LIFE HISTORY ATTRIBUTES OF BLACK BEARS (*URSUS AMERICANUS*) IN NORTHERN WISCONSIN

by

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ABSTRACT

Effective wildlife population management requires a thorough understanding of life history attributes of the species of interest. Specifically, data on reproduction and survival can allow managers to target sensitive population segments and effectively manage for desired population level outcomes. Effective management should be a priority for every wildlife species, especially for long-lived species with low reproductive rates, such as black bears.

The Wisconsin Department of Natural Resources (WDNR) manages Wisconsin's black bear population through a regulated annual harvest. The number of harvest permits issued each year is based on a black bear population projection generated from a population model, BEARPOP2. This model requires input parameters, such as reproductive rates and sex ratios. Currently, the WDNR is in need of up-to-date and accurate parameter estimates. In this study, I used data from a long-term mark-recapture study to estimate reproductive and survival rates of black bears in northern Wisconsin.

To estimate reproductive parameters, I analyzed 20 years of annual den survey data (1989-2008). I estimated average age of first reproduction, mean litter size, cub sex ratio, age- and year-specific pregnancy rates, and interbirth interval. Based on knowledge of bear biology, I tested for effects of age, winter severity, average precipitation, and average temperature on reproductive rates. Overall, productivity (mean litter size, pregnancy rates) of female black bears increased with age. Annual reproductive parameters were not related to environmental variables. All estimated reproductive parameters were comparable to those estimated for female black bears in

other regions. In particular, our estimated high mean litter size (2.46 cubs/litter), short interbirth interval (2 years), and relatively low average age of first reproduction matched estimates for black bears in regions with high quality habitat for the species.

To estimate survival rates of female black bears in northern Wisconsin, I generated encounter histories from 19-years of mark-recapture records (1989-2007). I generated a set of a priori known-fate (Kaplan-Meier) survival models using Program MARK. Based on knowledge of bear biology, I tested for effects of age, winter severity, average precipitation, and hunting effort on survival rates. I generated a set of eleven candidate models, and using an information-theoretic approach, I then generated a final set of three models. These models (an intercept-only model, a global model, and a model incorporating the effects of senescence) all have potential use for wildlife managers. The intercept-only model generated an overall survival estimate of 0.80 for female black bears. Survival of female cubs (0.70) was calculated as a simple proportion using data from annual den processing events.

Finally, I combined age-specific survival rates and fecundity to infer possible consequences to population dynamics. I used life table analysis to estimate an annual rate of increase of 3-4% for black bears in northern Wisconsin. I then conducted elasticity analysis and found that λ for the black bear population in Wisconsin is most sensitive to changes in cub and yearling survival. The information generated from this project is intended to aid the WDNR in both evaluating their progress toward management goals and updating their black bear population model.

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PREFACE

The two chapters comprising this thesis consist of separate, but closely related manuscripts that investigate life history attributes of black bears in northern Wisconsin. Data for these manuscripts were obtained from 19-20 years of field records from the ongoing Wisconsin Black Bear Research Project overseen by the University of Wisconsin-Stevens Point.

The Wisconsin Black Bear Research Project began in 1976 under the direction of Dr. Neil Payne, a wildlife professor at the University of Wisconsin-Stevens Point (UWSP), and Bruce Kohn, Wisconsin Department of Natural Resources, who directed studies in food habits and habitat use. In 1978, Dr. Raymond K. Anderson, also a professor of wildlife at UWSP, continued research on black bear ecology in Northern Wisconsin.

Anderson's research on these black bear populations had two primary objectives: to determine 1) the density at which black bears were most productive, and 2) if the population produced a "surplus" above a healthy density that could be removed through regular hunting. However, collection of annual den survey data allowed other projects to be implemented. Between 1980 and 1995, at least seven graduate students worked under the Wisconsin Black Bear Research Project. These students investigated a variety of topics relating to black bear ecology and population dynamics (Norton 1981; Massopust 1982; Bertagnoli 1986l; Kessler 1989; Storlid 1995; Trauba 1992; Fleming 1995).

Currently, the Wisconsin Black Bear Research Project is under the direction of Dr. Tim Ginnett, Associate Professor of Wildlife at UWSP. Ginnett has served as

Project Director for research that is promoting a better understanding of Wisconsin's black bears since 2001. Dr. Ginnett has advised several graduate students under the Wisconsin Black Bear Research Project (Gesch 2003; Hansen 2005; Schindler 2008).

In the first chapter of this thesis, I used 20 years (1989-2008) of data from visits to winter dens of female black bears to generate accurate estimates of black bear reproductive parameters. Specifically, I estimated mean litter sizes, mean age of first reproduction, fecundity rates, and cub sex ratios of black bears in northern Wisconsin. I also investigated potential relationships between reproductive parameters and environmental variables.

In the second chapter, I used encounter histories of female black bears from 19 years of data (1989-2007) to generate estimates of female black bear survival in Northern Wisconsin. I used Program MARK to construct known-fate a priori models relating female black bear survival to a number of variables and chose a “best” survival model based on Akaike’s Information Criterion. I then used results from my first chapter in combination with the generated survival estimates from my second chapter to construct life tables. From the life tables, I was able to estimate the intrinsic rate of population growth for black bears in Northern Wisconsin.

INTRODUCTION

Found in 39 states, every Canadian province and northern Mexico, the black bear (*Ursus americanus*) is the most common of the world's eight bear species. In some areas, a combination of high black bear abundance and an expanding human population has caused increased contact between black bears and humans. Consequently, the public often holds an ambivalent attitude toward the species. Some view the black bear as a potentially dangerous nuisance species, while others understand that black bears are important ecologically and economically as seed-dispersers and as a revenue-generating big game species (Gillin et al.1992; Pelton 2000). Because of the range of attitudes toward black bears, management is necessary to achieve a population that maximizes ecological benefit and hunter opportunity while minimizing unfavorable interactions between bears and humans.

Before wildlife managers can define a target black bear population size that balances public acceptance and biological needs, they must first estimate current abundance. Accurate estimation of black bear abundance is necessary because bears exhibit some of the lowest reproductive rates among terrestrial mammals (Bunnell and Tait 1981). As a result, overexploited populations of black bears will be slow to recover (Miller 1990). To avoid population estimation error and over harvest, management agencies should consider as many life history parameters as possible when designing population models. In particular, thorough understanding of survival and reproduction is essential to population analyses.

General Biology

Black bears are moderate-sized plantigrade mammals. Mean weights of adult males range from about 80-150 kg and are approximately 60-70% heavier than mean weights of adult females (Bunnell and Tait 1981). Body size of black bears may vary significantly with location and food supply (Pelton 2000). The predominant coloration of the species is black with a brownish muzzle and an occasional white chest blaze. Cinnamon, brown, blond, and white color phases are sometimes seen, but more frequently in the western and northern geographic range (Pelton 2000).

Despite being taxonomically classified in the order Carnivora, black bears typically consume various plant and animal foods. Their diets are often composed of items such as tubers, insect grubs, various hard and soft mast, carrion, and live prey such as white-tailed deer fawns (*Odocoileus virginianus*) and elk (*Cervus elaphus*) and moose (*Alces alces*) calves (Pelton 2000). Diet may vary by location, and proximity to humans may result in a black bear diet composed largely of garbage or other human food items (Hazard 1982).

In response to winter food shortages, female and male black bears typically become dormant. The level and duration of inactivity relates to latitude, but dormancy typically lasts 60 days or more (Pelton 2000). In Wisconsin, black bears are usually dormant for at least four months (WDNR 2007). Winter dens vary greatly in location and structure, and can range from cavities in hollow trees to sandy dugouts or shallow nest bowls (Weaver and Pelton 1994). During their period of inactivity, black bears exhibit a slightly decreased metabolism, but continue to use a great deal of energy without urination or defecation (Pelton 2000).

With the exception of sows with cubs or yearlings, black bears are usually solitary animals. Male and female black bears seldom encounter one another outside of the summer breeding season. In Wisconsin, peak black bear breeding season occurs between mid June and early July (Kohn 1982). Total gestation lasts seven months or more, and young are born in late January or early February while females are in winter dens.

Sexually mature female black bears typically breed every two years (Hellgren and Vaughn 1989). However, interbirth intervals of up to 3.2 years have been observed during periods of low food availability and high population density (Kasworm and Their 1994). After females give birth, they care for their young for 15-17 months, and then come into estrus after the family unit breaks up (Pelton 2000).

The age of primiparity in females varies according to nutrition and body size. Typically, female black bears reach sexual maturity between 2 and 7 years (Pelton 2000). No bears younger than 4.5 years were found to be in estrus in Montana (Jonkel and Cowan 1971). However, 2.5-year old females were observed breeding in Minnesota (Rogers 1987). The mean age of first reproduction of female black bears in Wisconsin was 3.9 years (Fleming 1997).

Litters of 2-3 cubs are most common among female black bears. Average litter size of black bears was 2.7 cubs/litter in Quebec, Canada (Samson and Huot 1995), 2.75 cubs/litter in Coahuila, Mexico (Doan-Crider and Hellgren 1996) and 2.44 cubs/litter in northern Wisconsin (Fleming 1997). Nutrition and body size of female black bears may influence litter size. Years with poor mast production often result in decreased litter sizes (Pelton 2000).

At birth, cub sex ratios in black bear populations are nearly always 1:1. In northern Wisconsin, cub sex ratios did not differ from an even ratio (Fleming 1997). However, a male:female cub sex ratio of 2.5:1 was observed in Oregon (Lindzey and Meslow 1977). The proportion of male cubs may be positively related to maternal weight (Noyce and Garshelis 1995).

The lowest survival rate among black bear age classes occurs in the cub age class (bears <1-year of age). Cub survival is highly dependent on the mother's experience, age, and body condition (Pelton 2000). Survival rates of black bear cubs range from 0.69 to 0.81 (Doan-Crider and Hellgren 1996; Trauba 1996; Wear et al. 2005).

Survival rates of black bears are most frequently calculated as annual rates and are defined as the proportion of individuals within a population surviving from one year to the next. Both natural and human induced mortality can affect black bear survival rates. Typically, black bear survival rates are most influenced by human induced causes of mortality such as hunting, depredation control, poaching, and vehicle collision (Pelton 2000).

At around 16 months of age, immature black bears leave their mothers and establish their own territories. Immature bears are typically less experienced, and are therefore more susceptible to mortality resulting from natural food shortages and severe weather conditions. Immature bears also may be subject to cannibalism by mature black bears (Gesch 2003). Yearling bears exhibited a survival rate of 0.81 in Virginia (O'Neill 2003) and 0.89-0.94 in Wisconsin (Kessler 1994).

Adult female black bears (≥ 3 years) exhibit the highest survival rates of any age class, with most estimates ranging from 0.90 to 0.97 (Bales et al. 2005; Dobey et al.; Kohler and Pierce 2005). High survival rates of adult females can often be attributed to timing of harvest seasons. Many states set black bear hunting seasons for late fall after most adult females have denned to protect females and their cubs from hunting mortality (O'Neill 2003).

The most variable survival rates occur in adult male black bears. Adult males (≥ 3 years) are more susceptible to human induced mortality because of both the timing of harvest and home range size. Adult male black bears have large home ranges and may be more likely to come in contact with hunters, campgrounds, garbage dumps, and residential areas. Estimates of adult male survival range from 0.59 to 0.76 (Hellgren and Vaughn 1989; Koehler and Pierce 2005; Lee and Vaughn 2005).

In summary, the black bear is a commonly occurring large mammal species in North America. Life history characteristics, such as diet selection, winter dormancy, and reproduction vary by region and habitat quality. Annual survival rates of black bears vary with age class and sex, but are typically quite high.

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CHAPTER I:

REPRODUCTIVE PARAMETERS OF BLACK BEARS IN NORTHERN WISCONSIN

Abstract. Between 1989 and 2008, 99 female black bears (*Ursus americanus*) were radio-collared and monitored in the Chequamegon-Nicolet National Forest, Wisconsin. Data from this 20-year period were used to estimate reproductive parameters for female black bears in northern Wisconsin. A relatively low mean age of first reproduction (4.11 years), high mean litter size (2.46 cubs/litter), and low interbirth interval (2 years) are likely indicative of high resource availability in the study area. Mean litter size was consistent with past estimates from northern Wisconsin and appeared to vary with sow age. Fecundity also increased with increasing sow age. Neither annual litter size nor annual pregnancy rates exhibited a significant linear trend with time. Annual reproductive parameters (mean litter sizes and pregnancy rates) were not related to annual environmental variables (winter severity, average precipitation, and average temperature). Reproductive parameter estimates from this study are intended to aid the Wisconsin Department of Natural Resources in effectively managing the black bear population in northern Wisconsin.

INTRODUCTION

Black bears exhibit some of the lowest reproductive rates among terrestrial mammals due to relatively late reproductive maturity, an extended reproductive period, and small litter size (Pelton 2000). As a result, black bear populations may be slow to recover from overexploitation (Miller 1990). Black bears are currently harvested in 29 states, including Wisconsin, and wildlife managers in these states must have a reliable abundance estimate to direct harvest goals (Garshelis and Hristienko 2006).

The Wisconsin Department of Natural Resources (WDNR) currently employs a black bear population model developed for Minnesota black bears. This model, BEARPOP2, uses an accounting approach requiring input parameters such as known harvest mortality, sex ratios, and litter sizes (Garshelis and Snow 1988). The final model output is not a direct estimate of population size, but rather a series of possible population projections given an initial population size provided by the model user. Known sex- and age-specific harvests along with assumed natural mortality are subtracted from the initial population to estimate the size and composition of the post-hunt population. Estimates of mean litter size and cub sex ratio are then used to estimate a post-birth season population, which is then reduced by estimated summer losses to generate the next pre-hunt population. The model user can determine, given the generated population trends, if the initial pre-hunt population is large enough to support the known losses. The initial population is adjusted to gain the best agreement between the estimated trend and trends determined independently from bait station surveys. By adjusting the initial population, the model user can reasonably estimate a feasible population trend for the state (Rolley and Woodford 2007).

Unfortunately, life history parameter inputs that make this model so comprehensive may also seriously jeopardize the accuracy of the model for Wisconsin managers. Many parameters, such as adult sex ratio, cub sex ratio, and mean litter size are from dated research or are assigned based on black bear research in Minnesota. As a result, many input parameters may not reflect Wisconsin black bear population dynamics.

The WDNR assumes that black bear population projections are accurate if the model trend is mirrored in bait station indices. However, the models have been suggesting a declining population in the northern 1/3 of the state for the past nine years, whereas the bait-station data have suggested a stable to increasing population (Rolley and Woodford 2007). Despite the discrepancy between model projections and bait station indices, the WDNR continues to issue a large number of black bear hunting permits each year. The total number of bears killed during hunting seasons increased from 460 in the fall of 1956 to 3,068 in 2006 (WDNR 2007). Because of the large number of black bears harvested in Wisconsin each year, an accurate population model is crucial to effective management. If abundance of black bears is overestimated, the WDNR may set harvest goals at an unsustainable level, and the Wisconsin black bear population may be seriously over-harvested. On the other hand, if abundance is underestimated, the WDNR may fail to manage the black bear population through hunting, which may lead to increased conflict between black bears and humans in Wisconsin.

If accurate estimates of input parameters were acquired, the WDNR's black bear population model would be much more robust. Fortunately, data from a long-term study of black bears in northern Wisconsin are available. From 1989 through 2008, the University of Wisconsin - Stevens Point conducted mark-recapture studies of black bears in the Chequamegon-Nicolet National Forest as a part of the Wisconsin Black Bear Research Project. My study has been constructed using data from the 20-year project, and the results are intended to aid the WDNR in accurate black bear population projection for the state of Wisconsin. My objectives were to (1) to estimate mean age of first reproduction, fecundity, year-specific pregnancy rates, age- and year-specific mean litter sizes, and cub sex ratios for northern Wisconsin black bears, and (2) determine if annual mean litter sizes and pregnancy rates were related to environmental variables such as winter severity and the previous year's precipitation and average temperature.

STUDY AREA

This study was conducted in the Great Divide district of the Chequamegon-Nicolet National Forest in north central Wisconsin (Figure 1). The study area is approximately 183,000 hectares, includes portions of Ashland, Bayfield, Price and Sawyer Counties, and is heavily forested. The forest is predominantly northern mesic with scattered areas of boreal forest and conifer lowlands. Major tree species of northern mesic forests include sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), bigtooth aspen (*Populus grandidentata),* and red maple (*Acer rubrum*). Lowland species include black ash (*Fraxinus nigra*), white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*) and eastern hemlock (*Tsuga canadensis*) (Storlid 1995). The area exhibits flat to rolling topography, with many lakes, rivers and wetlands. The area's soils are composed of sandy loam glacial till, silt-covered glacial till and sandy outwash soils. The average mean temperature is 4.5°C and the average annual precipitation is 80 cm (NOAA 2007).

METHODS

Field Methods

The mainland portion of the University of Wisconsin-Stevens Point Wisconsin Black Bear Research Project has been ongoing since 1989 (Massopust 1985, Kessler 1994, Storlid 1995, Trauba 1996, Fleming 1997, Gesch 2003, Hansen 2005). At present, this study is limited to female black bears because of their relevance to population dynamics. Because fecund individuals are those that contribute to population growth, female black bears are the individuals of interest when studying black bear survival and reproduction. Male black bears tend to roam too far outside the study area to be relocated and monitored regularly within time and budget constraints.

The first females were added to the study as a result of summer trapping. Bears were trapped in culvert traps throughout the study area and immobilized with an injection of a 5:1 mixture of ketamine:xylazine (6 mg/kg). Drugs were administered with a CAP-CHUR pistol (Palmer Chemical Company, Douglasville, Georgia, USA) or a jab stick. Researchers measured standard body features of each bear, tattooed the upper inside lip, attached uniquely numbered ear tags in both ears and extracted the first premolar for age estimation by cementum annuli analysis. All female bears were fitted with VHF radio-transmitter collars (ATS) equipped with leather spacers designed to break away after 18 months in the event of transmission failure. The same trapping and data collection methods were used to add females to the study when the number of collared females fell below ten.

Movement of radio-collared females was monitored during summer and fall. Locations of individuals were estimated at least once every two weeks using triangulation of radio signals from the ground. Signals were received on a vehicle-mounted model R4000 ATS receiver attached to a 5-element Yagi directional antenna. Aerial telemetry was used to supplement ground telemetry when a radio-collared bear could not be located from the ground.

In late November of each year, winter den sites were located. Specific locations of dens were obtained with the use of a handheld H-antenna in mid-winter. Dens were revisited in late February and early March. During each den visit, adult bears were sedated by injection of telazol (~4 mg/kg). Injections were administered via a CO_2 powered dart projector (Dan-Inject, Knoxville, TX, USA) or jab stick. Bears were sexed, weighed and monitored for heart and respiration rate and temperature. Chest and neck girth, total length, and footpads were measured. Cubs of the year were also sexed and weighed. A first premolar tooth was extracted from all bears of unknown age and sent to a lab for age estimation. Bears were marked with button ear tags and tattooed inside the lower lip with a permanent ID number. At each den visit, all yearling females of suitable weight were fitted with VHF radio-transmitter collars.

Dens of uncollared females within the study area were located from reports of local hunters and landowners. Bears within dens were processed in the manner described above, and females of suitable weight were fitted with VHF collars.

Between 10 and 25 individual sows were monitored each year. Locating as many dens as possible within the study area allowed for a large sample of female bears, which led to greater precision of life history parameter estimates.

Data Analysis

I estimated mean age at first reproduction using the Garshelis (1998) non-biased model. I included individuals whose reproductive status was verified during annual den visits or capture beginning at age 3. Only sows known to be previously nulliparous (never before observed with cubs) were included in the calculations.

Litter size was determined from a count of cubs in dens 1989-2008. Mean litter size was calculated as a mean of ratios. Due to small sample sizes for older black bear age classes, I pooled age-specific litter size results for female black bears age 7+. I used linear regression to test for a relationship between litter size and time (year).

I used a χ^2 test to determine if cub sex ratios differed from 50:50. Age-specific pregnancy rates were calculated as the proportion of available sows producing female cubs in each age class (1-15 Years), and pregnancy rates were calculated as the proportion of available sows producing each year (1989-2008). Available sows were those one year and older and without yearlings. I used linear regression to test for a relationship between age- and year-specific pregnancy rates and time (year).

I tested for differences in annual litter sizes and pregnancy rates relative to environmental variables. Specifically, I was interested in relationships between year-specific mean litter sizes and pregnancy rates and annual winter severity indices, the previous year's average precipitation and the previous year's average temperature (WDNR 2007; NOAA 2008). I used linear regression to test for significant ($P \leq 0.05$) relationships between reproduction and environmental variables from 1989 to 2006 (years with complete environmental data available).

All statistical analyses were performed using Microsoft Excel or SPSS statistical software (SPSS, Chicago, Illinois, USA). Statistical tests were considered significant if $P \leq 0.05$.

RESULTS

We monitored 99 female bears between 1989 and 2008. Of the 99 sows, 35 produced cubs, and 21 of the 35 sows produced cubs that survived to one year of age. Ages of radio-collared female bears ranged from 1 to 15 years. One 15-year old female dropped her radio collar, but was reported harvested 3 years later, making her 18-years old at harvest. The median age of known-age female bears was 3 years (n=77).

Mean age of first reproduction of 61 previously nulliparous known age sows was 4.11 years (Table 1). Four sows had their first litter at age 3, 8 at age 4, and 7 at age 5. The remaining 19 previously nulliparous known age sows were harvested, dropped their radio-collars, or had their radio-collars removed prior to producing their first litter. Three nonproducing 6 year olds that were added to the study at age 4 were not included as nulliparous individuals because they may have given birth before entering the study.

Litter size ranged from 1 to 4 cubs. Mean litter size of 92 observed litters was 2.46 ± 0.17 cubs/litter (Table 2) and litter size did not change systematically through time ($r^2 = 0.11$, 19 df, $P = 0.24$). Litter size varied with sow age, with older sows producing larger litters (Table 3). Age data were not available for nine productive sows, so these individuals were excluded from age-specific analyses.

The sex ratio of 184 cubs from the 92 litters was 1M:1.03F and did not differ significantly from 1:1 (χ^2=0.02, 1 df, $P > 0.05$) (Table 4). Four 3-year olds were observed with litters of one female cub each, thereby resulting in a composition of litters that was 100% female.

Age-specific pregnancy rates ranged from 0-1.0 (Table 5), and age-specific pregnancy rate was not significantly related to sow age (r^2=0.47, 14 df, $P = 0.18$). Year-specific pregnancy rates ranged from 0-0.67, but was not significantly related to time (year) (r^2=0.11, 19 df, $P = 0.15$).

Reproductive cycles were not skipped by female black bears in our study. Skips in cycles were considered to have occurred when the reproductive cycle was > 2 years in length. On four occasions, sows exhibited an interbirth interval < 2 years. On each occasion, the sow gave birth one year, lost the litter, and then gave birth again the next year. One sow gave birth in three consecutive years after losing each of the previous years' litters.

Reproductive parameters (year-specific litter size and pregnancy rates were not significantly related to any of the environmental variables (WSI, annual precipitation, and annual average temperature) (all P values > 0.22) (Table 6).

DISCUSSION

My research provides the first estimates of reproductive parameters for black bears in northern Wisconsin generated from long-term mark-recapture data. The primary source for reproductive information previously available for black bears in Wisconsin was produced from a 1982 study by Bruce Kohn of the Wisconsin DNR, who used harvest data in combination with field observations from 1975-1979 to make inferences about black bear population dynamics. Reproductive parameter estimates from my research will not only be more current than Kohn’s estimates, but will also provide more precise parameter estimates. My research is based on much larger sample sizes than previous research but also incorporates age-specific effects. As a result, wildlife managers may be able to target segments of the black bear population most important to population dynamics.

My estimates of black bear reproductive parameters are similar to those previously published. Mean age of first reproduction from my study was similar to that of black bears in Virginia (Hellgren and Vaughn 1989), Arkansas (Smith 1985), and earlier studies of black bears in northern Wisconsin (Kohn 1982; Fleming 1997). Four 3-year old females gave birth during my study, but all four litters had only one cub, and only one cub out of the four survived to the next year.

I found that reproductive parameters were not significantly related to environmental variables. Precipitation, temperature and winter severity may all influence mast production, and thereby influence black bears nutritional condition and reproductive capacity (Eiler et al. 1989). However, in northern Wisconsin, habitat quality may be high enough to support normal reproductive output even in years with relatively poor mast production. The predominance of deciduous forest, coniferous forest and forested wetland in northern Wisconsin likely provide excess mast and cover required by black bears (Hansen 2005). Black bears are also omnivorous, so they are able to switch to other food sources when mast availability is low.

Human-related factors may also influence black bear reproduction in northern Wisconsin. Areas of high human population density are beginning to overlap the primary range of black bears in Wisconsin so non-natural food sources are becoming increasingly available to black bears. In addition, baiting practices associated with black bear hunting have been in effect since 1985 in Wisconsin, and anecdotal evidence suggests that an increase in black bear body weight is due to bears feeding on bait piles. For example, in a study of black bears in Minnesota female black bears supplementing their diets with garbage had a lower mean age of reproduction, shorter interval between litters, and higher mean litter size than black bears feeding only on natural foods (Rogers 1993). Further research is necessary to determine whether high reproductive success in my study is due to high quality habitat or artificial food availability.

Body weight should be considered as a variable of interest in future reproductive analyses. Although a clear relationship between body weight and reproductive output of female black bears has been established in other parts of the country, analysis should be undertaken to see if such a relationship exists in the Wisconsin black bear population. Too much data were missing for me to analyze measured body weights and reproductive parameters. Kohn (1982) presented average live weight-at-age data for female black bears in Wisconsin that may be tentatively used to fill in gaps in weight data. Obtaining data on body weights should be a priority during future den visits to enable analyses.

Accuracy of my reproductive estimates requires that our marking system had no effect on the animals' behavior and reproduction. Radio-collars used in our study likely had little direct effect on either variable, but anecdotal evidence suggest that bear hunters may target radio-collared bears during the hound-training season. These female bears may have heightened stress levels that may reduce their reproductive capacity. Indirect effects of radio-collaring were not evident in this study, but should be monitored in the future.

I assumed that available females were one year or older and without yearlings, which was likely violated because most females did not reach sexual maturity until nearly four years of age. However female black bears may breed as early as 2 years old, so younger bears in our study area may be physiologically capable of reproducing much earlier (Collins 1973; Rayborne 1976; and Kordek and Lindzey 1980). Therefore, females younger than age four were available to reproduce, and I thought that including all marked females older than age one was warranted.

I considered bears captured between ages 1 and 3 to be previously nulliparous when estimating mean age of first reproduction. Reproduction before the age of three has never been recorded for a Wisconsin black bear (Fleming 1997). Any error caused by incorrectly assuming females under the age of 3 to be nulliparous would therefore likely be minor.

Another possible shortcoming of my study was that I used repeated observations. Ideally, observations within a sample should be independent when estimating accurate and representative parameters. Because we followed the same bears year after year, our study may be confounded by attributes of individual bears that do not reflect the entire population. Reproductive capacity may be greatly influenced by factors specific to an individual, such as physical condition or behavior. Therefore, collecting data from the same individuals may not represent the whole population. However, the alternative of collecting data from a large number of individuals on single occasions is not feasible in terms of funding or time. In addition, our sample size (99 individuals) was larger than most other studies of black bears, which likely compensated for any issues related to lack of independence.

MANAGEMENT IMPLICATIONS

A long-term study such as this has the potential to be greatly beneficial for wildlife managers. Long-term studies allow researchers to accurately observe natural patterns of a long-lived species like the black bear. The long-term nature of this study also allowed us to capture data on a variety of black bear age classes, which will allow wildlife managers in Wisconsin to target highly productive segments of the black bear population either to reduce the population or to encourage population growth.

Although reproductive parameters provide information on the health of a population, other factors like survival may be of equal or greater importance (Freedman et al. 2003). Our estimates of reproductive parameters will be used in combination with cub, juvenile, and adult survival to construct a life table for female black bears in northern Wisconsin (Chapter 2). From the life table, I estimated a rate of growth for the population to further assess the status of black bears in northern Wisconsin. My estimate of population growth should assist the WDNR in assessing progress toward management goals.

The results of my study are intended to aid the WDNR in producing a model that accurately projects the black bear population in Wisconsin. Some of our estimated reproductive parameters, such as mean litter size, differ from those currently used by the WDNR. For example, a mean litter size of 2.4 cubs/litter for black bears in northern Wisconsin (Kohn 1982) closely matches our estimate. However, I found that litter size varied with sow age, so the WDNR should incorporate age-specific mean litter size into their model. Other reproductive parameters I estimated do not differ greatly from WDNR estimates. Nonetheless, my results from a long-term mark-recapture study serve to validate previous estimates.

A large number of females in my study were harvested before age of first reproduction. The median age of female black bears in this study was 3 years, while mean age of first reproduction was approximately 4 years. This means that a relatively small number of sows are contributing to the next generation of female bears. Previously, the average age of first reproduction was 4.5-5.8 for female black bears in Wisconsin (Kohn 1982). My results may indicate a change in black bear age structure in Wisconsin that should be further investigated.

The oldest bear in my study, a 15-year old female, exhibited high reproductive success by producing 4 litters during 7 years in the study. Both her longevity and high reproductive success is likely only because her home range fell primarily within private property, which protected her from harvest. Most black bears in northern Wisconsin are exposed to high hunting pressure because much of the land in the area is open to public hunting. Research should be conducted to determine if reproductive success is related to property ownership (public vs. private) of female black bears in northern Wisconsin.

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TABLE 1. Production of first litters directly observed among radiocollared black bears in Northern Wisconsin, 1989-2008

Age (yr)	No. of nulliparous females available to reproduce	No. producing	% of nulliparous females producing	% of females in pop. Available to produce	% of females in population producing	Age weighted by % of population producing
3	36	4	11.1	100	11.1	0.33
4	17	8	47.1	88.9	41.9	1.68
5	8	7	87.5	47	41.1	2.1
					Sum	**4.11**[a]

[a]Mean age of first reproduction calculated using methods described by Garshelis (1998).

TABLE 2. Year-specific mean litter sizes for Northern Wisconsin black bears, 1989-2008, showing overall mean litter size.

Year	**Sows**	**Litters**	**Cubs**	**Mean litter size**	**S.E.**
1989	4	0	0	-	-
1990	7	3	6	2	0.58
1991	13	4	9	2.25	0.48
1992	13	2	4	2	1.00
1993	13	4	10	2.5	0.29
1994	14	3	8	2.67	0.33
1995	14	5	13	2.6	0.24
1996	15	3	7	2.33	0.88
1997	19	6	16	2.67	0.24
1998	24	4	8	2	1.00
1999	17	10	23	2.3	0.22
2000	12	1	4	4	0
2001	15	8	24	3	1.00
2002	16	6	14	2.33	0.40
2003	17	4	14	3.5	0.33
2004	21	7	14	2	0.26
2005	19	8	20	2.5	0.30
2006	19	6	17	2.83	0.40
2007	21	4	12	3	0.71
2008	12	4	11	2.75	0.48
total	**305**	**92**	**234**	**2.46**[a]	

[a] Mean of ratios.

TABLE 3. Mean litter size and standard errors for Northern Wisconsin black bears ages 1-7+, 1989-2008.

Age	**Litters**	**Average Litter Size**	**S.E.**
1	0	0	0
2	0	0	0
3	4	1.00	0
4	12	2.08	0.21
5	9	2.22	0.15
6	12	2.42	0.26
7+	37	2.86	0.11

TABLE 4. Sex composition of litters for female black bears in Northern Wisconsin, 1989-2008.

Year	Female Cubs	Male Cubs	Total Cubs	% Female	% Male
1989	0	0	0	0	0
1990	1	5	6	0.17	0.83
1991	3	6	9	0.33	0.67
1992	2	2	4	0.5	0.5
1993	5	5	10	0.5	0.5
1994	3	5	8	0.38	0.63
1995	8	5	13	0.62	0.38
1996	3	4	7	0.43	0.57
1997	9	7	16	0.56	0.44
1998	3	5	8	0.38	0.63
1999	12	11	23	0.52	0.48
2000	2	2	4	0.5	0.5
2001	14	10	24	0.58	0.42
2002	9	5	14	0.64	0.36
2003	2	12	14	0.14	0.86
2004	10	4	14	0.71	0.29
2005	14	6	20	0.7	0.30
2006	10	7	17	0.59	0.41
2007	3	9	12	0.25	0.75
2008	6	5	11	0.55	0.45
Total	**119**	**115**	**234**	**0.508547**	**0.491453**

TABLE 5. Age-specific pregnancy rates and standard errors of female black bears age 1-15 in Northern Wisconsin, 1989-2008. Pregnancy rates were calculated as the proportion of available sows producing in each age class. Available sows were considered to be those >1 year of age and without yearlings.

Age Class	**Sows with Cubs**	**Pregnancy Rate**	**S.E.**
0	0	0	0
1	0	0	0
2	4	0.1	0.048
3	12	0.5	0.10
4	9	0.69	0.13
5	12	0.92	0.07
6	5	0.83	0.17
7	9	0.75	0.13
8	5	1	0
9	5	1	0
10	4	1	0
11	3	0.75	0.25
12	3	0.75	0.25
13	1	0.5	0.5
14	2	1	0
15	0	0	0

TABLE 6. Results of linear regressions to test for relationships between reproductive parameters and environmental variables. Shown are the dependent variables, independent variables, degrees of freedom, r-square values, and P-values associated with each regression. Reproductive parameters (year-specific litter size and pregnancy rates were not significantly related to any of the environmental variables (WSI, annual precipitation, and annual average temperature) (all P-values > 0.05)

Dependent Variable	**Independent Variable**	**Degrees of Freedom**	R^2	**P-value**
Litter size	WSI	17[a]	0	0.90
Litter size	Precipitation	17	0.02	0.58
Litter size	Temperature	17	0.01	0.75
Pregnancy rate	WSI	17	0	0.96
Pregnancy rate	Precipitation	17	0.08	0.26
Pregnancy rate	Temperature	17	0.09	0.22

[a] I tested for relationships between variables from 1989 to 2006. Complete environmental data were available for this 18-year period.

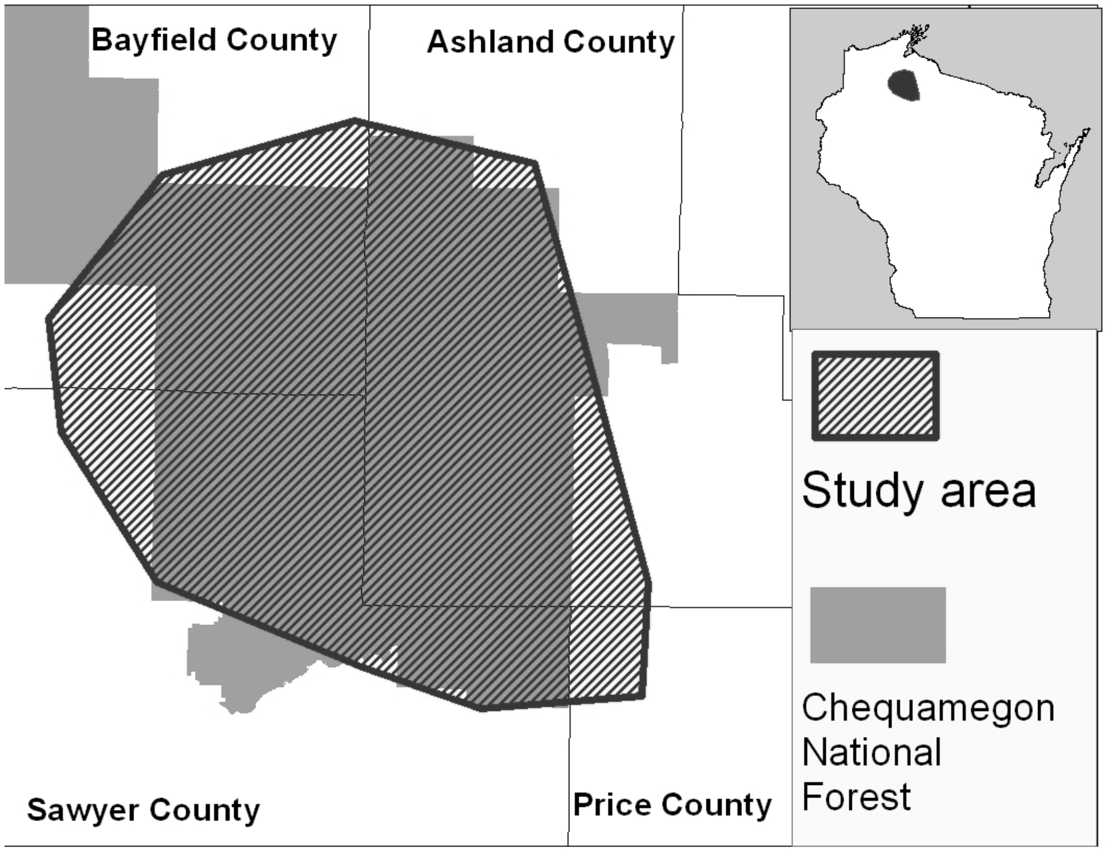

FIGURE 1. The Clam Lake study area—including land in Bayfield, Ashland, Sawyer and Price counties of Wisconsin. Most of the study area lies within the boundaries of the Chequamegon-Nicolet National Forest.

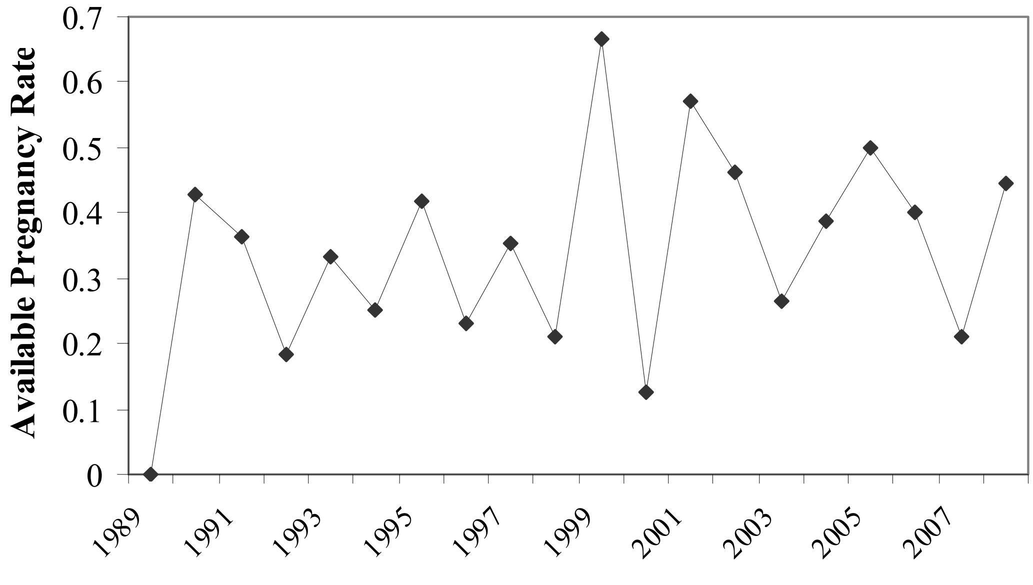

FIGURE 2. Year-specific pregnancy rates for female black bears in Northern Wisconsin, 1989-2008. Pregnancy rates were calculated as the proportion of available sows producing each year. Available sows were considered to be those >1 year old and without yearlings.

CHAPTER II:

SURVIVAL RATES OF BLACK BEARS IN NORTHERN WISCONSIN

Abstract. Between 1989 and 2007, 99 female bears were radio-collared and monitored in the Chequamegon-Nicolet National Forest, Wisconsin. Data from this 19-year period were used to estimate survival rates for female black bears in northern Wisconsin. I used Program MARK to test a set of a priori known-fate survival models and found that a model incorporating senescence best explained variation in survival, but the top three models were all equally plausible descriptions of black bear survival. A global model generating year-specific survival and an intercept-only model generating an overall average survival rate may be useful to wildlife managers. Overall survival of female black bears in northern Wisconsin was relatively low (~0.80) when compared to other hunted populations. Age-specific survival combined with estimated fecundity indicated that the annual population growth rate was λ = 1.03 – 1.04. The life table was then converted to a Leslie matrix for elasticity analysis. I found that λ for the northern Wisconsin black bear population was most sensitive to perturbations in cub and yearling survival. Results of my study should be combined with existing information on black bear population dynamics in Wisconsin to direct black bear population management.

INTRODUCTION

According to the Wisconsin Department of Natural Resources' (WDNR) population model, Wisconsin currently has approximately 14,000 black bears (WDNR 2007). Numbers of black bears within the state have risen dramatically over the past several decades. In 1985, the black bear harvest season was closed due to concern over population levels. Black bear harvest was tentatively reopened the following year, with only 844 permits issued. Since that time, the population has flourished and continues to be managed through harvest. The WDNR issued 4,660 permits for the 2008 black bear harvest season (WDNR 2007).

Despite implementation of a population model in the late 1990s, the status of the black bear population within the state remains uncertain. The population model suggests the population may be declining in the northern 1/3 of the state over the past nine years, whereas bait-station data suggest the population is stable or increasing (Rolley and Woodford 2007). Despite the discrepancy between model projections and bait station indices, the WDNR continues to issue a large number of black bear hunting permits each year. Up to date estimates of population parameters may reduce this uncertainty and enable the WDNR to accurately assess the status of the black bear population in Wisconsin.

Accurate estimates of female black bear survival rates are of particular importance to wildlife managers. Age-specific survival rates are necessary for population models and aid managers in targeting sensitive segments of a population. In addition, survival rates of subadult bears that represent recruitment into the reproductive adult population facilitate detailed study of population growth (Lee and Vaughn 2005).

Estimates of survival rates are not recent for Wisconsin black bears. Increasing overlap of black bear habitat with areas of high human population density warrants investigation into current black bear population dynamics within the state. The primary objective of this study was to estimate overall survival of female black bears in northern Wisconsin over a 19-year period from 1989-2007. Secondary objectives were to (1) use an information-theoretic approach to test for the effects of environmental and management factors on female black bear survival (Burnham and Anderson 1998), and (2) to combine age-specific survival rates with reproductive data (Chapter 1) to estimate rates of population growth through life table analysis.

STUDY AREA

This study was conducted in the Great Divide district of the Chequamegon-Nicolet National Forest in north central Wisconsin (Fig. 1). The study area is approximately 183,000 hectares, includes portions of Ashland, Bayfield, Price and Sawyer Counties, and is heavily forested. The forest is predominantly northern mesic with scattered areas of boreal forest and conifer lowlands. Major tree species of northern mesic forests include sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), bigtooth aspen (*Populus grandidentata),* and red maple (*Acer rubrum*). Lowland species include black ash (*Fraxinus nigra*), white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*) and eastern hemlock (*Tsuga canadensis*) (Storlid 1995). The area exhibits flat to rolling topography, with many lakes, rivers and wetlands. The area's soils are composed of sandy loam glacial till, silt-covered glacial till and sandy outwash soils. The average mean temperature is 4.5°C and the average annual precipitation is 80 cm (NOAA 2007).

METHODS

Field Methods

The mainland portion of the University of Wisconsin-Stevens Point Wisconsin Black Bear Research Project has been ongoing since 1989 (Massopust 1985, Kessler 1994, Storlid 1995, Trauba 1996, Fleming 1997, Gesch 2003, Hansen 2005). At present, this study is limited to female black bears because of their relevance to population dynamics. Because fecund individuals are those that contribute to population growth, female black bears are the individuals of interest when studying black bear survival and reproduction. Male black bears tend to roam too far outside the study area to be relocated and monitored regularly within time and budget constraints.

The first females were added to the study as a result of summer trapping. Bears were trapped in culvert traps throughout the study area and immobilized with an injection of a 5:1 mixture of ketamine:xylazine (6 mg/kg). Drugs were administered with a CAP-CHUR pistol (Palmer Chemical Company, Douglasville, Georgia, USA) or a jab stick. Researchers measured standard body features of each bear, tattooed the upper inside lip, attached uniquely numbered ear tags in both ears and extracted the first premolar for age estimation by cementum annuli analysis. All female bears were fitted with VHF radio-transmitter collars (ATS) equipped with leather spacers designed to break away after 18 months in the event of transmission failure. The same trapping and data collection methods were used to add females to the study when the number of collared females fell below ten.

Movement of radio-collared females was monitored during summer and fall. Locations of individuals were estimated at least once every two weeks using triangulation of radio signals from the ground. Signals were received on a vehicle-mounted model R4000 ATS receiver attached to a 5-element Yagi directional antenna. Aerial telemetry was used to supplement ground telemetry when a radio-collared bear could not be located from the ground.

In late November of each year, winter den sites were located. Specific locations of dens were obtained with the use of a handheld H-antenna in mid-winter. Dens were revisited in late February and early March. During each den visit, adult bears were sedated by injection of telazol (~4 mg/kg). Injections were administered via a CO_2 powered dart projector (Dan-Inject, Knoxville, TX, USA) or jab stick. Bears were sexed, weighed and monitored for heart and respiration rate and temperature. Chest and neck girth, total length, and footpads were measured. Cubs of the year were also sexed and weighed. A first premolar tooth was extracted from all bears of unknown age and sent to a lab for age estimation. Bears were marked with button ear tags and tattooed inside the lower lip with a permanent ID number. At each den visit, all yearling females of suitable weight were fitted with VHF radio-transmitter collars.

Dens of uncollared females within the study area were located from reports of local hunters and landowners. Bears within dens were processed in the manner described above, and females of suitable weight were fitted with VHF collars.

Between 10 and 25 individual sows were monitored each year. All dens were located within the study area to obtain comprehensive capture histories for each sow. Sows consistently located during each den survey with complete recapture histories were used to estimate survival. Locating as many dens as possible within the study area also allowed for a large sample size of female bears, which led to greater precision of life history parameter estimates.

Survival Analysis

I estimated survival rates from mark-recapture data using a known-fate model within program MARK (White and Burnham 1999). Known-fate analysis (Kaplan-Meier analysis) is based on the assumption that the death or detection of study animals is known with certainty. Use of a known fate model requires several assumptions: (1) animals of each sex and age class are randomly sampled, (2) survival times are independent among individuals, (3) capture of an animal or attachment of a radio collar does not influence survival, (4) censoring is random, and (5) newly-collared and previously-collared individuals have the same survival probability (Pollock et al. 1989).

Kaplan-Meier analysis is commonly used with radio telemetry studies because the fate of each animal can be known. If the fate of an individual is unknown, then that animal is censored from the study. Some black bears in the data set were censored because of incomplete capture histories resulting from failure of radio collars or loss of capture documentation.

The probability of survival between year *i* and *i*+1 (S) is the parameter of interest in a known-fate model. In my study, survival probability was expressed as a yearly survival rate, the probability that an animal survived from one den processing event to the next. The Kaplan-Meier model assumes that all animals are released at time 1 and are followed until they die or are censored. However, for my mark-recapture study, I used Pollock's staggered-entry design, because animals were added to the study over a 19-year period (Pollock et al. 1989).

The Kaplan-Meier survival estimator is

$$\hat{S}_t = \prod_{i=1}^{t} \left[1 - \left(\frac{d_i}{r_i} \right) \right]$$

where $\hat{S}_t$ is the finite survival rate for year *t*, d_i is the number of deaths recorded during year *i*, r_i is the number of individuals alive and at risk during year *i* (Krebs 1999).

Data must be formatted as encounter histories for input into Program MARK. Known-fate encounter histories are constructed with paired entries of 1s and 0s. The first position is a 1 if the individual is alive at the start of the time interval and a 0 if the individual was not yet a part of the study at the beginning of the time interval. The second position in the paired entry is a 0 if the animal survived to the end of the time interval and a 1 if it died somewhere in the time interval. For example, an individual with the encounter history "101010" was added to the study at the first time interval and survived until the end of the study, while an animal with the encounter history "101011" was added to the study at the first time interval, but died during the third interval. My study of black bear survival included 19 years of data (1989-2007), so encounter histories were 36 paired entries for each tagged individual.

Linear models were constructed to explain variation in survival estimates. The basic linear form for these models was:

$$Yi = \beta_0 + \beta_1 x_1 + \beta_n x_n \ldots + \varepsilon$$

where β_0 is the intercept, $\beta_{1\ldots n}$ are the coefficients of survival effects $x_{1\ldots n}$, and ε is random error. Survival (S) was estimated by the equation:

$$S = \frac{e^{\beta_0 + \beta_1 x_1 + \beta_n x_n \ldots + \varepsilon}}{1 + e^{\beta_0 + \beta_1 x_1 + \beta_n x_n \ldots + \varepsilon}}$$

As explanatory variables are added to the model, the model becomes increasingly complex with more survival estimates. Program MARK uses an interface called the "design matrix" to effectively handle construction of complex models. The design matrix allows a user to delineate which variables will be incorporated into the model. By altering the design matrix, I generated models using biologically relevant variables.

Explanatory variables included age, hunting effort, harvest order, annual winter severity, and annual precipitation. Age data were obtained from den survey data for each collared individual or from results of cementum annuli analysis. Annual hunting effort was quantified by the number of black bear hunting permits issued each year during 1989-2007. Harvest order was defined as the yearly order prescribed by the WDNR for the two types of black bear hunting ("with the aid of dogs" versus "methods not utilizing the aid of dogs"). The WDNR specifies dog hunters and "other" hunters are each entitled to an exclusive one-week hunt every other year at the beginning of the bear hunting season. For example, in 2007, hunters using dogs were allowed to hunt exclusively from September 5 to October 2, while hunters utilizing other methods were allowed to hunt from September 12 to October 9. This order will be switched to favor hunters not utilizing dogs in 2008. Harvest order was a binary variable in my models, with a 1 for years when hunters with dogs were assigned the first week and a 0 for years when hunters utilizing other methods were assigned the first week.

Records of winter severity for the study area were obtained from the WDNR. Winter severity was represented by the winter severity index (WSI). The WSI is calculated by adding the number of days with 18 inches or more of snow on the ground to the number of days when the minimum temperature was 0°F or below between December 1 and April 30. A winter with an index of less than 50 is considered mild, 50 to 79 is moderate, 80 to 99 is severe and over 100 is very severe. Annual precipitation data from the Ashland, Wisconsin weather station, the station nearest to the study area, were obtained from National Oceanic and Atmospheric Administration website (NOAA).

I generated a set of a priori candidate models that related survivorship to potential explanatory variables. I initially constructed eleven models within Program MARK—an intercept only model, a global model, a linear time model, and eight models incorporating potential explanatory variables (Table 1). I did not estimate goodness of fit because such testing is currently unavailable for known fate models in

Program MARK or elsewhere (Devries et al. 2003). I used an information theoretic approach to select the most parsimonious model (Burnham and Anderson 1998).

Because cubs were not collared, I could not calculate their survival within Program MARK. I estimated cub survival (S_c) as

$$S_c = n_{t+1} / n_t$$

Where n_t is the total number of cubs alive at time t and n_{t+1} is the total number of cubs alive at time $t+1$

Population growth and elasticity analysis

I estimated the intrinsic rates of population change using life table analysis to explore the effects of age-specific survival and fecundity on the black bear population in northern Wisconsin. I constructed two life tables using cohort methods described by Caughley (1977), one using a constant adult survival rate and one using age-specific survival rates. I calculated fecundity rates (m_x) using reproductive data for female black bears ages 0-15 (Chapter 1). I estimated fecundity as the mean number of female cubs born per inter-birth interval to adult females [m_x = (number of cubs born)(% female cubs) / interbirth interval]. Cub sex ratio was 1:1 and interbirth interval was 2 years (Chapter 1). I calculated l_x, the probability at birth of surviving to age x for each age 0-15 and reproductive value (V), the expected reproduction of an individual from their current age onward. I then numerically solved Euler's equation ($1 = \sum e^{-rx} l_x m_x$) to generate the intrinsic rate of increase (r) for each life table (Caughley 1977).

I constructed Leslie matrices using fecundity and survival rates for female black bears age 0-15 in northern Wisconsin. I constructed a separate Leslie matrix for each set of life table values. I then generated elasticity values for both Leslie matrices (Caswell 2001).

RESULTS

Mortality

We monitored a total of 99 female bears between 1989 and 2007. Ages of radio-collared female bears ranged from 1 to 15 years. One 15-year old female dropped her radio collar, but was reported harvested 3 years later, thereby making her 18-years of age at harvest. The median age of known-age female bears was 3 years (n=77).

We recorded 66 deaths of radio-collared females during the study, 59 as a result of black bear hunting and 7 from other causes. Other causes included 1 car kill, 1 death caused by another bear, 2 deaths from unknown causes, and 3 research-related deaths. Twenty-one bears in the study suffered unknown fates either as a result of removed or dropped collars or transmitter failures. Twelve female bears are still radio-collared in the study area as of April 2008.

Survival

The top ranked model, S(age^2), was only three AICc points better than the next top ranked model, S(hunting effort) (Table 2). However, all models incorporating explanatory variables, with the exception of S(age^2), generated beta estimates with 95% confidence intervals including zero, thereby indicating little or no difference among models (Table 3). Therefore, I removed all models with parameters having confidence intervals containing zero, which left only three models: S(age^2), S(.), and S(t-full) (Table 4).

As a result of reducing my candidate model set, more model weight was given to S(age^2). This 3-parameter model included the effect of senescence on female black bear survival (Fig. 2). Survival estimates generated from this model ranged from 0.70 to 0.87 (Table 5). The intercept-only model provided an average survival estimate of 0.81. The global model provided year-specific survival rates (1989-2007) that ranged from 0.71 to 1.0 (Table 6).

Population growth and elasticity analysis

Fecundity rates (m_x) ranged from 0 to 0.67 and reproductive values (V_x) from 1 to 3.42 (Table 7, Table 8). Six to eight year old females exhibited the highest reproductive values (2.95 – 3.42). Net reproductive rates were R_0 = 1.33 and 1.20 and intrinsic rates of increase were *r* = 0.03 and 0.04 for the two life tables. Finite population growth rates were λ = 1.03 and 1.04.

The total of the fertility elasticities was only 0.13 - 0.14 (13-14%), while the elasticities to survival summed to 0.86 – 0.87 (86-87%) (Figure 3, Figure 4). The largest elasticities for both Leslie matrices corresponded to survival of cubs (P_0=0.13) and yearlings (P_1=0.14).

DISCUSSION

Survival

My research provides current estimates of age-specific survival of female black bears in northern Wisconsin generated from long-term mark-recapture data. For long-lived organisms such as black bears, data from a long-term study such as this one likely provide valuable insights into population dynamics. The results of this research are intended to aid the WDNR in assessing their current black bear management efforts.

Although my results indicated that a model incorporating age-specific effects was best, survival estimates from all three candidate models may be of use to wildlife managers. The global model provides year-specific survival estimates and may be useful for examining population trends. The intercept only model provides an overall average survival rate for all the females in the study, so may serve as an easily reportable overall rate for the adult female black bear population in the state. Finally, my age-specific survival rates are useful for life table analyses and population modeling.

The average survival estimate and age-specific survival estimates for my study were relatively low. Survival rates of adult female black bears in other regions, even in those where harvest is utilized as a management tool, are generally higher at around 0.90 (Bales et al. 2005; Koehler and Pierce 2005; Samson and Huot 1995). High levels of harvest mortality are likely the cause of lower adult female survival in Wisconsin. In 2007, the total black bear harvest success rate in Wisconsin was about 62%, which is approximately 30% higher than the rate reported for the state of

Minnesota. High harvest success and subsequent high adult female mortality in Wisconsin may be due to the allowance of black bear hunting with the aid of hounds, although more research would be necessary to establish a firm relationship between hound hunting and adult female mortality.

Because high harvest success most likely causes lower adult female survival, I was surprised that the hunting effort model poorly explained variation in survival. This may be due to inadequacy of the variable in representing female hunting mortality. Typically, black bear harvest is skewed toward male bears, so the number of permits issued may not adequately correspond to hunting pressure on females. Future survival analysis should consider variables that represent female-only harvest. Harvest mortality may also be better represented by harvest success rates in the future. Harvest success rates were not consistently available for the time period of this study. A compensatory interaction between harvest and survival rates of female bears may not be explained in my models.

However, effects of hunting may be examined indirectly through the senescence model, in which younger bears exhibited lower survival rates that may caused by exposure to heightened harvest pressure. Younger bears are typically less experienced and may have lower quality home ranges. These disadvantages may translate into a heightened incidence of harvest for young bears. In a 1982 study by the Wisconsin DNR, 2 and 3-year old bears were harvested at greater rates than older bears (Kohn 1982). This difference may be due to a greater abundance of individuals in these age classes, but inexperience and increased exposure to humans may also play a role.

In my model, 7 and 8-year old bears exhibited the highest survival (~0.87). This estimate approaches estimates for adult females in other regions and may indicate that older adult females in Wisconsin are somehow evading hunting pressure. Some females in my study area had home ranges that fell primarily within private property. As a result, these females were often protected from hunting pressure. This may be a simple cause and effect relationship or female bears may have adapted behaviorally to avoid areas with high levels of harvest pressure. Female black bears with cubs are known to be particularly wary of human presence. Research should be conducted to investigate whether females can translate harvest pressure into habitat suitability and establish home ranges in areas safe from harvest pressure.

One major shortcoming of my study was the high incidence of collar loss and transmitter failure. Individuals with lost collars or transmitter failure had unknown fates and were censored during known-fate analysis. If the number of unknown fates could be minimized, inferences could be stonger regarding the incidence of natural mortality. More effective collar and transmitter designs should be considered to minimize unknown fates in the future.

Population growth and elasticity analysis

The results of elasticity analysis of female black bears in northern Wisconsin closely matched results of other researchers, who found that λ of long-lived species such as black bears were sensitive to changes in juvenile survival (Powell et al. 1996; Heppell 2000). In particular, cub survival from birth to one year had the most influence on λ of black bears in North Carolina (Powell 1996).

Life table analyses assumes that the population intrinsic rate of increase is stable through time (Caughley 1977). This assumption is likely valid for my study. Neither litter size (Chapter One) nor survival varied with time, so the rate of increase was likely constant for the population during the study period. Likewise, elasticity analysis was an appropriate choice for our data. Fertility and survival data work on different scales, so assessing the response of λ to proportional, rather than absolute, changes was more appropriate.

One possible shortcoming of my life table analysis was small sample size. My sample size may be low when considered for life table analysis (Caughley 1977); however, when compared to other studies of black bears, my sample size is relatively high, with over 100 individuals incorporated into my life tables.

MANAGEMENT IMPLICATIONS

Although adult female survival was relatively low, the WDNR seems to have little need for concern over population levels. The results of my study indicate a slightly increasing black bear population in northern Wisconsin. A positive rate of increase may mean that female black bears are dispersing outside the study area. Some individuals of unknown fate in our study may be animals that dispersed. Signal loss as a result of travel outside the study area may have led to unknown fate in some instances.

My results indicating population increase may not reflect WDNR management goals. The current estimate of black bear abundance within the state is 14,000 individuals, which is the highest abundance of black bears ever estimated within the state. While the population model may need updating, the estimate may be reason for the WDNR to attempt population reduction. Complaints of nuisance black bears have increased in the past decade, and may confirm a need for population reduction.

Results from life table and elasticity analysis will allow managers to target vital rates that are particularly important to rates of population growth. Elasticity values indicated that perturbations to cub and yearling survival will have the greatest effect on λ. If managers wish to enhance λ for the black bear population in northern Wisconsin, they should protect young bears. Protecting young bears would likely entail protecting sows with cubs. Young bears may also benefit from a later harvest season or changes in hound hunting regulations.

Prescribing greater protection to sows with cubs may have a dual effect on the northern Wisconsin black bear population, by increasing survival of young bears and ensuring reproductive output of older females. Reproductive values indicated that females around age 6 exhibited the highest reproductive potential (3.42). Increasing the survival of older females through protection of sows with cubs may lead to a greater increase in λ for the northern Wisconsin population.

Currently, harvest of sows with cubs is illegal in Wisconsin, but this regulation may not prevent hunters from harvesting sows with cubs. Between 1989 and 2008, seven sows with cubs in our study were believed to have been harvested. These sows had cubs with them in their winter dens, but were harvested later in the same year during bear hunting season. Some of these cubs may have died before hunting season, thereby leaving the sow available for legal harvest. However, several of these sows were likely harvested illegally. The WDNR should implement greater enforcement of harvest regulations and restrict black bear harvest utilizing hounds to prevent both intentional and accidental harvest of sows with cubs.

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TABLE 1. A set of a priori models generated to explain variation in female black bear survival in northern Wisconsin, 1989-2007. Shown are the model structures and number of parameters associated with each model.

Model Structure	Number of Parameters
{S(age^2)}	3
{S(hunting effort)}	2
{S(t-linear)}	2
{S(.)}	1
{S(age)}	2
{S(harvest order)}	2
{S(harvest order, hunting effort)}	3
{S(WSI)}	2
{S(precipitation)}	2
{S(WSI, precipitation)}	3
{S(t-full)}	16

TABLE 2. Initial model list for female black bear survival in northern Wisconsin, 1989-2007. Shown are the model structures, AIC_c, ΔAIC_c, AIC_c weight, model likelihood and number of parameters associated with each model.

Model Structure	**Parameters**	**AIC_c**	**ΔAIC_c**	**AIC_c Weight**	**Model Likelihood**
{S(age^2)}	3	263.81	0	0.26	1
{S(hunting effort)}	2	265.07	1.26	0.14	0.53
{S(t-linear)}	2	265.15	1.34	0.14	0.51
{S(.)}	1	265.30	1.5	0.13	0.47
{S(age)}	2	265.58	1.77	0.11	0.41
{S(harvest order)}	2	267.00	3.19	0.05	0.20
{S(harvest order, hunting effort)}	3	267.04	3.23	0.05	0.20
{S(WSI)}	2	267.04	3.24	0.05	0.20
{S(precipitation)}	2	267.30	3.49	0.05	0.17
{S(WSI, precipitation)}	3	269.09	5.28	0.02	0.07
{S(t-full)}	16	276.56	12.75	0.00	0.00

TABLE 3. The initial model set and associated beta estimates. Also shown are the standard errors and 95% confidence intervals for each model.

Model Name	**Beta**	**Beta Estimate**	**Standard Error**	**Lower CI**	**Upper CI**
S(age^2)	linear	0.30	0.13	0.09	0.52
S(age^2)	quadratic	-0.02	0.01	-0.03	-0.00
S(hunting effort)	hunting effort	-0.18	0.12	-0.38	0.02
S(t-linear)	time	-0.05	0.03	-0.10	0.01
S(age)	age	0.06	0.05	-0.02	0.14
S(harvest order)	harvest order	0.18	0.31	-0.33	0.69
S(harvest order, hunting effort)	harvest order	-0.17	0.12	-0.37	0.03
S(harvest order, hunting effort)	hunting effort	0.14	0.31	-0.38	0.65
S(WSI)	WSI	0.00	0.00	-0.01	0.01
S(precipitation)	precipitation	0.00	0.03	-0.05	0.06
S(WSI, precip.)	WSI	0.00	0.00	-0.01	0.01
S(WSI, precip.)	precipitation	0.00	0.03	-0.06	0.06

TABLE 4. Model selection results for yearly female black bear survival (S) in northern Wisconsin, 1989-2007. Shown are the top candidate set of models, with the model structure, AIC_c, ΔAIC_c, AIC_c weight, model likelihood and number of parameters associated with each model.

Model Structure	**Parameters**	**AIC_c**	**ΔAIC_c**	**AIC_c Weight**	**Model Likelihood**
{S(age^2)}	3	263.81	0	0.68	1
{S(.)}	1	265.30	1.5	0.32	0.47
{S(t-full)}	16	276.56	12.75	0.00	0.00

TABLE 5. Survival estimates for female black bears ages 0-15 in northern Wisconsin, 1989-2007. Also shown are standard errors and 95% confidence intervals for each estimate.

Age	Estimate	Standard Error	Lower CI	Upper CI
0[a]	0.70	0.05	0.60	0.81
1	0.73	0.04	0.64	0.81
2	0.78	0.03	0.71	0.83
3	0.81	0.02	0.75	0.86
4	0.84	0.03	0.78	0.88
5	0.85	0.03	0.79	0.90
6	0.86	0.03	0.80	0.91
7	0.87	0.03	0.80	0.92
8	0.87	0.03	0.80	0.92
9	0.87	0.03	0.79	0.92
10	0.86	0.04	0.77	0.92
11	0.85	0.04	0.74	0.92
12	0.83	0.06	0.69	0.92
13	0.81	0.08	0.62	0.91
14	0.77	0.10	0.51	0.91
15	0.72	0.14	0.39	0.91

[a] Cub survival was calculated as 1-(number of cub deaths/total number of cubs born). Survival rates for ages 1-15 were calculated using Program MARK.

TABLE 6. Year-specific survival rates 1989-2007 of female black bears in northern Wisconsin. Also shown are standard errors and 95% confidence intervals for each estimate.

Year	Estimate	S.E.	Lower CI	Upper CI
1989	1.00	0	1.00	1.00
1990	1.00	0	1.00	1.00
1991	0.83	0.11	0.52	0.96
1992	0.82	0.12	0.49	0.95
1993	1.00	0	1.00	1.00
1994	0.80	0.10	0.53	0.93
1995	0.80	0.10	0.53	0.93
1996	0.73	0.11	0.47	0.90
1997	0.93	0.07	0.63	0.99
1998	0.80	0.09	0.57	0.92
1999	0.60	0.13	0.35	0.81
2000	0.83	0.11	0.52	0.96
2001	0.93	0.07	0.63	0.99
2002	0.71	0.12	0.44	0.89
2003	0.73	0.11	0.47	0.90
2004	0.68	0.11	0.45	0.85
2005	0.83	0.09	0.59	0.95
2006	0.88	0.08	0.63	0.97
2007	0.74	0.10	0.50	0.87

TABLE 7. Life table for female black bears ages 0-15 in northern Wisconsin utilizing age-specific survival.

Age	**m_x**[a]	**p_x**[b]	**l_x**[c]	**l_xm_x**	**xl_xm_x**	**V**[d]
0	0	0.70	1	0	0	1
1	0	0.73	0.70	0	0	1.48
2	0	0.78	0.52	0	0	2.09
3	0.25	0.81	0.40	0.10	0.30	2.78
4	0.52	0.84	0.33	0.17	0.68	3.24
5	0.56	0.85	0.27	0.15	0.76	3.37
6	0.60	0.86	0.23	0.14	0.85	3.42
7	0.55	0.87	0.20	0.11	0.78	3.38
8	0.69	0.87	0.18	0.12	0.98	3.37
9	0.65	0.87	0.15	0.10	0.90	3.18
10	0.85	0.86	0.13	0.11	1.14	3.03
11	0.69	0.85	0.12	0.08	0.87	2.62
12	0.67	0.83	0.10	0.07	0.78	2.36
13	0.83	0.81	0.08	0.07	0.88	2.11
14	1.00	0.77	0.07	0.07	0.92	1.65
15	0.88	0.72	0.05	0.04	0.66	0.88
				R_O[e]	1.33	
				R[f]	0.04	
				λ[g]	1.04	

[a] Fecundity (m_x) was calculated as the age specific litter size multiplied by the percent female offspring per female of age *x* divided by the interbirth interval (interbirth interval was 2 years and cub sex ratio was 1:1).
[b] Age specific survival (p_x) generated from the S(age^2) model in Program MARK. Cub survival was calculated as $S_c = n_{t+1} / n_t$
[c] Survivorship from birth to age class *x* (l_x). Derived from $l_{x+1} = p_x(l_x)$
[d] Reproductive value (V) was calculated as $(\sum e^{(-rx)*(lxmx)})/(e^{(-rx)} * l_x)$
[e] Net Reproductive rate (R_O). Calculated as $\Sigma l_x m_x$. R_O is the average number of female offspring produced by an average female during her lifetime.
[f] Intrinsic rate of increase (*r*). Derived from Euler's equation within Microsoft Excel.
[g] Finite population growth rate (λ). Calculated as $\lambda = e^r$.

TABLE 8. Life table for female black bears ages 0-15 in northern Wisconsin utilizing constant adult survival.

Age	**m_x**[a]	**p_x**[b]	**l_x**[c]	**$l_x m_x$**	**$x l_x m_x$**	**V**[d]
0	0	0.70	1.00	0	0	1.00
1	0	0.81	0.70	0	0	1.46
2	0	0.81	0.57	0	0	1.86
3	0.25	0.81	0.46	0.11	0.25	2.37
4	0.52	0.81	0.37	0.19	0.52	2.71
5	0.56	0.81	0.30	0.16	0.56	2.79
6	0.60	0.81	0.24	0.14	0.60	2.85
7	0.55	0.81	0.19	0.11	0.55	2.86
8	0.69	0.81	0.15	0.11	0.69	2.95
9	0.65	0.81	0.12	0.08	0.65	2.88
10	0.85	0.81	0.10	0.08	0.85	2.84
11	0.69	0.81	0.08	0.06	0.69	2.54
12	0.67	0.81	0.06	0.04	0.67	2.36
13	0.83	0.81	0.05	0.04	0.83	2.16
14	1.00	0.81	0.04	0.04	1.00	1.69
15	0.88	0.81	0.03	0.03	0.88	0.88
				R_O[e]	1.20	
				R[f]	0.03	
				λ[g]	1.03	

[a] Fecundity (m_x) was calculated as the age specific litter size multiplied by the percent female offspring per female of age *x* divided by the interbirth interval (interbirth interval was 2 years and cub sex ratio was 1:1).
[b] Constant adult survival (p_x) generated from the S(.) model in Program MARK. Cub survival was calculated as $S_c = n_{t+1} / n_t$
[c] Survivorship from birth to age class *x* (l_x). Derived from $l_{x+1} = p_x(l_x)$
[d] Reproductive value (V) was calculated as $(\sum e^{(-rx)*(lxmx)})/(e^{(-rx)} * l_x)$
[e] Net Reproductive rate (R_O). Calculated as $\Sigma l_x m_x$. R_O is the average number of female offspring produced by an average female during her lifetime.
[f] Intrinsic rate of increase (*r*). Derived from Euler's equation within Microsoft Excel.
[g] Finite population growth rate (λ). Calculated as $\lambda = e^r$.

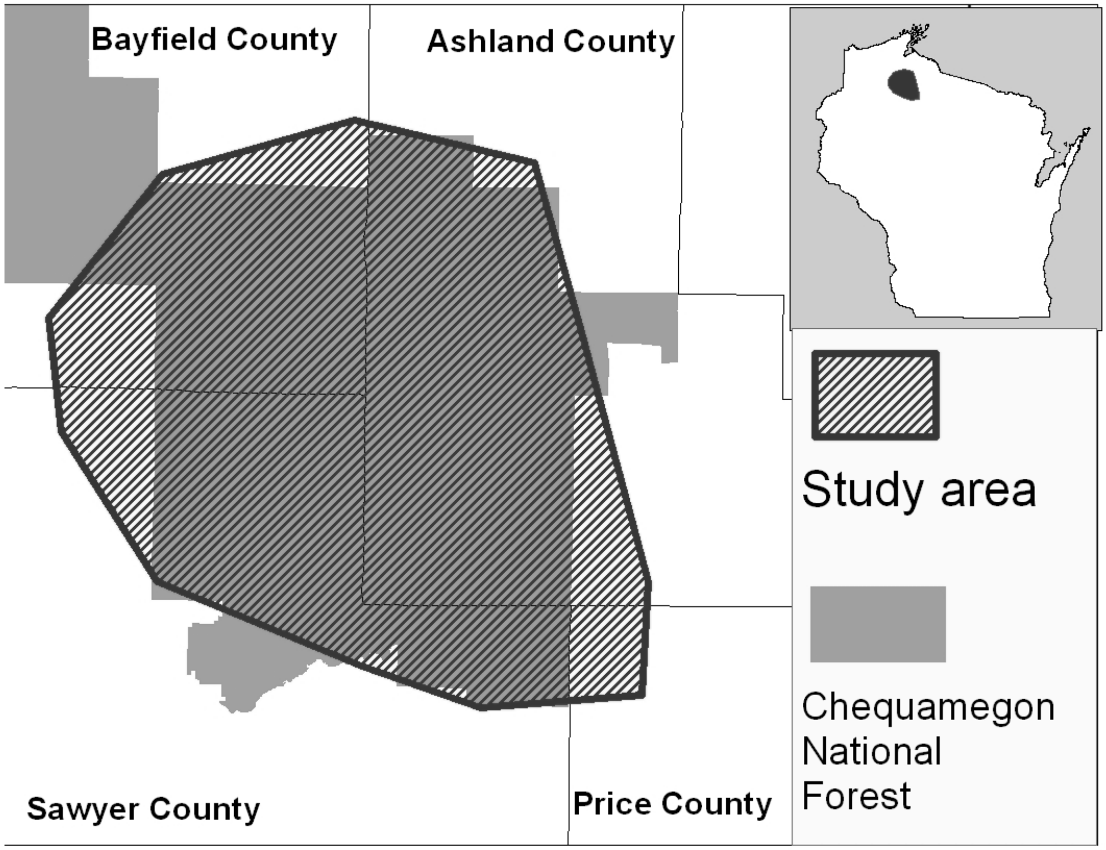

FIGURE 1. The Clam Lake study area—including land in Bayfield, Ashland, Sawyer and Price counties of Wisconsin. Most of the study area lies within the boundaries of the Chequamegon-Nicolet National Forest.

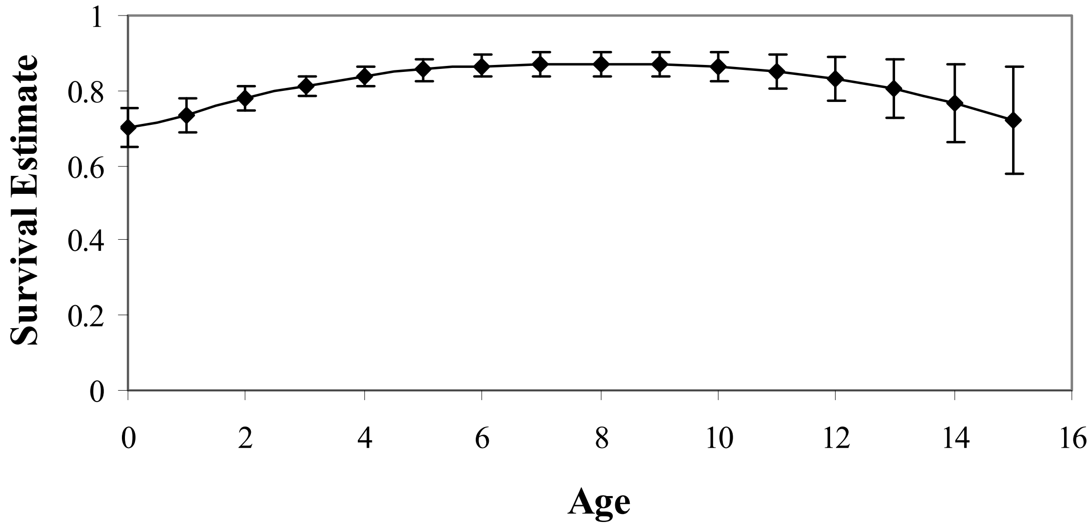

FIGURE 2. Survival estimates and associated standard errors of female black bears age 0-15 in northern Wisconsin, 1989-2007.

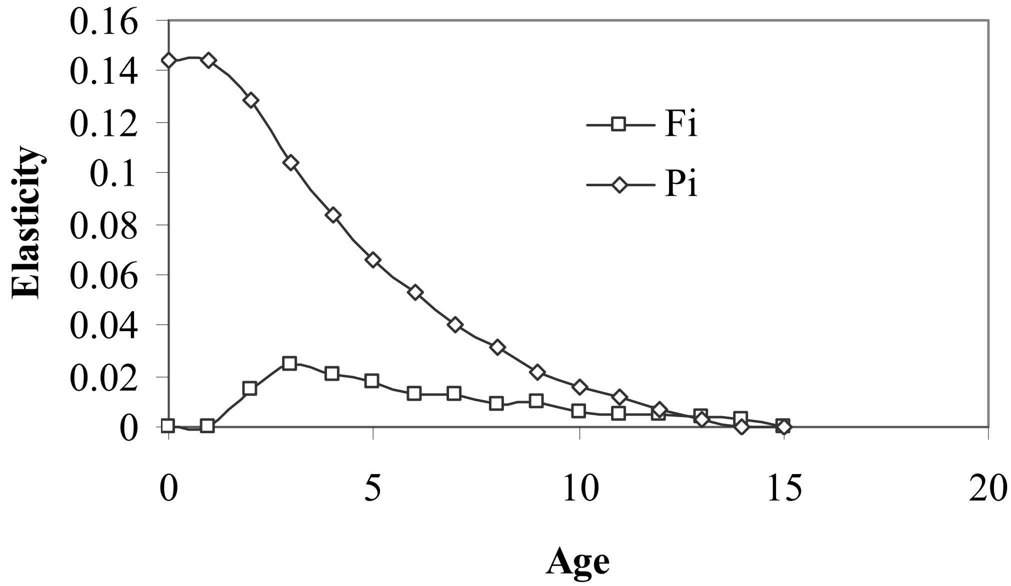

FIGURE 3. Elasticities of λ to changes in survival (P_i) (in this case, constant adult survival) and fertility F_i for female black bears in northern Wisconsin, 1989-2007.

FIGURE 4. Elasticities of λ to changes in age-specific survival (P_i) and fertility (F_i) for female black bears in northern Wisconsin, 1989-2007.

APPENDIX A: Reproductive data for female black bears age 1-15 in northern Wisconsin 1989-2008.

Age	Sows	Sows without yearlings	Sows with cubs	Sows with female cubs	Total cubs	Total pregnancy rate	S.E.	Available pregnancy rate	S.E.	Mean litter size	S.E.
1	59	59	0	0	0	0	0	0	0	0	0
2	48	48	0	0	0	0	0	0	0	0	0
3	40	40	4	4	4	0.10	0.05	0.10	0.05	1.00	0
4	25	24	12	9	25	0.48	0.10	0.50	0.10	2.08	0.21
5	21	13	9	8	20	0.43	0.11	0.69	0.13	2.22	0.15
6	18	13	12	10	29	0.67	0.11	0.92	0.08	2.42	0.26
7	15	6	5	5	11	0.33	0.13	0.83	0.17	2.20	0.25
8	13	12	9	7	25	0.69	0.13	0.75	0.13	2.78	0.29
9	12	5	5	5	13	0.42	0.15	1.00	0	2.60	0.25
10	10	5	5	4	17	0.50	0.17	1.00	0	3.40	0.24
11	8	4	4	2	11	0.50	0.19	1.00	0	2.75	0.25
12	6	4	3	2	8	0.50	0.22	0.75	0.25	2.67	0.33
13	6	4	3	1	10	0.50	0.22	0.75	0.25	3.33	0.33
14	3	2	1	1	4	0.33	0.33	0.50	0.50	4.00	0
15	3	2	2	2	7	0.67	0.33	1.00	0	3.50	0.50

APPENDIX B: Elasticity values for fertility (F) and survival (P) generated from a leslie matrix with constant adult survival for female black bears in northern Wisconsin.

Age	**F**	**P**	**Elasticity (F)**	**Elasticity (P)**
0	0	0.70	0	0.14
1	0	0.81	0	0.14
2	0.20	0.81	0.02	0.13
3	0.42	0.81	0.02	0.10
4	0.45	0.81	0.02	0.08
5	0.49	0.81	0.02	0.07
6	0.44	0.81	0.01	0.05
7	0.56	0.81	0.01	0.04
8	0.52	0.81	0.01	0.03
9	0.68	0.81	0.01	0.02
10	0.55	0.81	0.01	0.02
11	0.54	0.81	0	0.01
12	0.67	0.81	0	0.01
13	0.81	0.81	0	0
14	0.70	0.81	0	0
15	0	0.81	0	0

APPENDIX C: Elasticity values for fertility (Fi) and survival (Pi) generated from a leslie matrix with age-specific survival for female black bears in northern Wisconsin.

Age	F	P	Elasticity (F)	Elasticity (P)
0	0	0.70	0	0.13
1	0	0.73	0	0.13
2	0.19	0.78	0.01	0.12
3	0.42	0.81	0.02	0.10
4	0.46	0.84	0.02	0.09
5	0.52	0.85	0.02	0.07
6	0.48	0.86	0.01	0.06
7	0.60	0.87	0.01	0.05
8	0.57	0.87	0.01	0.04
9	0.74	0.87	0.01	0.03
10	0.59	0.86	0.01	0.02
11	0.57	0.85	0.01	0.01
12	0.69	0.83	0.01	0.01
13	0.81	0.81	0.01	0
14	0.67	0.77	0	0
15	0	0.72	0	0