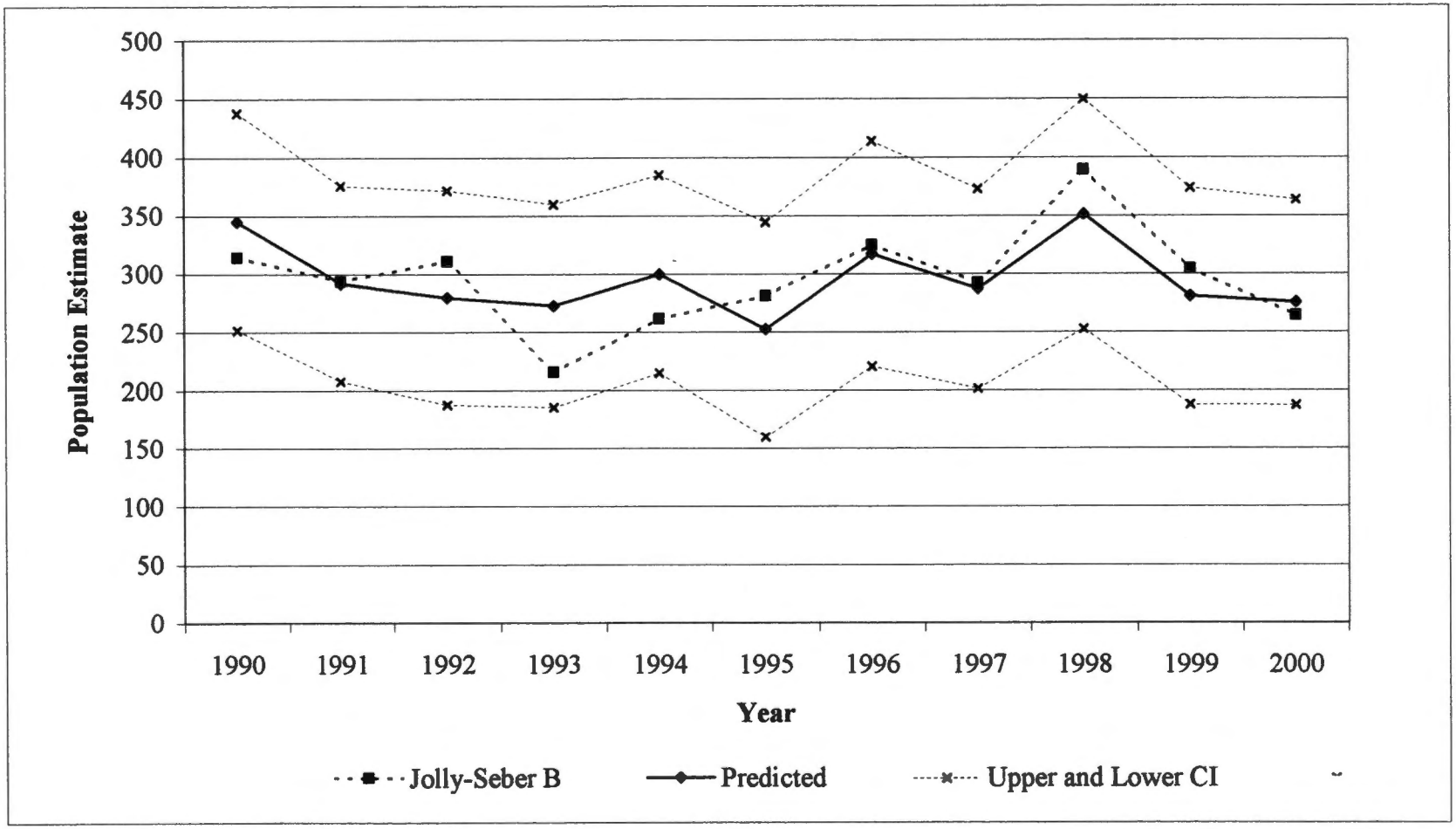


Figure 4.6. Predicted black bear population estimates with 95% confidence intervals (CI) based on regression with the Whitehead index (Model 16), Great Smoky Mountains National Park, 1990–2000. Observed Jolly-Seber (Model B) population estimates are shown for reference.

CHAPTER V

DISCUSSION

Black Bear Population Estimates and Hard Mast Surveys

Long-term population studies are important to detect relationships between mast production and population abundance over time. The long-term black bear mark-recapture study in Great Smoky Mountains National Park provided a unique dataset to examine such relationships. Similar to many other field studies of large carnivores, that database had its limitations. Otis et al. (1978) and White et al. (1982) suggested that optimal mark-recapture studies should minimize the perimeter-to-area ratio of the study area by approximating a circle or square in shape, cover a large enough area to sample at least 50 individuals, and saturate the entire study area with a minimum of 4 trapsites per home range. That sampling design should result in a high capture probability that is equal for all individuals within the study area, unless temporal or behavioral responses exist. Because of logistical problems primarily related to access, the study in Great Smoky Mountains National Park did not represent an ideal sampling design. The nearly linear traplines resulted in high perimeter-to-area ratios and a non-contiguous study area (Eason 2002). Some traplines changed over the course of this study, so comparisons could only be made for areas consistently trapped throughout the entire study period, which limited the area for which population estimates could be derived. Only three areas, containing nearly linear traplines, were consistently sampled during 1981–1999 (Figure 2.1). Population estimates based on this dataset likely included sampling biases, which should be considered when examining results. For example, black bear home ranges may

only partially overlap trapsites and bears may easily move in and out of the linear study areas without being captured. Furthermore, the majority of trapsites were located along ridge tops, where fluctuation in food availability may affect the potential for captures. A good soft mast crop, for example, may cause untagged bears to move into the study area, possibly biasing population estimates high. In poor mast years, bears may move out of the area, which may reduce the number of new bears captured, thus biasing the estimate low. Another possible bias in the population estimates could be learned trap response. Once trapped, some bears become "trap smart", making it more difficult to recapture them. This trap response bias may be reduced by the 14-day trapping period and long-term nature of the study, which allows "trap smart" bears multiple opportunities to be recaptured (Coley 1995, Pedersen 1995).

Estimates of the black bear population from 1990–2000 were based on a larger and more contiguous study area (Figure 3.1). Standard errors were lower for the population estimates from 1990–2000 (Tables 4.4 and 4.5). Overall, these estimates likely included less sampling bias and were more precise compared with the 1981-1999 estimates.

Black bear population estimates from the study area were compared to the mast data collected for the entire national park. I used mast survey data from the entire national park to increase sample size and to better capture variation in the mast indices. Coley (1995) also studied relationships between black bear population estimates and mast production in the national park, but only used survey routes within the study area. Only a small number of trees were sampled within the study area and the mast index showed little variation, resulting in erratic relationships that were difficult to interpret. By

comparing bear population estimates from the study area in the northwestern quadrant to mast indices for the entire national park, I assumed that bear densities were relatively uniform throughout the national park. Eason (2002) estimated black bear density in two study areas of Great Smoky Mountains National Park, one in Tennessee (used in this study) and the other in North Carolina. He found that density estimates for the two areas did not differ markedly using 3 common estimators (Lincoln-Petersen, Bailey's binomial, and Jolly-Seber). Thus, my assumption of uniform density was probably reasonable.

Mast indices are widely used for sampling large areas where information about mast production is needed. Although poor and excellent mast years were observed (Pozzanghera 1990), the Whitehead index never achieved a rating of 0 or 10, the lowest and highest possible scores, respectively. The Whitehead index consistently rated mast production as fair, despite large annual variation (Table 4.1). Visual surveys are time consuming and provide indirect estimates of acorn crop yield, which may be biased by differences in observers (Greenberg and Parresol 2000). Thus, the importance of examining new methods of mast production is evident. Greenberg and Parresol (2000) found that the proportion of trees bearing acorns was a significant and strong predictor of acorn crop yield (no. of acorns/m^2 basal area) in any given year, and this proportion was highly correlated with the number of acorns on fruiting trees. Because application of the equation only requires observation of the presence or absence of acorns, this method is less vulnerable to observer bias, although observers may miss small numbers of acorns. The Greenberg and Parresol (2000) equation was based on mast data from three national forests located in the southern Appalachians (Cherokee, Pisgah, and Chattahoochee). Because these national forests surround Great Smoky Mountains National Park, I

assumed the regression models of Greenberg and Parresol (2000) were applicable to the national park. The major forest components that may have differed between these areas were the spruce-fir component and, to some extent, the northern hardwood component.

Population Abundance and Acorn Production

The Whitehead index and mast regression index were correlated ($P < 0.001$) for white oak, northern red oak, and a combination of the 2 species, which show these two mast production methods may be comparable. When comparing indices for the period 1981–1999 (Table 4.6), the mast regression index explained more of the variation in the data ($R^2 = 0.53$) than models based on the Whitehead index ($R^2 = 0.42$), and was found to be more significant ($P = 0.001$, $P = 0.005$). However, the mast regression index produced slightly better predictions compared with the Whitehead index (Root MSE = 48.81 and 50.60 respectively). For the time period 1990–2000, the Whitehead index explained more of the variation in the data, although other diagnostical statistics were similar to the mast regression model (Table 4.7). The two methods showed similar results, therefore using the mast regression index may not be an improvement over the Whitehead index.

Population estimates from the 1990–2000 period were more precise and may have been more accurate, which may have caused some differences in results compared with the 1981–1999 period. Indeed, models for the 1990–2000 period predicted population estimates better and exhibited a better fit than models for the 1981–1999 period. Therefore, my interpretation of the regression models will focus on the 1990–2000 period.

For the period 1981–1999, both the mast regression index and Whitehead index were positively associated with the current year's white oak mast, after correcting for autocorrelation. Relationships between summer population data and mast data from the fall of the same year are difficult to interpret because black bear population estimates are derived from data collected before hard mast is produced. Therefore, this variable may actually be a surrogate for other factors associated with black bear population abundance. For example, availability of shrub-borne soft mast may be correlated with white oak acorn production. Soft mast is a vital resource used by black bears from late spring to early fall and may require similar environmental conditions as white oak in order to flower. Spring temperature has the greatest effect on white oak acorn production, and was seen through flower to fruit survival rather than flower initiation (Sharp and Sprague 1967). Indeed, peak flowering times for oak species and shrub-borne soft mast species, such as huckleberries (*Gaylussacia* spp.), blueberries (*Vaccinium* spp.), and blackberries (*Rubus* spp.) are similar (Inman 1997). Soft mast, particularly huckleberries, are abundant in areas around most trapsites (personal observation). The majority of traplines follow major ridges, and many soft mast producing species occur on these same ridges. An increase in soft mast production may attract a disproportionate number of untagged bears from surrounding areas, increasing the population estimate. My data seems to follow this pattern when comparing the proportion of white oak trees with acorns (Table 4.2) to the Jolly-Seber population estimates (Table 4.4 and 4.5). The Jolly-Seber population estimates tend to increase or decrease as the proportion of white oak trees with acorns increase or decrease.

My results indicated that hard mast from previous years was also important, particularly for the 1990–2000 period (Table 4.7). For both mast survey methods, population estimates for 1990–2000 were best predicted by including a 2-year lag time on the white oak variable. The effects of a good acorn crop may not become apparent in the population until several years later. For example, female bears are more likely to produce cubs following a good mast crop. This birth pulse may not be seen until 2 summers later when the 1.5-year-old bears are captured. The opposite situation also may occur. Subsequent to a mast failure, female bears may not produce cubs the following winter, and this lack of reproduction may be seen 2 years later when only a small or no cohort of 1.5-year-old bears show up in the capture sample.

White oak mast from 2 years before was an important variable in many models and often showed a more significant relationship with black bear population abundance than northern red oak. This finding may support the notion that white oak masting events may correspond more to population dynamics. White oak seems to exhibit more pronounced fluctuations in yearly mast crops (Figure 4.1), which may have a greater affect on the bear population. Indeed, the proportion of white oak trees with acorns (Table 4.2) exhibited high variability, with bear population estimates following similar trends (Tables 4.4 and 4.5), whereas the proportion of northern red oaks with acorns remained fairly stable (Table 4.2).

Northern red oak from the previous year was included in the best model for the Whitehead index during 1990–2000 (Table 4.7 and B.1), and was in the top 4 models for the mast regression index (Table B.2) for that time period. Adding this variable to the model of white oak from two years ago during 1990–2000 (Model 10, Table B.1) resulted

in an improved model (Model 16, Tables 4.7 and B.1). This finding may demonstrate the importance of multiple mast producers to bear populations. The proportion of northern red oak trees with acorns (Table 4.2) remained stable in years that the proportion of white oak trees with acorns was low. Greenberg (2000) found that the effect of crop failure of one oak species in a mixed oak stand often is dampened by the presence of other species. Northern red oak mast showed a positive association in the regression models, possibly reflecting a population response due to mortality. For example, when a poor mast crop occurs, black bears may exhibit wide-ranging movements, increasing their vulnerability to mortality. Resident (marked) bears, particularly females, in the study area may be less vulnerable to this type of mortality than younger bears. This disparity in mortality would be evident in the population estimates for the following summer due to a decrease in total captures and an increase in the recapture rate, resulting in lower population estimates. An alternative explanation of the importance of northern red oak mast from the previous year may be related to a potential trap bias. As discussed previously, good mast crops may influence cub production during the following winter. Given the length of this study, it is reasonable to assume that most resident females in the study area have been captured and marked. Females with cubs have more restricted home ranges than females without cubs. Therefore, in years following a good mast crop of northern red oak, the capture rate of these marked females may be low, giving new bears a greater opportunity to move into the area and be captured, thereby increasing the population estimate.

Management Implications

This study indicates that white oak from 2 years ago and northern red oak from the previous year may have a positive association with black bear population abundance. These variables were a significant factor for both mast production methods and within both time periods. However, black bear reproduction and survival are not solely related to variation in acorn crops, which may explain the difficulty in detecting strong relationships. First, black bears show a behavioral plasticity that allows them to exploit continually changing food sources, ranging from herbaceous material in early spring (90%) and late spring (45%), shrub-borne soft mast during summer (60%), tree-borne soft mast during early fall (30%), and hard mast during late fall (70%; Eagle and Pelton 1983). Such plasticity has also been observed in Virginia (Kasbohm et al. 1996) and Minnesota (Noyce and Garshelis 1997). In the southern Appalachians, the most likely alternate food sources during fall are black cherry (*Prumus serotina*) and grapes (*Vitis* spp.) (Inman 1997). These alternate foods may reduce the impacts of severe oak mast failures on the black bear population. Secondly, factors not related to food sources, such as interactions with other bears or exposure to humans and roads may play a role in black bear population dynamics (Carr 1983, Pozzanghera 1990). Future studies should examine those additional factors to better understand the relationship between black bear population trends and food resources.

Despite these confounding factors, my results indicate that relationships exist between acorn production and bear abundance. The occurrence of major oak mast crop failures or highly abundant crops causes substantial effects in the black bear population. The presentation from the regression analyses may be used by wildlife managers to better

anticipate how the black bear population in Great Smoky Mountains National Park may respond to changes in mast production.

The Whitehead index and mast regression index showed few differences in their relationships with black bear abundance. Based on the results of my study, both methods seemed effective to help interpret black bear population trends. However, basal area measurements proved to be a limiting factor in this study. The lack of these measurements made it impossible to use the yield equation presented by Greenberg and Parresol (2000). The results obtained from the mast regression index may not accurately reflect results that would have been obtained by using the entire yield equation. More studies should be done to determine whether an index of acorn yield would improve results enough to warrant a switch in mast survey methods. Using a yield index, such as the equation by Greenberg and Parresol (2000), requires establishing vegetation plots rather than sampling individual trees. However, plot sampling may be more efficient in terms of personnel time while providing improved acorn yield estimates. Therefore, managers should consider including basal area measurements in future mast surveys.

CHAPTER I

SURVIVAL OF FEMALE BLACK BEARS

Introduction

Black bear survival, particularly among females, is an important parameter for population studies. Female survival has not been thoroughly studied in Great Smoky Mountains National Park. However, each year 20–25 radio-collared females are monitored during the denning period. These radio-collared bears can be located during other times of the year to estimate survival and to determine causes of mortality. Radio-telemetry provides researchers with an excellent opportunity to estimate annual survival rates and causes (Vangilder and Sheriff 1990). This information can be valuable to determine when mortality occurs, and whether certain age classes are more susceptible to different types of mortality.

Study Area

The study area was in the northwestern section of Great Smoky Mountains National Park. This 328-km^2 study area stretches west of highway 441 to the northwestern boundary of Great Smoky Mountains National Park and from the northern boundary of the national park to the North Carolina-Tennessee border (Figure 1.1).

Since 1968, the black bear population in the study area has been continuously sampled through livetrapping, although sampling regimes have varied over time due to differing study objectives (Pelton and van Manen 1996). The conditions of the study area differed somewhat from other portions of the national park only due to lower

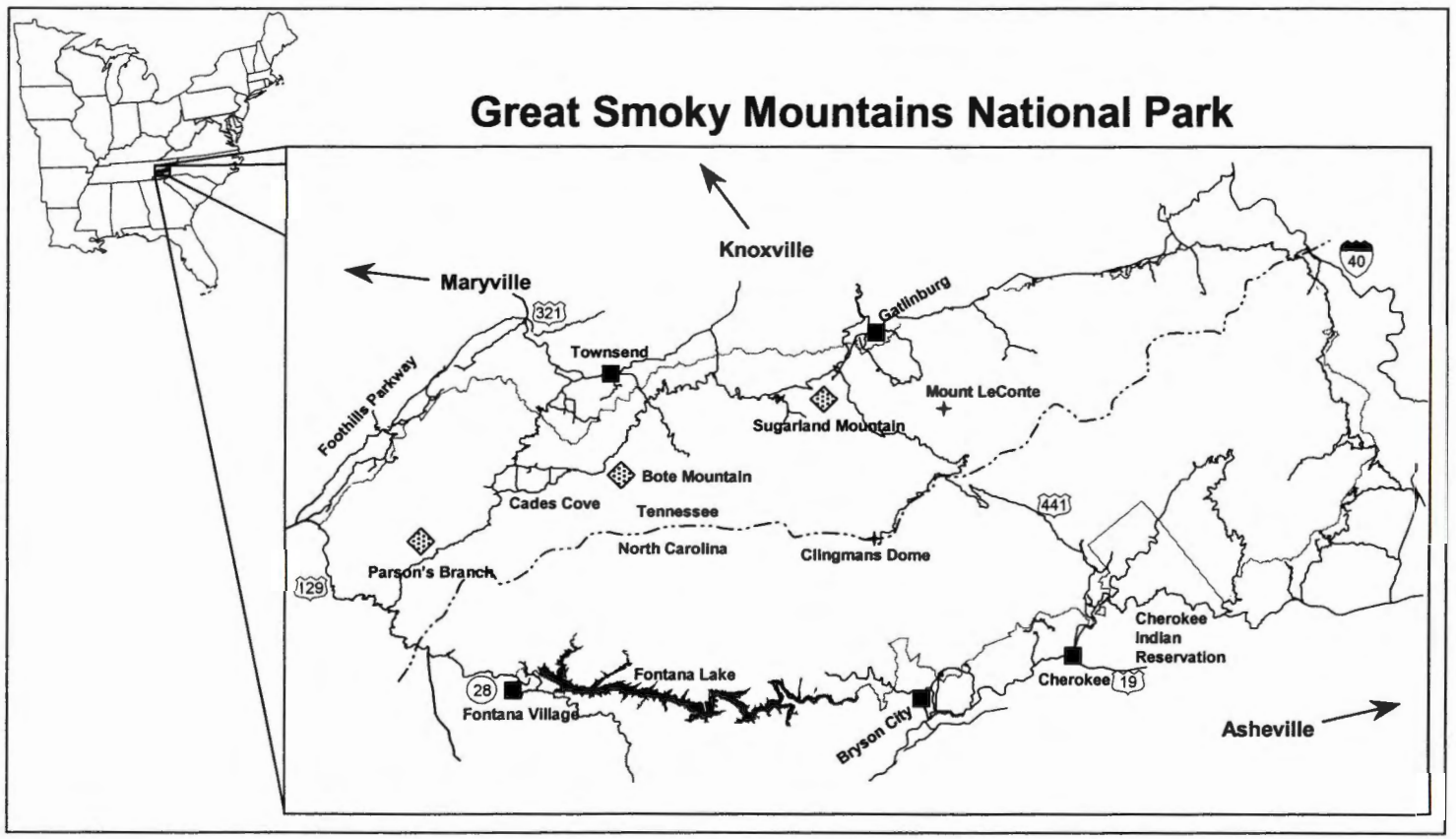


Figure 1.1. Great Smoky Mountains National Park and the 3 areas used for ground telemetry.

elevations and a greater percentage of xeric oak and pine cover types (Eason 2002). The topography of the national park is complex, including many steep ridges separated by fast-flowing streams (King and Stupka 1950). Elevations range from 329 m to 1,552 m. Four dominant cover types occur on the study area, consisting of pine, xeric oak, cove hardwood, and mixed mesic hardwood (Table 1.1, MacKenzie 1993).

Methods

From 1999 through 2001, adult female black bears captured for the mark-recapture study conducted in Great Smoky Mountains National Park were fitted with radio collars (MOD–500; Telonics, Mesa, Arizona, USA). Radio-collars were attached with cotton spacers covered with duct tape; deterioration of the cotton typically resulted in a collar drop after 2.5–3 years after which the transmitter was retrieved. Cotton spacers have been used in other studies to ensure that collars are not worn permanently (Mace and Waller 1998, Hellgren et al. 1988). All radio collars were outfitted with 2 mercury-tip sensors that serve as motion-sensitive activity monitors. When the radio collar was rotated upward (heads up), it emitted a faster pulse signal (~96 beeps/minute); when rotated downward (heads down) it emitted a slower pulse signal (~72 beeps/minute) (Telonics, Mesa, Arizona, USA). Additionally, if the collar was stationary for approximately 4 hours it would switch to a "mortality" signal. The pulse rate in this mode (~32 beeps/minute) is approximately half that of the active mode (~72-96 beeps/minute). Because bears rarely are completely inactive for more than a few hours, other than during the den season, such a signal would likely indicate a mortality or dropped collar. If the mortality signal was heard, I searched for the radio

Table 1.1. Percentage of forest types within the black bear study area and Great Smoky Mountains National Park (GSMNP) (based on MacKenzie 1993).

Forest Type	Study Area	GSMNP
Spruce-Fir	0.0	2.3
Northern Hardwood	1.7	9.4
Cove Hardwood	20.8	33.4
Mesic Oak	3.0	10.3
Mixed Mesic Hardwood	17.0	16.0
Tulip Poplar	7.7	2.7
Xeric Oak	22.0	10.0
Pine-Oak	2.4	2.4
Pine	23.6	11.2
Open	1.8	2.3

transmitter to determine whether it was a mortality or a dropped collar.

From October 1999 through April 2001, I located radio-collared female bears once every month (Table 1.2). Thirty-two radio-collared females were used in the survival analysis. Because the exact location of the bear is not important, only the signal from the collar was recorded. Activity and mortality were assessed by determining the pulse rate of each signal.

Ground telemetry was used to find as many female bears as possible. All female radio signals were scanned on a TR-2 scanner (Telonics, Mesa, Arizona, USA). Scanning for radio-collar signals started when entering the national park by vehicle. Antennas were placed outside both windows of the vehicle for continuous scanning. Foot trails were used to hike to ridge tops along a determined route in 3 areas: Sugarland Mountain, Bote Mountain, and Parson's Branch Road (Figure 1). Higher elevations were favored to avoid signal blocking from nearby ridges. All radio-collar signals were scanned at each of the 3 sampling areas. Once a signal was heard, the number of beeps was counted for one minute (beeps per minute) to determine active, inactive, or mortality mode. The date, bear identity number, beeps per minute, and location were recorded for each radio-collar signal received.

Because signals of some bears could not be consistently received, aerial telemetry was incorporated into the study in May 2000. Bears whose signals could not be received by ground telemetry were subsequently searched using aerial telemetry. I designed a data recording system that allowed the pilot to easily collect data while flying. All radio transmitter frequencies were programmed into the TR-2 scanner. The scanner was

Table 1.2. Radio transmitter signals of female black bears received using ground telemetry and aerial telemetry[a], Great Smoky Mountains National Park, October 1999–April 2001.

		1999			2000												2001			
Bear No.	Area	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
611	Parson's Branch						G			A		G	G	AG	AG		AG	F(B)		A
1538	Parson's Branch	G	G	GA	G	G				A		G	G	AG	AG		AG		F(B)	
1549	Parson's Branch		G	GA			G			A		G	G	A	A		A		F(B)	
1366	Parson's Branch			GA	G	G				A		GA		G	AG					A
1391/1211	Parson's Branch	G	G	GA								G	G	G	G		G			
1519	Meigs Mountain			A								G	G	A	A				F(B)	A
1448	Sugarland Mountain	G	G	GA		G				A		GA	G	AG	G		A		F(B)	A
1400	Sugarland Mountain		G	GA		G	G	G		A		G	G	AG	G	G	GA		F(B)	
1348	Sugarland Mountain	G	G	GA								G	G	G	G	G	GA			A
1570	Sugarland Mountain	G	G	G		G						G	G	G	G	G	GA			
1291	Sugarland Mountain	G	G	GA								A	A	G	G	G	G			
1436	Sugarland Mountain			G									A		G	G	G		F(D)	
1425	Sugarland Mountain	G	G	GA		G		G		A			G	G	G	G	G		F(D)	
784	Sugarland Mountain	G																		
1213	Bote Mountain	G	G	GA								G	G	G	G	G		F(B)		A
1495	Bote Mountain		G	GA						A		G	G	G	F(D)					
1481	Bote Mountain		G	GA	G	G				A		G	G	G(D)	G	G	F(D)			
1440	Bote Mountain			GA	G					A		G	G	G	G	G				
1344/1579	Bote Mountain	G		GA																
1430	Abrams/Rabitt Creek			A			G			A		A	A	A	A		A			A
1080/1528	Schoolhouse Gap	G		A										G	G	G			F(B)	A
1524	Green Camp Gap	G	G	GA						A		A	A		A		A			
1523	Green Camp Gap		G	A			G			A		G	A	A	A			F(B)		A
1351	Curry Mountain	G	G	GA				G		A		A	G	AG	G					
1514	Curry Mountain	G	G	GA								G	G	G	G		GA	F(D)		
1522/1360	Lumber Ridge	G	G	GA			G						A					F(D)		

[a] G = ground telemetry, [b] A = aerial telemetry, [c] F = found transmitter, [d] B = bear, [e] D = dropped transmitter

connected to a hand-held cassette recorder to record the number of beeps per minute when a transmitter signal was received. A small microphone was also connected to the receiver to allow the pilot to verbally record the bear number on the cassette, while recording the transmitter signal. The pilot scanned through frequencies during the entire flight, and each signal was recorded for approximately one minute. All recorded tapes were labeled with the flight date. I subsequently listened to the tape and recorded the female bear frequencies received and whether the radio transmitter was in active, inactive, or mortality mode. During May and July flights could not be conducted due to adverse weather conditions and ground telemetry was not performed because of livetrapping for the mark-recapture study.

Visits to winter den sites substituted for aerial and ground telemetry during February, March, and April; as many female bears as possible were located to determine general health and reproduction. Radio collars were replaced when needed if immobilization of the female was possible.

Several techniques exist to estimate animal survival using radio telemetry data (Trent and Rongstad 1974, Heisey and Fuller 1985, Pollock et al. 1989, White and Garrott 1990). The basis of all these techniques is the placement of a radio transmitter on an animal, and use of radio telemetry at specified time intervals to determine the fate of the sampled animals. Because bears are radiocollared over a 2-month period each summer, most animals do not enter the study at the same time. Taking this into consideration, I chose the Kaplan-Meier staggered entry design (Pollock et al. 1989). This design, which is widely used in medical studies subject to censoring, can be used to overcome the problem of radio or animal loss (Pollock et al. 1989). The staggered entry

procedure allows animals to be added to the study after it has begun. Allowances must be made for animals lost or censored (removed from analysis) because of radio failure, radio loss, or emigration from the study area. Pollock et al. (1989) suggested that all animals whose radio signals are lost should be censored, although they can be included in survival estimation up to the final location. Another modification that can be made to the Kaplan-Meier staggered entry procedure is to correct the number of animals at risk (number of animals detected) to account for uncertain relocation of individuals (Bunck et al. 1995). The Kaplan-Meier staggered entry design is based on the assumption that the relocation probability of animals with a functioning transmitter is 1; however, this is not always necessary or reasonable. If an animal that has been censored is found in subsequent time periods, it is then known to have been alive during earlier periods in which it was not found. However, if the relocation history is corrected to show the animal was alive the entire time, it can bias the survival estimate. Bias occurs in this case because correcting such relocation histories is more likely to occur for animals that are alive rather than dead (Bunck et al. 1995). I avoided this bias by using a modified Kaplan-Meier technique (Bunck et al. 1995), and included only relocated animals in the number of animals at risk instead of including animals that were not relocated but observed during subsequent periods (Bunck et al. 1995). Assumptions associated with this method are (Bunck et al. 1995): (1) the sample is representative of the population being studied, (2) the animal's survival is not influenced by the radio transmitter, (3) radio-tagged animals have independent fates, (4) right censoring (losing track of animals after a certain time) is independent of the animal's fate, and (5) each animal's survival time is known (except for right-censored animals).

Results

Of the 32 bears with radio-collars entered into this study six bears were censored: signals of two females on the North Carolina side of Great Smoky Mountains National Park were heard only once during a telemetry flight in December 1999 and were eliminated from my study. Four other bears were only heard once at the beginning of my study and were not detected again; these bears were removed from the analysis.

Signals from an average of 14 female black bears were heard each month (Table 2). Signals of nine radio collars switched to mortality mode during the course of the study. Of these, three radio transmitters could not be retrieved, and the remaining 6 were dropped collars. No evidence of mortality was observed at any of the locations where dropped collars were found. No mortalities were observed throughout the study, and the survival rate of female black bears was 1.0.

Discussion

Throughout the range of the black bear, hunting is the primary source of mortality among black bear populations (Elowe et al. 1991). Because hunting is not allowed in Great Smoky Mountains National Park, the black bear population is relatively unexploited. However, some mortality from hunting is observed through tag return by hunters, and is greatest when fall mast failures cause bears to move out of the national park into the surrounding areas. Males travel over larger distances than females, which exposes them to a greater risk of mortality from vehicle collision and legal harvest (Eason 2002). Although mortality due to natural causes, intra-specific competition, starvation, and vehicle collisions has been documented within the study area, such occurrences have

been extremely infrequent. The results of my study suggest that such mortalities are indeed rare among adult female bears. Eason (2002) also found that survival of the female segment of the black bear population in the same study area was high. In a 5-year study, Eason (2002) observed an average survival rate of 0.905; the survival rate was 1.0 during two of those years. Other studies have also found high survival among females in bear protected areas, such as sanctuaries (Powell et al. 1996).

The large home ranges of bears make it difficult to detect all radio signals within a short amount of time. In my study the length of time between observations (1 month) may have been too long to determine causes of mortality in cases where the transmitter could not immediately be found. On the other hand, for long-lived species such as black bears, observations at intervals of more than 1 month may be adequate to document survival. More intensive research is needed to immediately find collars on mortality signal to determine causes of mortality that may be lost over time. Because of the extreme topography of the study area, aerial telemetry was crucial to detect radio signals. Expanding the use of aerial telemetry during future monitoring may reduce the number of censored bears and improve the ability to detect mortalities. Due to the longevity of bears, longer-term research will be needed to better document trends in female black bear survival in Great Smoky Mountains National Park.

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Appendix A. Results of regression analysis of mast data based on the Whitehead index (Table A.1) and mast regression index (Table A.2) and black bear population estimates based on the Jolly-Seber method (Model A), Great Smoky Mountains National Park, 1981–1999.

Table A.1. Regression results based on the Whitehead index and black bear population estimates, Great Smoky Mountains National Park, 1981–1999.

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
1	Northern red oak and white oak	43.46	0.05	0.23	188.41	none
2	Northern red oak and white oak, 1-year lag	37.44	0.12	0.15	190.16	none
3	Northern red oak and white oak, 2-year lag	1.82	0.94	0.00	193.61	3 -
4	Northern red oak	8.10	0.70	0.01	192.62	3-
5	Northern red oak, 1-year lag	31.21	0.09	0.18	189.58	none
6	Northern red oak, 2-year lag	-8.85	0.66	0.01	193.38	3 -
7	White oak	35.50	0.00	0.42	183.53	none
8	White oak, 1-year lag	4.07	0.77	0.01	192.87	3 -
9	White oak, 2-year lag	9.14	0.49	0.03	193.05	3 -
10	Northern red oak	4.69	0.78	0.42	185.43	none
	White oak	35.29	0.01			

Table A.1. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
11	Northern red oak	8.40	0.71	0.01	184.45	3 -
	White oak, 1-year lag	3.06	0.84			
12	Northern red oak	3.30	0.89	0.03	173.75	3 -
	White oak, 2-year lag	8.85	0.60			
13	Northern red oak, 1-year lag	-9.32	0.68	0.45	175.19	none
	White oak	42.09	0.02			
14	Northern red oak, 1-year lag	32.69	0.09	0.20	191.17	none
	White oak, 1-year lag	7.40	0.57			
15	Northern red oak, 1-year lag	32.48	0.10	0.21	180.79	none
	White oak, 2-year lag	3.95	0.76			
16	Northern red oak, 2-year lag	- 11.33	0.51	0.45	165.20	none
	White oak	36.27	0.01			
17	Northern red oak, 2-year lag	- 31.89	0.27	0.10	182.93	3 -
	White oak, 1-year lag	17.72	0.37			

Table A.1. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
18	Northern red oak, 2-year lag	-7.78	0.70	0.04	194.86	3 -
	White oak, 2-year lag	8.73	0.52			

[a] AIC = Akaike's Information Criterion

[b] Durbin Watson statistic measures whether serial correlation exists: none = no significance ($P > 0.05$), a number (e.g., 3) indicates the specified order where significance was found; a (-) or (+) after the number indicates the relationship was negative or positive, respectively.

Table A.2. Regression results based on the mast regression index and black bear population estimates, Great Smoky Mountains National Park, 1981–1999.

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
1	Northern red oak and white oak	13.87	0.01	0.36	185.26	4 +
2	Northern red oak and white oak	13.78	0.01	0.36	187.14	4+
	Autoregression term 1	0.08	0.77			
3	Northern red oak and white oak	14.88	0.00	0.45	187.06	4+
	Autoregression term 1	0.16	0.57			
	Autoregression term 2	0.36	0.21			
4	Northern red oak and white oak, 1-year lag	9.20	0.12	0.16	190.07	3 -
5	Northern red oak and white oak, 2-year lag	9.96	0.94	0.18	190.32	3 -
6	Northern red oak	18.57	0.21	0.10	190.94	3 -
7	Northern red oak, 1-year lag	29.27	0.04	0.25	188.12	none
8	Northern red oak, 2-year lag	14.16	0.37	0.05	192.67	3 -
9	White oak	19.29	0.01	0.39	184.38	4 +

Table A.2. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
10	White oak	19.37	0.01	0.39	186.36	4+
	Autoregression term 1	-0.04	0.90			
11	White oak	22.54	0.00	0.53	184.99	none
	Autoregression term 1	0.05	0.85			
	Autoregression term 2	0.52	0.06			
12	White oak, 1-year lag	7.58	0.32	0.06	191.83	3 -
13	White oak, 2-year lag	12.65	0.09	0.18	190.33	3 -
14	Northern red oak	2.69	0.85	0.39	186.33	4 +
	White oak	18.63	0.02			
15	Northern red oak	2.37	0.87	0.39	188.32	4+
	White oak	18.76	0.03			
	Autoregression term 1	-0.02	0.96			

Table A.2. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
16	Northern red oak	-5.07	0.70	0.54	186.84	2+
	White oak	24.32	0.00			
	Autoregression term 1	0.03	0.90			
	Autoregression term 2	0.58	0.04			
17	Northern red oak	17.73	0.26	0.15	182.11	3 -
	White oak, 1-year lag	6.55	0.43			
18	Northern red oak	12.74	0.46	0.19	170.96	3 -
	White oak, 2-year lag	10.64	0.24			
19	Northern red oak, 1-year lag	-4.53	0.87	0.41	176.32	4 +
	White oak	21.79	0.11			
20	Northern red oak, 1-year lag	27.56	0.08	0.25	190.00	4 +, 3 -
	White oak, 1-year lag	2.29	0.76			
21	Northern red oak, 1-year lag	26.87	0.06	0.35	177.72	none
	White oak, 2-year lag	10.15	0.17			

Table A.2. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
22	Northern red oak, 2-year lag	5.63	0.74	0.40	166.53	4 +
	White oak	19.94	0.02			
23	Northern red oak, 2-year lag	5.52	0.76	0.40	168.53	4+
	White oak	19.99	0.02			
	Autoregression term 1	-0.01	0.96			
24	Northern red oak, 2-year lag	- 16.64	0.21	0.64	165.43	none
	White oak	27.30	0.00			
	Autoregression term 1	0.05	0.84			
	Autoregression term 2	0.72	0.01			
25	Northern red oak, 2-year lag	- 16.45	0.65	0.07	183.36	3 -
	White oak, 1-year lag	13.39	0.42			
26	Northern red oak, 2-year lag	5.28	0.74	0.18	192.20	3 -
	White oak, 2-year lag	11.66	0.16			

[a] AIC = Akaike's Information Criterion

[b] Durbin Watson statistic measures whether serial correlation exists: none = no significance ($P > 0.05$), a number (e.g., 3) indicates the specified order where significance was found; a (-) or (+) after the number indicates the relationship was negative or positive, respectively.

Appendix B. Results of regression analysis of mast data based on the Whitehead index (Table B.1) and mast regression index (Table B.2) and black bear population estimates based on the Jolly-Seber (Model B), Great Smoky Mountains National Park, 1990–2000.

Table B.1. Regression results based on the Whitehead index and black bear population estimates, Great Smoky Mountains National Park, 1990–2000.

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
1	Northern red oak and white oak	24.15	0.23	0.15	115.41	none
2	Northern red oak and white oak	26.94	0.20	0.19	116.94	3-
	Autoregression term 1	- 0.20	0.61			
3	Northern red oak and white oak	27.26	0.23	0.20	118.91	3-
	Autoregression term 1	- 0.19	0.66			
	Autoregression term 2	- 0.06	0.90			
4	Northern red oak and white oak, 1-year lag	15.69	0.46	0.06	116.56	none
5	Northern red oak and white oak, 2-year lag	24.63	0.23	0.15	115.43	none
6	Northern red oak	3.66	0.82	0.01	117.19	none
7	Northern red oak, 1-year lag	15.84	0.30	0.12	115.89	none
8	Northern red oak, 2-year lag	4.36	0.79	0.01	117.17	none
	White oak	22.50	0.13	0.24	116.00	none

Table B.1. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
9	White oak, 1-year lag	-5.54	0.71	0.02	117.09	none
10	White oak, 2-year lag	22.76	0.07	0.32	113.03	none
11	Northern red oak	4.58	0.74	0.31	115.24	none
	White oak	23.40	0.10			
12	Northern red oak	2.39	0.89	0.02	119.06	none
	White oak, 1-year lag	-4.98	0.76			
13	Northern red oak	1.88	0.89	0.32	115.00	none
	White oak, 2-year lag	22.64	0.09			
14	Northern red oak, 1-year lag	-5.82	0.78	0.30	115.29	none
	White oak	27.20	0.18			
15	Northern red oak, 1-year lag	15.38	0.35	0.12	117.80	none
	White oak, 1-year lag	-3.85	0.80			

Table B.1. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
16	Northern red oak, 1-year lag	19.37	0.14	0.49	111.82	none
	White oak, 2-year lag	24.84	0.04			
17	Northern red oak, 2-year lag	9.98	0.63	0.26	99.04	none
	White oak	23.82	0.20			
18	Northern red oak, 2-year lag	17.45	0.48	0.08	118.35	none
	White oak, 1-year lag	-16.71	0.45			
19	Northern red oak, 2-year lag	6.39	0.66	0.34	114.76	none
	White oak, 2-year lag	23.13	0.08			

[a] AIC = Akaike's Information Criterion

[b] Durbin Watson statistic measures whether serial correlation exists: none = no significance ($P > 0.05$), a number (e.g., 3) indicates the specified order where significance was found; a (-) or (+) after the number indicates the relationship was negative or positive, respectively.

Table B.2. Regression results based on the mast regression index and black bear population estimates, Great Smoky Mountains National Park, 1990–2000.

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
1	Northern red oak and white oak	7.24	0.19	0.18	115.06	none
2	Northern red oak and white oak, 1-year lag	3.18	0.59	0.03	116.89	none
3	Northern red oak and white oak, 2-year lag	8.96	0.09	0.29	113.45	none
4	Northern red oak	7.55	0.59	0.03	116.88	none
5	Northern red oak, 1-year lag	11.27	0.44	0.07	116.48	none
6	Northern red oak, 2-year lag	11.67	0.43	0.07	116.46	none
7	White oak	9.38	0.22	0.16	117.06	none
8	White oak, 1-year lag	2.08	0.78	0.01	117.16	none
9	White oak, 2-year lag	11.40	0.08	0.30	113.27	none
10	Northern red oak	1.77	0.90	0.20	116.81	none
	White oak	9.36	0.23			

Table B.2. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
11	Northern red oak	9.35	0.54	0.06	118.61	none
	White oak, 1-year lag	3.47	0.67			
12	Northern red oak	9.16	0.45	0.35	114.45	none
	White oak, 2-year lag	11.72	0.08			
13	Northern red oak, 1-year lag	-10.49	0.65	0.22	116.52	4-
	White oak	13.85	0.25			
14	Northern red oak, 1-year lag	-21.70	0.22	0.39	116.09	none
	White oak	19.58	0.05			
	Autoregression term 1	-0.47	0.25			
15	Northern red oak, 1-year lag	11.04	0.49	0.07	118.48	none
	White oak, 1-year lag	0.38	0.96			
16	Northern red oak, 1-year lag	15.29	0.23	0.43	113.13	3+
	White oak, 2-year lag	12.53	0.06			

Table B.2. (continued)

Model	Variable(s)	Parameter estimate	*P*	R^2	AIC[a]	Durbin-Watson[b]
17	Northern red oak, 1-year lag	15.20	0.26	0.43	115.13	3+
	White oak, 2-year lag	12.54	0.07			
	Autoregression term 1	-0.01	0.98			
18	Northern red oak, 1-year lag	15.69	0.29	0.50	115.87	3+
	White oak, 2-year lag	14.64	0.05			
	Autoregression term 1	-0.03	0.95			
	Autoregression term 2	0.37	0.42			
19	Northern red oak, 2-year lag	17.25	0.39	0.26	99.06	none
	White oak	11.22	0.26			
20	Northern red oak, 2-year lag	22.09	0.39	0.10	118.06	none
	White oak, 1-year lag	-6.54	0.60			
21	Northern red oak, 2-year lag	3.24	0.82	0.31	115.19	none
	White oak, 2-year lag	10.85	0.13			

[a] AIC = Akaike's Information Criterion

[b] Durbin Watson statistic measures whether serial correlation exists: none = no significance ($P > 0.05$), a number (e.g., 3) indicates the specified order where significance was found; a (-) or (+) after the number indicates the relationship was negative or positive, respectively.

VITA

Jaime Suzanne Chadwick was born on November 26, 1976 in Kingsport, TN. She graduated from Dobyns-Bennett High School in Kingsport, TN in 1995. She attended the University of Tennessee, Knoxville as a zoology student in the fall of 1995. The following year she decided to pursue a degree in wildlife and fisheries science and graduated with a Bachelor of Science degree in May 1999. The following summer, Jaime began her Master's research at the University of Tennessee on black bears in the Great Smoky Mountains National Park. She received her Master's of Science degree in Wildlife and Fisheries Science in December 2002. Jaime is married to Dr. Frank Chadwick and they reside in Knoxville, TN.

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