# POPULATION ECOLOGY OF BLACK BEARS IN THE ALLEGHANY MOUNTAINS OF VIRGINIA

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## ABSTRACT

The Cooperative Alleghany Bear Study (CABS) was a 10-year study conducted on 2 areas and designed to investigate the ecology of a hunted population of American black bears (*Ursus americanus*) in the Alleghany Mountains of western Virginia.  Over the course of our research, we handled 1,041 individual bears ≥18 months old and gathered reproductive data from females during 424 bear-winters.  My analyses of 183 litters indicate that reproductive rates were high with relatively large litters ($\bar{x}$ = 2.49 cubs / litter) and younger (3–4-year-old) females having smaller litters than older (≥ 5 years old) females.  Overall cub sex ratios did not differ from 1M:1F; however, female cubs were over-represented in 4-cub litters.  Most cubs were born in January ($\bar{x}$ = January 17) and younger females had later parturition dates than older females. Bears on our study areas had relatively early ages at primiparity ($\bar{x}$ = 3.8 years old) and few missed reproductive opportunities.  Hard mast failure apparently resulted in periodic reproductive failures and subsequent reproductive synchrony, which I tracked using 5 indices.  The amplitude of oscillations in reproductive synchrony dampened through time after each synchronizing event.  The population contained substantially more females than males; however, males were more vulnerable to trapping than were females.  Population size was determined using genetic and photographic capture-recapture estimators.

Density estimates were relatively high and approached 1 bear / km$^2$.  Annual survival rates were high for cubs (0.87) and females (0.91).  For males, annual survival rates were lower, particularly for 1–3-year-olds (0.57).  Excluding hunting mortality, natural survival rates were high (0.98) for all ≥1-year-old bears on our study areas.  The results of Leslie Matrix and Program RISKMAN models indicated a growing population.  A Leslie Matrix model incorporating the effects of a 5-year-cyle of mast-failure-induced reproductive failure yielded a $\lambda$ = 1.13.  To reach the objective of 0 population growth prescribed for some areas of Virginia, increased levels of hunting mortality on adult  (≥3-year-old) females would likely be necessary.

# ACKNOWLEDGEMENTS

# FOREWARD

Research presented is this dissertation was gathered and analyzed as a component of the Virginia Cooperative Alleghany Bear Study (CABS). Data were collected from 1994–2003 on 2 study areas located in the Alleghany Mountains of western Virginia. These data were collected by personnel working for the Virginia Department of Game and Inland Fisheries (VDGIF), graduate students at Virginia Polytechnic Institute and State University (Virginia Tech), and numerous technicians and volunteers. This dissertation was made possible by their hard work and dedication of these personnel and builds on many components of their analyses. These previous research topics include: responses of black bears (*Ursus americanus*) to dogs (Higgins 1997*b*), habitat use and home range size, survival and dispersal of yearling bears (Lee 2003), population viability (O'Neil 2004), reproduction and cub survival (Echols 2000), reproduction and denning ecology on the northern (Godfrey 1996) and southern (Ryan 1997) study areas, diet and effects of anthropogenic feeding (Gray 2001), and population dynamics (Klenzendorf 2002), habitat use and home range size (Higgins 1997*a*, Olfenbuttel 2005).

In this dissertation, I use new data collected by my cohort and myself (2000–2003) in conjunction with data gathered by my predecessors (1994–1999) to examine the population ecology of black bears in western Virginia. Chapter 1 focuses on quantifying the reproductive parameters and associated covariates. Chapter 2 examines the sex and age structure and discusses difficulties in quantify these parameters. Chapter 3 details our attempts to quantify density

and population growth rate on our 2 study areas.  Chapter 4 examines age- and sex-specific survival rates using a variety of methodologies.  Finally, Chapter 5 examines population harvest and growth rates using 2 modeling techniques and discusses how stabilization of population growth might be achieved.

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# CHAPTER 1: REPRODUCTIVE ECOLOGY

**ABSTRACT**

Quantifying reproductive parameters for American black bears (*Ursus americanus*) is complicated because of their low reproductive rates and because parturition and several months of subsequent neonatal development occur in secluded dens. The Cooperative Alleghany Bear Study (CABS) was an intensive 10-year research project conducted on 2 study areas that addressed the population ecology of black bears in western Virginia. From 1994–2002, we handled 326 ≥2-year-old female black bears 672 times during summer trapping and subsequently followed 176 of these individuals through 424 den seasons. We examined 183 litters consisting of 455 cubs. Bears were documented in estrus from late May through August with a peak during early July. Parturition dates ranged from late December to mid February with most births occurring in mid January. Three- and 4-year-olds gave birth, on average, 12 days later than older bears. Unbiased mean age at primiparity was 3.8 years. Mean litter size was 2.49 (S.E. ± 0.06) cubs / litter, with 3- and 4-year-olds having smaller litters than older bears. We tracked reproductive synchrony using 5 indices including proportion of females producing cubs in the den, proportion of adult females nursing cubs when handled during the summer, recruitment as indexed via population reconstruction from harvest, proportion of 23-month-old bears in the harvest, and proportion of 2-year-olds trapped during summers. We documented a resetting of this synchrony, apparently as a result of an exceptionally poor hard

mast crop in 1997.  Amplitude of oscillations in synchrony dampened through

time after the synchronizing events (mast failures in 1992 and 1997).   Female

age and hard mast availability were primary influences on reproductive

parameters.  My analyses and documentation of these relationships should allow

managers to better understand, forecast, and manage bear populations.


**INTRODUCTION**

Understanding and quantifying reproductive parameters has been

recognized as a cornerstone of successful wildlife management.  The first

management mechanism defined in *Game Management* is  "productivity…the

rate at which mature breeding stock produces other mature breeding stock"

(Leopold 1933:22).  Quantifying parameters is relatively simple for species that

reproduce frequently and have easily-observed offspring.  Black bears (*Ursus*

*americanus*), however, have slow reproductive rates (Bunnell and Tait 1981) and

study for multiple years (LeCount 1982), or even decades (Pelton and van

Manen 1996) may be necessary to draw valid inferences.  Complicating research

efforts, black bears give birth in secluded dens.  Entering bear dens to acquire

reproductive data can involve considerable risk to both researcher and study

animal (Godfrey et al. 2000).

Because of these difficulties, obtaining sufficient sample sizes to elucidate

patterns and evaluate influences on bear reproduction has been difficult for

researchers.  For example, parturition date has only been quantified only once in

the published literature (Alt 1983) and any relationships to potentially influential factors, such as female age and nutritional availability, were not described.

Previous black bear research in Virginia focused on unhunted populations in the Shenandoah National Park in western Virginia (Carney 1985, Kasbohm et al. 1996) and the Great Dismal Swamp in coastal Virginia (Hellgren and Vaughan 1989a).  In the Alleghany Mountains that run along the western border of the state, bear hunting is a long-standing tradition.  Over the 20 years preceding the initiation of our study (1974–1993; Figure 1.1), harvest nearly quadrupled from approximately 200 bears / year to over 800 bears / year (Martin and Steffen 2000).  However, the substantial but unexpected drops in harvest that occurred in 1990 and 1992 were puzzling.  Thus, because management decisions based solely on harvest data without underlying knowledge of population parameters and their influences on population dynamics may not be biologically sound (Lubow et al. 1996), biologists from the Virginia Department of Game and Inland Fisheries (VDGIF) and researchers from Virginia Tech initiated the Cooperative Alleghany Bear Study (CABS) to investigate the population ecology of black bears in western Virginia.  My objectives in this portion of my research were to explore the reproductive ecology of black bears in western Virginia, quantify reproductive parameters, and examine these parameters and their influences in relation to the observed pattern in harvest.

**STUDY AREAS**

Our research was conducted on 2 study areas (Figure 1.2) in the Alleghany Mountains of western Virginia, USA. The centers of the 2 study areas were approximately 160 km apart; both were located largely on the George Washington-Jefferson National Forests. The northern study area was centered near Reddish Knob at 38° 28' N, 79° 15' W. It was approximately 840 km$^2$ primarily in Augusta and Rockingham Counties. The southern study area was 1,544 km$^2$ and was centered near Mountain Lake at 37° 22' N, 80° 31' W. It was composed primarily of Craig, Giles, and Montgomery Counties. Elevations on these 2 study areas ranged from 480–1,360 m (Kozak 1970) and common tree species included: eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipfera*), eastern white pine (*P. strobus*), mountain laurel (*Kalmia latifolia*) and scrub oak (*Q. ilicifolia*; Rawinski et al. 1994). At Mountain Lake, the center of the southern study area, high temperatures ranged from an average high of 24°C in July to an average low of -9°C in the January with total precipitation averaging 125 cm, including 134 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va5828). The closest weather station to our northern study area was at Dale Enterprises in the lowlands of Rockingham County. Because it was in the lowlands, weather averages were likely warmer and drier than

conditions in the adjacent mountains where our research was conducted.  At Dale Enterprises (38$^{o}$45' N, 78$^{o}$93' W), temperatures ranged from an average high of 30°C in July to an average low of -5°C in January with total precipitation averaging 90 cm, including 63 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va2208).

Hunting season lengths varied slightly (≤ 7 days) among years.  Generally, September was marked by bear-hound training season during which bears could be pursued and treed with hounds, but not harvested.  The second week of October through the first week of November was archery-hunting season, during which bears could be harvested using archery equipment.  Gun season, during which bears could be killed with firearms, but not with the aid of dogs, was the last week of November.  Hound-hunting season, during which bears could be killed using firearms and with the aid of dogs, consisted of the first few days of December through the first Saturday in January.  One bear tag / year / hunter was sold with the combined deer, bear, and turkey license.  To be legally harvested, bears had to weigh ≥45.5 kg live weight or ≥34.1 kg with all internal organs removed.  Adult females with cubs could not be legally harvested.  Law required that all harvested bears be checked at registered check stations.  Checking a bear involved recording any tags, tattoos, and/or transmitters, determining sex of the individual, and removing a premolar for subsequent age determination.

## METHODS

### General

We captured bears with Aldrich spring-loaded foot snares and culvert traps (Johnson and Pelton 1980) from late May through late August 1994–2002. We initiated trapping on our northern study area in 1994 and on our southern study area in 1995. We sedated captured bears with a mixture of ketamine hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45.5 kg; White et al. 1996) administered via dart pistol, blowpipe, or jab stick. After bears were sedated, we determined their sex, weighed them, recorded morphometric measurements, and examined females for signs of estrus or lactation. To determine age, we removed a premolar (Willey 1974), which was sent to Matson's Laboratory (Milltown, Montana, USA) for cementum annuli analysis. We also tattooed bears' upper lips, and attached individually-numbered, plastic, perma-flex, stud-style eartags (National Band and Tag, Newport, Kentucky, USA) to all bears ≥6 months old. We attached motion-sensitive radio transmitters to bears selected in an attempt to keep our sex ratio of transmittered animals at approximately 1M:3F. Bears ≥1 year old received collars (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA, Wildlife Materials International, Murphysboro, Illinois, USA) that were equipped with breakaway cotton spacers (Hellgren et al. 1988) or eartag transmitters (Servheen et al. 1981) from ATS. We administered a tetracycline antibiotic to prevent infection and serve as a permanent biomarker

in teeth and bones (Johnson 1964, Garshelis and Visser 1997).  Finally, we administered yohimbine hydrochloride (5mg/ml; 2 ml/45.5 kg) to reverse the xylazine hydrochloride.  Each week, we monitored and attempted to locate bears wearing transmitters.

Biologists from VDGIF conducted surveys in late August to early September to quantify annual hard mast production (Sharp 1958, Coggin and Peery 1973).  Mast surveys involved examination of the same trees annually and quantifying the mean number of acorns / 10 limbs / tree (Fearer et al. 2002).  I used mast survey data collected by VDGIF (D. Martin, personal communication) for the 3 mast survey regions overlapping our study areas to examine autumn hard mast availability.

In the late fall and winter, we used radio telemetry to locate dens of female bears wearing transmitters.  We returned to and entered (Godfrey et al. 2000) these dens in January–April to gather reproductive data, change transmitters on adults, attach transmitters to cubs (Echols 2000, Vashon et al. 2003) and yearlings, and deploy remote cameras (Bridges et al. 2004).  The Virginia Polytechnic Institute and State University Animal Care and Use Committee (98-069-F&W) approved all animal handling protocols.

**Estrus**

I evaluated the proportions of ≥2-year-old bears trapped during summers that were visibly in estrus versus those that were not in estrus.  We evaluated visible signs of estrus including vulval swelling, vascularization (based on coloration), and discharge.  Breeding season estimation was based on the

proportion of female bears >2 years old that were not with cubs (where not
lactating or showed visible evidence of nursing) visibly in estrus during each
interval from 1994–2002. Because annual trapping effort timing was inconsistent
and sample sizes for females were small, I could not examine annual variation
nor could I use a daily time step to examine estrus timing. Thus, to obtain
sufficient sample sizes, I pooled years and study areas and subdivided the
summer trapping season into 10, 10-day intervals beginning May 22 and ending
August 31. I tested for differences in distribution of estrus timing on the 2 study
areas using a non-parametric Kolmogorov-Smirnov (K.S.) test.

**Parturition date**

I estimated parturition date using a regression model that we developed
using known-age captive black bear cubs (Bridges et al. 2002). This model
employs cub hair length and ear length to estimate time of birth for individuals.
For multi-cub litters, I estimated parturition date for each individual and used the
mean date for the entire litter. I hypothesized that variation in parturition date
might be due to mast-failure-induced nutritional stress, female age class, or litter
size. Accordingly, I subdivided our sample into 2 age classes (3–4-year-olds
versus ≥5-year-olds), 2 litter size groups (1–2-cub-litters versus 3–4-cub-litters)
and 2 year groups (1998, immediately following a mast failure in 1997 versus all
other years). I tested for effects of these factors and for interactions between
these factors using factorial ANOVA and then compared least square means
(L.S. $\bar{x}$ ) and associated variance derived from these ANOVAs.

**Primiparity**

I calculated age at primiparity using 2 methods. First, I used an unbiased estimator (Garshelis et al. 1998) based on den observations and data obtained from summer trapping. This method assumes that females that would have produced their first litters at older ages are more likely to be lost from a study due to radio failure, emigration, or death. It includes 4 steps: 1) calculating the percentage of previously nulliparous (have not previously given birth to a litter) females in each age class that gave birth to their first litter of surviving cubs, 2) using results from step 1 to estimate the percentage of females in the total population that were available to have a litter at each age class, 3) multiplying the percent of the population available to have a first litter by the percent that actually had a first litter and 4) taking the results from step 3 and multiplying them by the corresponding ages and then taking the sum of these calculations. Differences between study areas were tested using a log-rank test (Garshelis et al. 1998). The second method I employed was based on the mean age at first reproduction from den-site observations of female bears at ages 3 and 4.

Evidence of reproduction was based on reproductive data obtained during winter observations of denned female bears. Evidence of reproduction from summer trapping data was based on a combination of nipple elongation indicating evidence of nursing (Brooks and McRoberts 1997), lactation, and/or observations of cubs with females.

**Litter size**

I calculated age-specific reproductive output based on the number of cubs observed during den-site observations of parous females.  Because young bears may have different reproductive characteristics than older bears (McLaughlin et al. 1994, Noyce and Garshelis 1994, Costello et al. 2003), I hypothesized that reproductive output might vary due to age class.  Additional possible sources of variation might be related to year and study area.  I used a 3-way ANOVA pooling study areas to examine effects of years, age class, study area and their interactions.  I then examined results from these ANOVAs with factorial treatment arrangement and their associated least square means and 95% confidence intervals (C.I.) to determine if these factors influenced litter sizes.

**Reproductive synchrony and failures**

I examined reproductive synchrony using 5 annual indices:  proportions of females with cubs in their dens, proportions of ≥3-year-old females with cubs when handled during summers, the recruitment index calculated from VDGIF's population reconstruction (C. Godfrey, unpublished data), proportions of harvest composed of 23-month-olds, and proportions of 2-year-olds relative to all other age classes handled in each summer.  Bears appearing to be barren (sterile) and those with known reproductive history alteration due to researcher interference (Hellgren and Vaughan 1989*b,* Godfrey et al. 2000) were not included in reproductive synchrony analyses.

Proportions of females with cubs in their dens were calculated using pooled study areas and based on the number of females documented with cubs

during winter den work divided by total number of females ≥3 years old whose reproductive status we could determine each winter. This proportion was used to index reproduction at time $_t$ (e.g., observations from 1998 were used to index reproduction for that year). I did not include data from 1995 or 1996 in this calculation because trappers during the first trapping seasons (summers 1994 and 1995 on the northern and southern study areas, respectively) attempted to collar primarily estrous females and thus using these proportions would reflect collaring bias and not the entire population.

Proportions of females with cubs in the summer was based on the number of female bears captured during summer that exhibited signs of nursing or were observed with cubs divided by the total number of ≥3-year-old females handled. A combination of the presence of milk, swelling of mammary tissue, teat elongation from nursing, and observations of cubs with the female was used to determine if a bear was with cubs. I assumed that relative trap vulnerability of females with and without cubs did not vary annually. Like den-site observations, this proportion was used to index reproduction at time $_t$ (e.g., observations from 1998 were used to index reproduction for that year).

I used data from a population reconstruction based on harvest data (Downing 1980) calculated by VDGIF (C. Godfrey, personal communication) to index reproductive output / female. This reconstruction was based on harvest data from our northern study area (Rockingham and Augusta Counties) and used multiple years of harvest to build annual recruitment indices for each preceding year. It produces a number based on the number of offspring that must have

been born (because they were harvested) divided by the number of adult females that must have been present (because they were harvested) and yields an index for time $_t$ (e.g., population reconstruction recruitment index 1998 was used to index reproduction during the winter of 1998).

The proportion of 23-month-olds in the harvest was calculated by dividing the number of 23-month-olds harvested each year by the total harvest for the 5 counties comprising our study areas. This statistic was used as an index to reconstruct cub production from the previous year's winter at time $_{t-1}$ (e.g., 23-month-olds harvested in fall of 1999 were used to index reproductive output during the winter of 1998). I assumed that relative sex- and age-specific vulnerability to harvest did not vary annually.

Proportion of 2-year-olds captured in summer was calculated for pooled study areas by dividing the number of 2-year-olds handled during summer trapping by the total number of individuals handled each summer. This index was used to reconstruct cub production from the winter 2 years prior to the trapping session or time $_{t-2}$ (e.g., 2-year-olds handled in summer of 2000 were used to index reproduction during the winter of 1998). I assumed that relative sex- and age-specific vulnerability to capture did not vary annually.

After constructing these indices, I examined them using 3 methods. First, I z-transformed the 5 indices and plotted the mean and 95% confidence interval (C.I.) for the indices available for each year. Next, I used Spearman's rank order correlation for each pair containing $\geq 5$ temporally matched data points to measure the degree of association between indices. Finally, I examined whether

synchrony oscillations, if present, dampened through time by plotting the absolute values of the z-values for the 2 5-year periods following likely synchronizing events (mast failures in 1992 and 1997) and examining their degree of association using Spearman's rank order correlation.

Missed breeding intervals were calculated based on those females who were observed in the den ≥2 winters at ≥3 years of age and included evidence of ≥1 reproduction.  Observation of ≥2 winters was required because a lack of cubs in the den only reflected a missed opportunity if the individual was known to have had yearlings the previous year.  If previous year(s) reproductive status(es) were not known, a lack of cubs in the den could be due to separation from yearling cubs during the preceding autumn.  Females ≥3 years of age were required because 3-year-olds represented minimum age at first reproduction on our study areas.  Evidence of ≥1 reproduction was required because some bears appeared to be barren and thus missed all possible reproductive opportunities.

Bears meeting these criteria were divided into those missing a reproductive opportunity, those not missing an opportunity, and those that were indeterminate.  In instances of missed opportunities, the year of breeding failure was documented.  A bear was considered barren if she was observed in the den without young (cubs or yearlings) during ≥3 years at ages ≥4 and showed no evidence of nursing during summer handlings.

## RESULTS

### General

We handled 326 female black bears (2–25 years of age) 672 times from late-May–August, 1994–2002. We gathered data from 176 females (2–24 years old) during 424 bear-winters (defined as an observation on an individual female and her associated reproductive output gathered from January–April) during January–April, 1995–2003. I used age and sex data from 2,057 bears harvested from the 5 counties constituting our 2 study areas to examine reproductive synchrony. Hard mast production during our study was lowest in 1997 and showed a less-pronounced drop in 2002 (Figure 1.3). Prior to our study, a mast failure occurred in 1992.

### Estrus

Timing of estrus was based on 430 observations of 326 bears from late May–August, 1994–2002. Females began coming into estrus in late May. We observed a peak in estrus during early July followed by a gradual decline through August (Figure 1.4). Patterns were not statistically different between study areas (K.S. $D = 0.30$, $P = 0.68$).

### Parturition date

I estimated parturition date for 383 cubs from 150 litters born to 99 individual females ranging from 3–24 years old during 1996–2003. Morphometric measurements required for age estimation were not taken in 1995. I excluded 1 outlier, a 24-year-old female whose single cub was born on February 18 (14 days

later than any other litter), from further analyses because she was 5 years older

than any other female and her litter's birth date might have exerted

disproportionate leverage on subsequent calculations.  For the remaining 149

litters, estimated parturition date ranged from December 26 to February 4 with a

mean and median of January 17 and a mode of January 22.  Litters were born

from late December (2.7%) into February (6.0%) with most births occurring in

January (91.3%).  Distribution of birth dates was roughly bimodal with peaks in

early-mid and mid-late January (Figure 1.5).

Results from analysis of variance indicated adult female age class (3– 4-

year-olds versus ≥5-year-olds) influenced parturition date ($F_{1,141}$ = 13.81, $P$

<0.001; Table 1.1).  The mast failure year (1998 versus all other years), litter size

class (1–2 cubs versus 3– 4 cubs), 2-way interactions between age class and

litter size class, 2-way interactions between year and litter size class, and 3-way

interaction between all female age classes, litter size class, and mast failure did

not suggest significant differences ($F_{1,141}$ = 0.00–1.33, $P$ = 0.25–0.98; Table 1.1).

Further examination of the effect of age class revealed that 3– 4-year-old

females had later parturition dates (L.S. $\bar{x}$ = January 28, S.E. ± 3 days, 95% C.I.

= January 22 – February 2) than ≥5-year-olds (L.S. $\bar{x}$ = January 16, S.E. ± 1

day, 95% C.I. = January 13–18; Figure 1.6).

The 2-way interaction between mast failure and age class was not

strongly supported ($F_{1,141}$ = 1.85, $P$ = 0.18; Table 1.1).  Further examination of

these interaction effects on parturition dates revealed L.S. $\bar{x}$ dates were slightly

later for 3– 4-year-olds following the mast failure (L.S. $\bar{x}$ = February 1, S.E. ± 4

days, 95% C.I. = January 24 – February 8) than for non-failure years (L.S. $\overline{x}$ = January 24, S.E. ± 4 days, 95% C.I. = January 15 – February 1), however, small sample size for 1998 (*n*=6) and associated large and overlapping confidence intervals indicate statistical power was low and differences were not statistically different.  Confidence intervals for ≥5-year-olds during the mast failure (L.S. $\overline{x}$ = January 15, S.E. ± 2 days, 95% C.I. = January 11–20) strongly overlapped with confidence intervals during non-failure years (L.S. $\overline{x}$ = January 16, S.E. ± 1 day, 95% C.I. = January 14–18).

**Primiparity**

Using an unbiased estimator (Garshelis et al. 1998) and pooling study areas, mean age at primiparity was 3.8 years.  I compared study area estimates using a log-rank test (Garshelis et al. 1998) and found females on our southern study area reproduced earlier (3.4 years) than females on our northern study area (3.9 years; $\chi_1^2$ = 6.59, *P* = 0.02).  I could not examine annual variation or relationship to mast crop due to inadequate annual sample sizes.

Using only den-site observations, primiparity for bears on our study areas occurred most frequently at 3 and 4 years of age.  Nineteen of 31 (61%) 3-year-olds observed in the den had cubs and none had yearlings.  Twenty-eight of 45 4-year-olds (62%) had cubs and 8 of 45 (18%) had yearlings (indicating successful reproduction at age 3).  Using only den-site observations on 16 bears observed at ages 3 and 4, consecutively, age of primiparity was 3.3 years old.

**Litter size**

We observed 455 cubs from 183 litters produced by 115 females. Pooling all years, study areas, and age classes yielded a mean litter size of 2.49 (S.E. ± 0.06) cubs / litter. Three-year-olds had smaller litters ($\bar{x}$ = 1.50, S.E. ± 0.17) than 4-year-olds who had smaller litters ($\bar{x}$ = 2.00, S.E. ± 0.13) than 5-year-olds ($\bar{x}$ = 2.53, S.E. ± 0.12; Table 1.2). There was no substantial difference between litter size of 5-year-olds and those ≥6 years old.

Analysis of variance to test effects of pooled age classes (3–4-year-olds versus ≥ 5-year-olds; pooled due to missing cells in 3-year-old age classes), study areas (northern versus southern), and year class (1998 following the mast failure versus all other years) suggested age class affected reproductive output ($F_{1,175}$ =7.35, $P$ = 0.01; Table 1.3). There was no effect of study area, year class, or any 2-way interactions among the 3 groupings or the 3-way interaction including all groupings ($F_{1,175}$ =0.12 – 0.74, $P$ = 0.27–0.89; Table 1.3). Further examining differences due to age class, litter size was smaller for 3–4-year-olds (L.S. $\bar{x}$ = 1.95, S.E. ± 0.22, 95% C.I. = 1.51–2.39) than ≥5-year-olds (L.S. $\bar{x}$ = 2.63, S.E. ± 0.11, 95% C.I. = 2.41–2.85).

**Reproductive synchrony and failures**

Reproductive synchrony was evident from proportions of females with cubs from annual den-site observations, proportions of females nursing during summer handlings, population reconstruction recruitment indices, proportions of 23-month-old bears harvested, and proportions of 2-year-olds handled during summers (Table 1.4). Most of these indices were correlated with each other

(Table 1.5).  Peaks in reproduction occurred during even numbered years from 1992–1996 and, following the autumn 1997 mast failure, were replaced by peaks during odd numbered years from 1999–2003 (Figure 1.7).  The observed synchrony prior to the 1997 mast failure might have been associated with a mast failure in 1992 (Figure 1.3).  The amplitude of the oscillations in the synchrony cycle dampened through time after the synchronizing event (mast failures in 1992 and 1997; Figure 1.8).  Absolute values of mean z-values were correlated between paired years (1993 and 1999, 1994 and 2000, 1995 and 2001, 1996 and 2002, 1997 and 2003; $P$ = 0.04, $r_s$ = 0.90).

Subsequent to primiparity, 4 of 47 (8.5%) reproductively active adult females (3–20 years old) were documented missing 1 reproductive opportunity each.  Three of the 4 missed intervals occurred in 1998 following the mast failure of 1997.  Two of 99 (2.0%) adult females had not successfully reproduced by age 9 and may have been barren.

## DISCUSSION AND MANAGEMENT IMPLICATIONS

### Estrus

Our estrus observations did not differ by study area.  The incidence of estrus climbed quickly through the month of June, peaked in early July, and then gradually tapered off through August (Figure 1.4).  The timing of estrus we documented was consistent with results of previous studies indicating early summer peaks in estrus across the black bear's range including northern Mexico (Doan-Crider and Hellgren 1996), Tennessee (Eiler et al. 1989), Idaho (Reynolds

and Beecham 1980), Washington (Lindzey and Melsow 1977), Minnesota (Rogers 1987), Ontario (Kolenosky 1990) and Alaska (Schwartz and Franzmann 1991). Photoperiod is thought to regulate breeding season in most mammals (Sadleir 1973). Because peaks in breeding season generally occurred immediately following the summer solstice, these results seemingly support the hypothesis of a photoperiod-based *zeitgeiber.*

Because birth date can heavily influence juvenile survival for most mammalian species, breeding season is timed so that young are born at an optimum time that maximizes their survival probability (Lack 1954). However, for species such as bears that delay implantation of blastocysts (Hamlett 1935), breeding season is essentially independent of parturition date and thus subject to a different suite of selection pressures. Although researchers repeatedly confirm that an early summer breeding season seems nearly universal, few have considered why this season is selected.

Compared with species that do not delay implantation, relatively few theories have attempted to address timing of breeding in species employing delayed implantation. Sandell (1990) proposed that mate-competition theory might play a role in breeding season timing for species that delay implantation. This theory suggests that breeding season in species employing delayed implantation is based on when males are best able to compete for females and that this will occur "when high-quality resources are easily available." The implication is that during times of high resource access, males can improve their condition and focus their energies on competition for females. Females then

have a larger selection of males from which to choose a mate.  Competition

through fighting among male bears has been demonstrated to be a primary factor

in their mating access and success (Kovach and Powell 2003).  Superficially, the

late June and early July peak in estrus would seem to deviate from this theory as

late spring and early summer are not generally considered times of high nutrient

availability (Beeman and Pelton 1980, Eagle and Pelton 1983).  However, though

black bears are largely herbivorous and are not considered effective predators of

adult ungulates (Rogers 1987), they are effective predators of neonates (Kunkel

and Mech 1994, Ballard et al. 1999).  Evidence of the importance of neonatal

ungulates in black bear diets during late spring and early summer is abundant

and consistent across the bears' range.  Some examples include black bears

accounting for at least 50% of white-tailed deer (*Odocoileus virginianus*) fawn

mortality in early-mid June in New York (Mathews and Porter 1988); neonate

mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) as a primary

component of early summer scats in Oregon (Bull et al. 2001); over 70% of

marked elk calves killed by black bears in Idaho (Schlegel 1976); and a

suggested causal relationship between black bear reproductive output and

consumption of moose (*Alces alces*) calves from late May–late June in Alaska

(Schwartz and Franzmann 1991, Miller 1994).  Thus, if mate-competition theory

operates in black bears, early summer is a period of high protein availability due

to fawning seasons and associated access to neonatal ungulates throughout the

black bear's range.  This period "when high-quality resources are easily

available" coincides with the onset of estrus.  Supporting this suggested

mechanism, polar bears (*Ursus maritimus*) are the only bear species known to breed primarily in seasons other than summer and their breeding is concurrent with seal-pup birthing period in early spring (Sandell 1990).

An alternative and more parsimonious theory proposed by Rogers (1987) suggests that breeding season in black bears is proximally constrained by spring den emergence and distally constrained by autumnal focus on hyperphagia. This essentially leaves only the summer available for breeding. This simpler theory would likewise place breeding season consistently during early- to mid-summer.

**Parturition date**

Quantitative estimates of parturition dates for black bears are rare in the published literature (Bridges et al. 2002). This is likely because of the intensive researcher time investment required to estimate black bear parturition date based on auditory observation outside den sites. Alt (1983) provided 1 of the few published quantitative assessments of parturition date. Similar to my results, he found that most births took place during January. Unlike the roughly bimodal distribution I found, he reported birth dates were distributed on a clearly bell-shaped curve. However, he did not report the age structure of the population of parturient females.

I found a roughly bimodal parturition date distribution (Figure 1.5) with younger females (3–4-year-olds) giving birth an average of 12 days (based on L.S. $\bar{x}$ ) later than older (≥5-year-olds) females. Because parturition date frequently affects offspring survival in large mammals (Smith and Anderson 1998, Testa et al. 2000) the later birth dates associated with young female bears

might affect survival of their offspring.  There is evidence that den emergence date is positively correlated with parturition date (Bridges et al. 2004).  If litters from young females are born later they might emerge from the den later and accordingly have less time in the summer to gain weight and learn survival skills.  Thus, they might experience lower survival rates.  Though evidence is statistically weak ($F_{1,141}$ = 1.85, $P$ = 0.18; Table 1.1) young females gave birth 8 days later (based on L.S. $\overline{x}$ ) following mast failure than during other years, possibly suggesting young female parturition dates are more strongly affected by mast failure than older (≥5-year-olds) females where no substantial difference (1 day) in birth date was apparent.  The lack of statistical significance could be due to lack of effect or due to lack of statistical power because our sample of 3–4-year-old females following mast failure was small ($n$=6),

Researchers planning den work might consider female age in determining when to schedule den visitations to ensure cubs have been born and are developed enough to be safely handled.   The single outlier from our distribution was a 24-year-old female that gave birth approximately 2 weeks later than any other litter.  This individual was 5 years older than any other female whose reproduction was documented in our research.  Bears of this age may be approaching reproductive senescence (Schwartz et al. 2003).  Though any inference from a single observation is purely speculative, this data point might suggest that implantation timing could be affected as individuals approach senescence.

Examination and quantification of factors influencing implantation and birth date is an under-explored aspect of black bear reproductive biology. Timing of parturition is thought to be based on timing of implantation and may be influenced by photoperiod in delayed implanters (Sadleir 1973, Racey 1981). There is evidence suggesting timing of den emergence is based on cub age and development (Bridges et al. 2004), however, because birth date has been quantified so infrequently, this relationship is not definitive. Accurate quantification of both parturition and den emergence dates are needed to explore this relationship. Additionally, manipulative experiments, likely involving captive bears, ultrasound, and tracking hormonal profiles while controlling for age, nutritional, and environmental variables (e.g., temperature and light) will likely be necessary to more thoroughly examine influences on implantation timing and parturition date.

**Primiparity**

Our estimated unbiased age at primiparity, 3.8 years, is consistent with the reports of first reproduction most frequently occurring at ages 3 or 4 documented across the eastern United States (Alt 1989, Eiler et al. 1989, Elowe and Dodge 1989, Hellgren and Vaughan 1989a, Kasbohm et al. 1996, Willey et al. 1996;Table 1.6). It was earlier than western (Jonkel and Cowan 1971, Kasworm and Thier 1994, Costello et al. 2003) and northern black bear populations (Rogers 1987, Kolenosky 1990, Miller 1994) where primiparity frequently occurred at ages 5–8.

Mean age at primiparity, though frequently reported, is more difficult to accurately quantify than it might appear as Garshelis et al. (1998) demonstrated in their review of the topic. Their conclusion was that reported estimates were frequently biased low, and in general, I agree that their technique offers an improvement over the simpler techniques employed previously. However, I removed 2 apparently barren (did not reproduce by 9 years of age) females from my calculations of primiparity. Sterility, if undocumented, could increase the number of females available to reproduce at each age class as used in the Garshelis et al. (1998) method and could thus result in overestimates in age at primiparity. In populations with higher age of primiparity or longer intervals between litters, it would take more years of observation and may be more difficult to determine if an individual is barren. Because long-term research projects are uncommon in the black bear literature (Pelton and van Manen 1996), time limitation may present a problem for bear researchers attempting to use the Garshelis et al. (1998) method. Thus, I suggest that researchers use the Garshelis et al. (1998) method when their data set allows, but in addition, that they report a modal age at primiparity. A modal age is less sensitive to outliers, sterility, and study length, and might provide a simple alternative for inter-project comparison, especially in those too short in duration to allow for use of the Garshelis et al. (1998) method. Additionally, because bears generally give birth within a few weeks of their birthday, a modal estimate, unlike a mean, consistently provides a biologically realistic number.

**Litter size**

Mean litter size from our study (all data pooled; 2.49 ± 0.06) was within the range observed (2.1–3.0; Table 1.6) in other populations in the eastern United States (Eiler et al. 1989, Elowe and Dodge 1989, Hellgren and Vaughan 1989*a*, Kolenosky 1990, McLaughlin et al. 1994, Kasbohm et al. 1996).  Larger mean litter sizes of 3.0 and 2.8 were reported in Pennsylvania (Alt 1989) and northern Mexico (Doan-Crider and Hellgren 1996), respectively, and smaller mean litter sizes (1.6–1.9; Table 1.6) were reported in the western United States (Jonkel and Cowan 1971, Lindzey and Melsow 1977, Reynolds and Beecham 1980, LeCount 1982, Kasworm and Thier 1994, Costello et al. 2003).

Using data from 4 different and nonequivalent measures (corpora lutea, counts of embryos, counts in dens, and counts of yearlings), as well as data from wild and captive bears interchangeably, Bunnell and Tait (1981) examined regional differences in reproductive output.  Though I question whether mixing these 4 different measures was an appropriate approach, they were the first to describe regional differences in reproduction parameters from populations of American black bears throughout North America.  Using only litter size from den-site observations, I likewise found substantial differences in regional populations. Reproductive output from our study population fell roughly in the middle of the range of observations from eastern North America, but was substantially higher than reproductive output estimates from the western United States (Table 1.6).

Litter size for young (3- and 4-year-old) females was smaller than the litter size for older (≥5 years old) females.  Similarly, younger bears were reported to

have smaller litter sizes in Pennsylvania (Kordek and Lindzey 1980), Ontario (Kolenosky 1990), Massachusetts (Elowe and Dodge 1989), Maine (McLaughlin et al. 1994), Minnesota (Noyce and Garshelis 1994), and New Mexico (Costello et al. 2003).  However, researchers found similar litter sizes in young and old bears in Alaska (Schwartz and Franzmann 1991, Miller 1994) and Arkansas (Clark and Smith 1994).  I could not determine the influence of maternal weight in my analysis of litter size because extracting and weighing females from tree dens (the den structure type used most frequently during our study) was generally impractical.  Our lack of weight data should not have been a problem in these analyses as Noyce and Garshelis (1994) concluded age, not weight, was primarily responsible for female reproductive output and that previous associations using weight were likely spurious.

Control of litter size has been the subject of much theoretical speculation. Optimal litter size hypothesis (Lack 1948, Lack 1954, Alexander 1996) suggests the mean litter size should reflect the size at which the maximum number of young survive and that this litter size usually is below the biological maximum. However, experiments have often failed to support this hypothesis (Risch et al. 1995) and have indicated litter sizes larger than the mean may be most productive.  The lack of difference I found in cub survival (Chapter 3) from large versus small litter size would seemingly support this conclusion.

It is widely accepted that litter sizes for very small, young, and old animals are frequently less than average for the population (Lack 1948, Sadleir 1973, Clutton-Brock 1988), but may still conform to optimality theory if age or size of

the female influence survival rates of their offspring (Lack 1954).  Because old females are relatively rare in bear studies, it is difficult to clearly demonstrate the effects of old age on reproduction.  Reproductive senescence is difficult to document in bear research where sample sizes of old-aged individuals are often small or lacking (Schwartz et al. 2003).  Pooling data from studies conducted around the world, Schwartz et al. (2003) documented reduced reproductive output and eventual senescence in brown bears (*Ursus arctos*).  The only female we observed in the den at >20 years of age did not have cubs at 23 and had 1 cub at 24.

In the black bear literature, the most commonly reported reproductive parameter was mean litter size.  While mean litter size is useful for examining general regional trends, I found that age distribution of parous females was rarely reported.  Because evidence strongly suggests female reproductive output is not consistent across age classes, researchers reporting an overall mean are assuming that their sample was representative of the population.  However, if sample sizes are small, biased, or if efforts are made to maintain transmitters on individual bears throughout their lives, means may be more representative of age structure of the sample of collared females than of the population as a whole.  My results underscore the importance of taking age structure into account when reporting and modeling reproduction in black bears.  For example, mean litter size for the first year of our study was small (1.69; SE ± 0.24; Table 1.7), and, had this study been shorter in duration, might have lead to the spurious conclusion that our population exhibited lower-than-average reproductive output.

However, upon further analysis, it became apparent that median age of parturient females in 1997 (4 years old) was substantially younger than median age for all other years (6–10 years old).  The addition of older age-class bears in subsequent years and corresponding increase in mean litter size (Table 1.7) indicate that this year of seemingly low reproductive output likely was the result of our study animal age structure.

No effect of mast failure on litter size was evident from our data (Table 1.3).  However, 3 of the 4 missed reproductive intervals occurred following the mast failure years.  These results suggest that mast failure did not affect litter size, but likely did affect the proportion of available females that produced litters.

**Reproductive synchrony and failures**

Reproductive synchrony based on den-site observations has been reported for black bear populations in Washington (Lindzey and Melsow 1977), New York (Free and McCaffrey 1972), Florida (Dobey et al. 2005) and Maine (McLaughlin et al. 1994).  Concurrent observation of percentages of females with cubs in dens, females with cubs in the summer, population reconstruction recruitment indices, proportions of 23-month-olds in harvests, and proportions of 2-year-olds trapped in summers, allowed me to document reproductive synchrony with a variety of relatively independent indices.  This combination of indices provided stronger confirmation than use of any 1 of these indices would have allowed (Table 1.4).  All indices were positively correlated with each other (Table 1.5).  The significant positive correlations documented among indices suggests that having data for all 5 indices is likely unnecessary to document

synchrony and that readily available harvest-based indices, such as proportions

of 23-month-olds and population reconstruction recruitment indices, could be

used to document and track reproductive synchrony in the future.  Modal ages of

females trapped during summers likewise appear to reflect synchronous

reproduction (Chapter 2).  Because the mast failure of 1997 fell in the middle of

our study, I was able to document a seldom-observed reset in synchrony

whereby pulses of cubs went from being produced during even numbered years

(1992, 1994 and 1996) to odd numbered years (1999, 2001, and 2003).  A poor

mast year in 1992 (Figure 1.3) may have set the even-year cycle I documented in

the early years of the study.  Similarly, a regional mast failure in 1988 (Pack and

Igo 2004) may have resulted in poor cub production in 1989 and again in 1991

(due to synchrony).  The corresponding lack of 23-month-olds available to

harvest in 1990 and 1992 likely was responsible for the previously unexplained

pattern observed in Figure 1.1.

Of importance to researchers and managers, the costs and risks

associated with den work (Godfrey et al. 2000) do not appear to be necessary to

document reproductive synchrony.  Data based on den-site observations was not

as consistent in documenting synchrony as were data from trapping and harvest

and this may have caused earlier researchers examining our data set to

conclude that our population did not exhibit reproductive synchrony (Klenzendorf

2002).  This may be due to disruption of females' breeding schedules because of

previous den abandonments associated with research activities (Hellgren and

Vaughan 1989*b*, Godfrey et al. 2000), from efforts to transmitter bears in estrus

during the early years of our study, or from undocumented post-emergence litter losses.

Three of the 4 females we documented missing a reproductive opportunity missed following the 1997 mast failure. Similarly, Eiler et al. (1989) in Tennessee reported that nearly all missed reproductive opportunities followed poor mast years. Females from our study that did have litters following the 1997 mast failure did not exhibit a reduction in litter size (Table 1.7). This suggests reproductive response to mast failure may operate on a threshold principle similar to that proposed by Costello et al. (2003), with females either producing normally sized litters or no cubs at all. The paucity of missed reproductive intervals we documented is likewise consistent with results from Ontario (Kolenosky 1990), Maine (McLaughlin et al. 1994), and Virginia (Kasbohm et al. 1996).

Interbirth interval, defined as the length of time between consecutive litters from an individual female, is a frequently reported reproductive parameter in bear research. In western populations where bears frequently reproduce at >2-year-intervals (LeCount 1982, Kasworm and Thier 1994, Costello et al. 2003), calculated intervals may be useful indices of reproductive output. However, I agree with Miller (1994), who concluded calculated interbirth intervals frequently overestimate the frequency of reproduction and that this index is frequently oversimplified and misunderstood, particularly in the more highly productive populations found in eastern North America (Kolenosky 1990, McLaughlin et al. 1994, Kasbohm et al. 1996).

In highly productive populations where adult females rarely miss a reproductive opportunity (e.g, Kasbohm et al. 1996), calculation of interbirth interval can be <2.0 (Klenzendorf 2002).  Because black bears only reproduce at <2.0-year-intervals when they experience complete litter loss, interbirth interval may not be a measure of reproductive output so much as a measure of litter survival rates.  Cub survival is affected by many factors such as intraspecific predation (Echols 2000) that may have little relationship to the reproductive potential of their mother, thus making interbirth interval a misleading index. Additionally confounding this measure, litter loss caused by researcher activities, such as maternal litter abandonment (Hellgren and Vaughan 1989*b*, Godfrey et al. 2000), must be both recognized and reported.  Researchers seldom mention abandonments in their publications, and I believe the incidence of maternal abandonment is both under-recognized and under-reported.   Finally, as I observed and as has been substantiated in previous research (Eiler et al. 1989, McLaughlin et al. 1994, Costello et al. 2003), female bears may miss reproductive opportunities in response to mast failures.  Thus, in populations where reproductive opportunities are rarely missed except following mast failures (Eiler et al. 1989, McLaughlin et al. 1994), estimates of interbirth interval may reflect mast failure frequency more than female bears' reproductive potential. Effects of mast failure might be magnified in areas approaching carrying capacity (K) and it is possible that effects of mast failure are becoming more important and influential in western Virginia's relatively high density (Chapter 3) and growing population (Chapters 3 and 5) population.

The method I used to examine reproductive frequency is based on calculating frequency of missed reproductive opportunities in lieu of mean interbirth intervals.  Calculating missed reproductive opportunities is relatively simple and based on 2 components: 1) because females may be barren (as documented in our study), an adult female must have evidence of prior reproduction and 2) her reproductive status must be documented during ≥2 years.  For example, a female known to have had cubs in the past that is alone in 2 consecutive years or is with yearlings in year 1 and alone in year 2 has missed a reproductive opportunity.  However, a female alone in the den may have missed an opportunity, may have experienced complete litter loss after breeding season, or may be have denned separately from her yearlings; thus, a single den-site observation of a lone female does not provide meaningful information on reproductive frequency.  An additional advantage of this approach is that instead of giving a mean number, it provides the year(s) reproductive opportunities were missed and thus allows researchers to examine covariates such as annual food availability.  Elucidating the causes of missed reproductive opportunities, which in our study appear to result from hard mast failure and likely are due to subsequent nutritional stress, in conjunction with the proportion of breeding females affected, offers more mechanistic insight than simply calculation an average interbirth interval.

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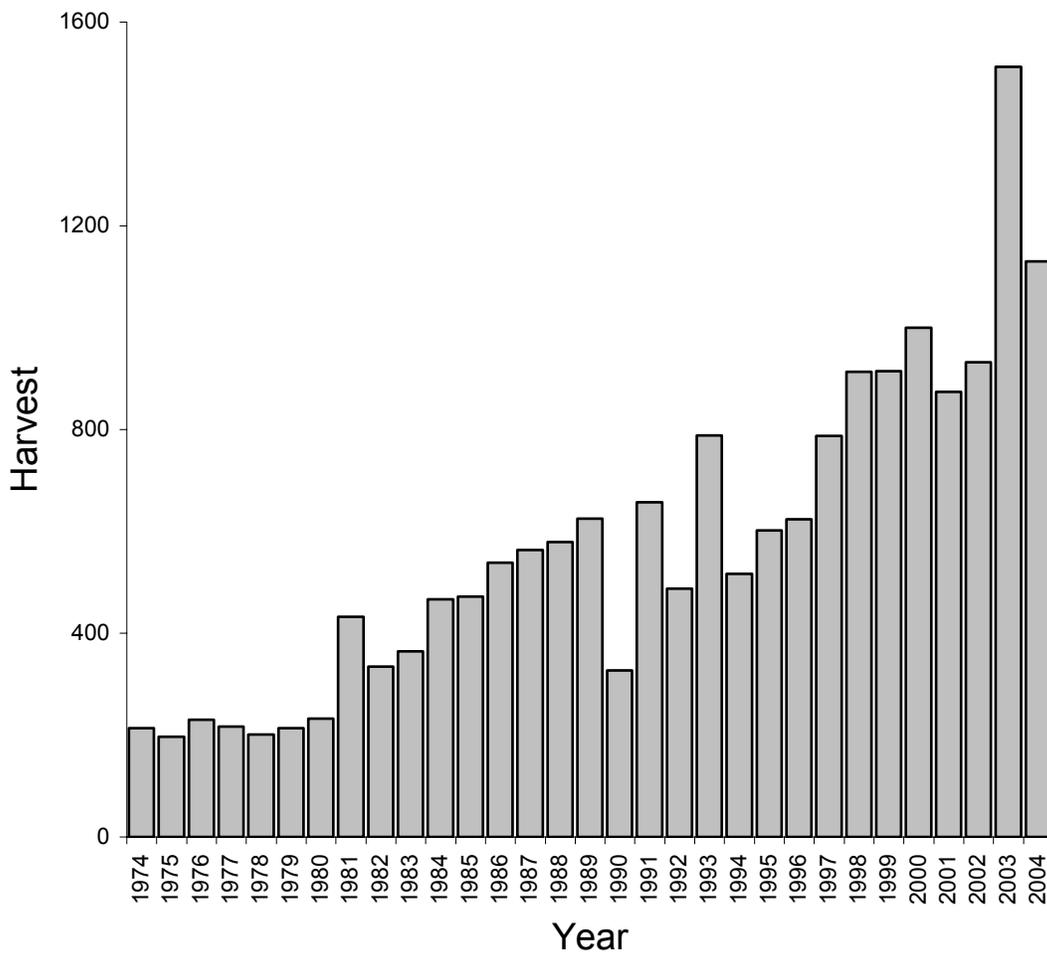
Figure 1.1.  Total black bear harvest for Virginia, USA, 1974–2004.   The

unexplained dips in 1990 and 1992 were a source of concern for managers.

Hunting regulations changed in 2003 were associated with the increase in

harvest in 2003 and 2004.
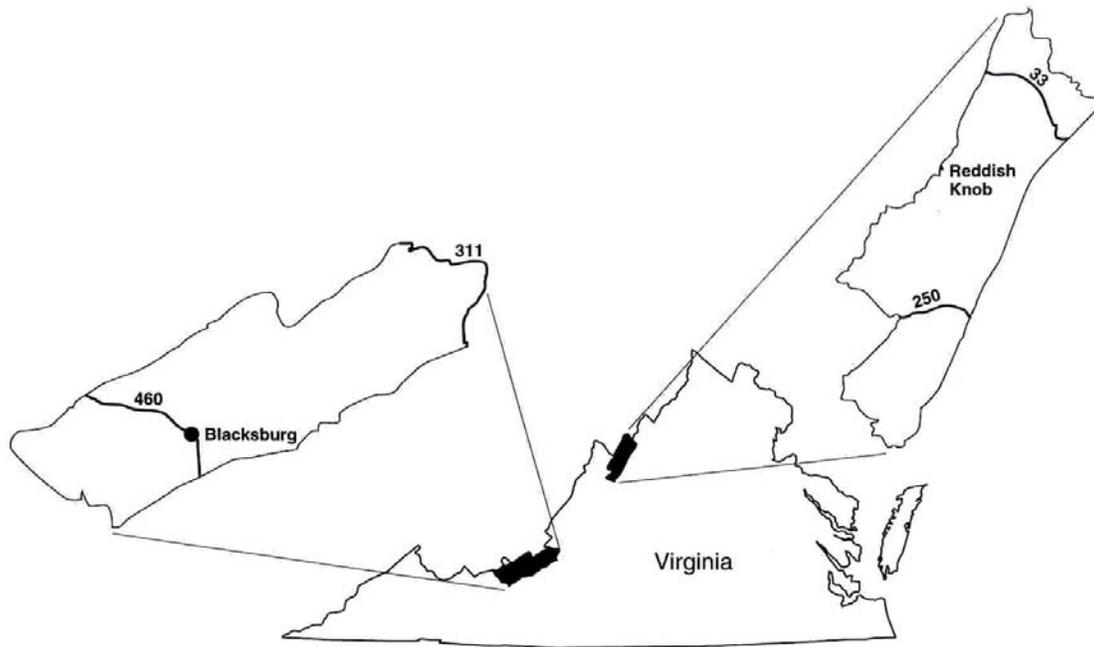
Figure 1.2.  Study areas of the Cooperative Alleghany Bear Study in western

Virginia, USA.  We conducted research on the northwestern study area from

1994–2003 and on the southwestern study area from 1995–2003.
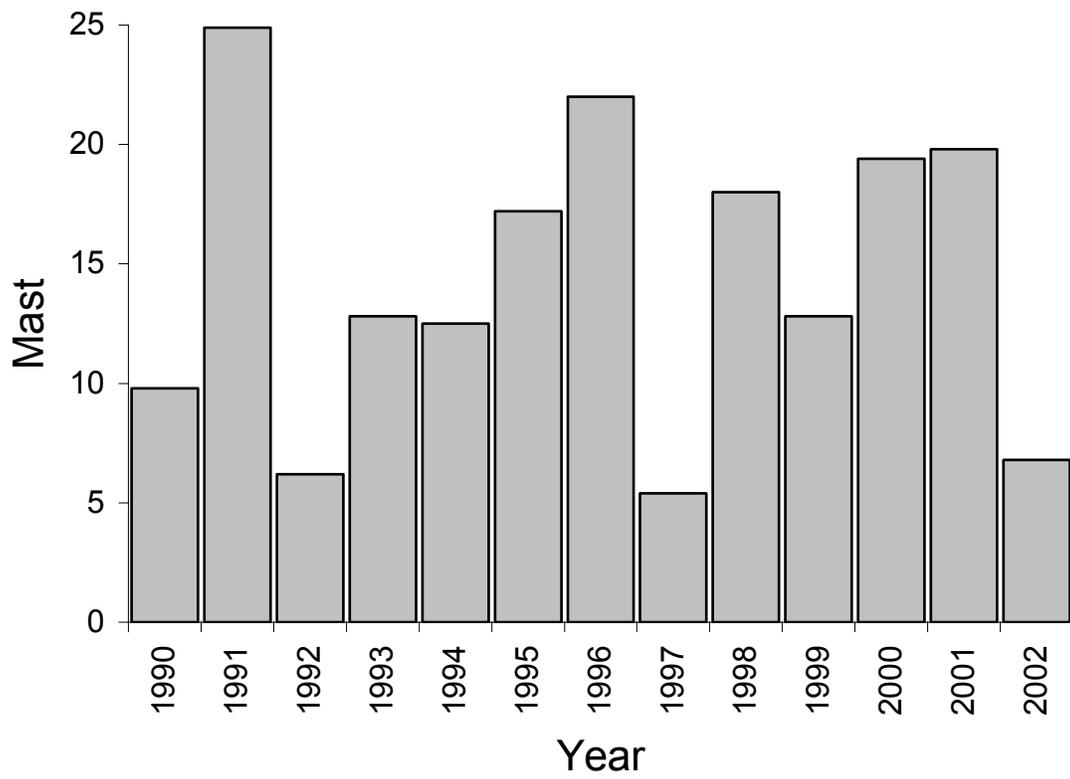
Figure 1.3. Mean number of acorns / 10 limbs / tree sampled on the 5 counties comprising our 2 study areas in the Alleghany Mountains of western Virginia, USA.
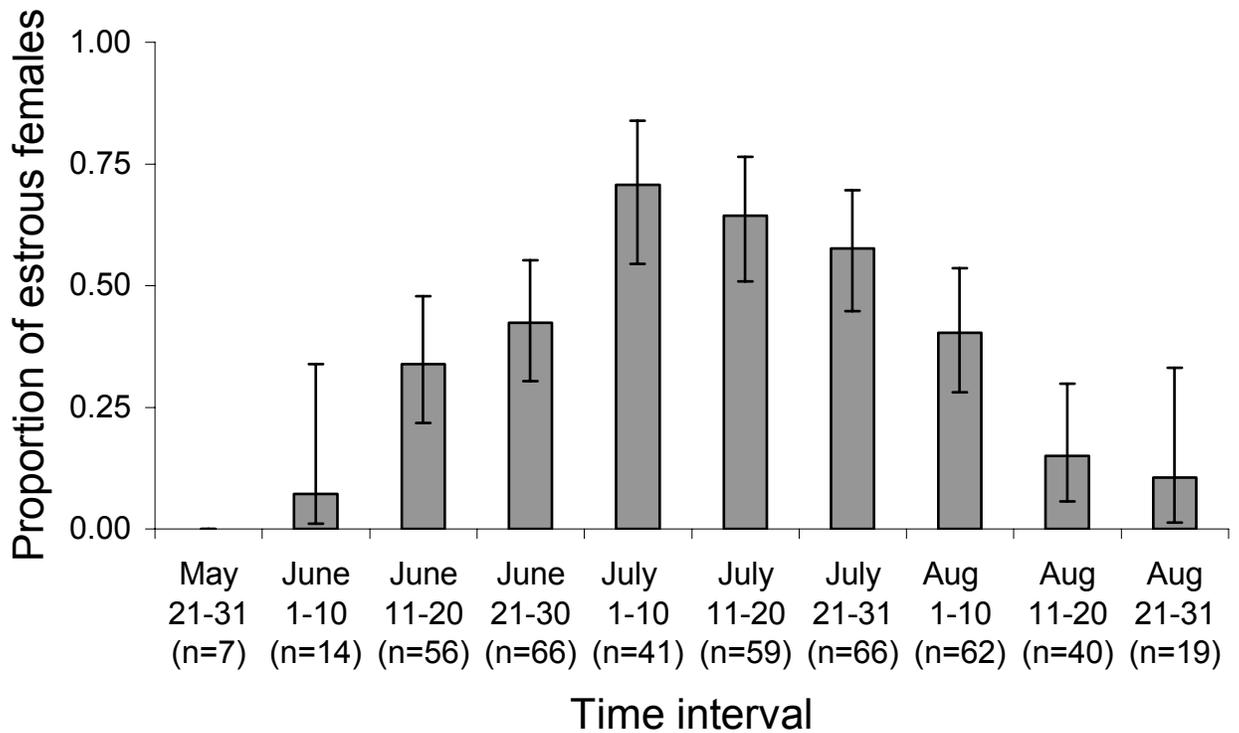
Figure 1.4. Proportion of females in estrus with associated 95% confidence intervals based on visual inspection of 326 ≥2-year-old available (not nursing cubs) individual female black bears 430 times, from May–August, 1994–2002 in western Virginia, USA.
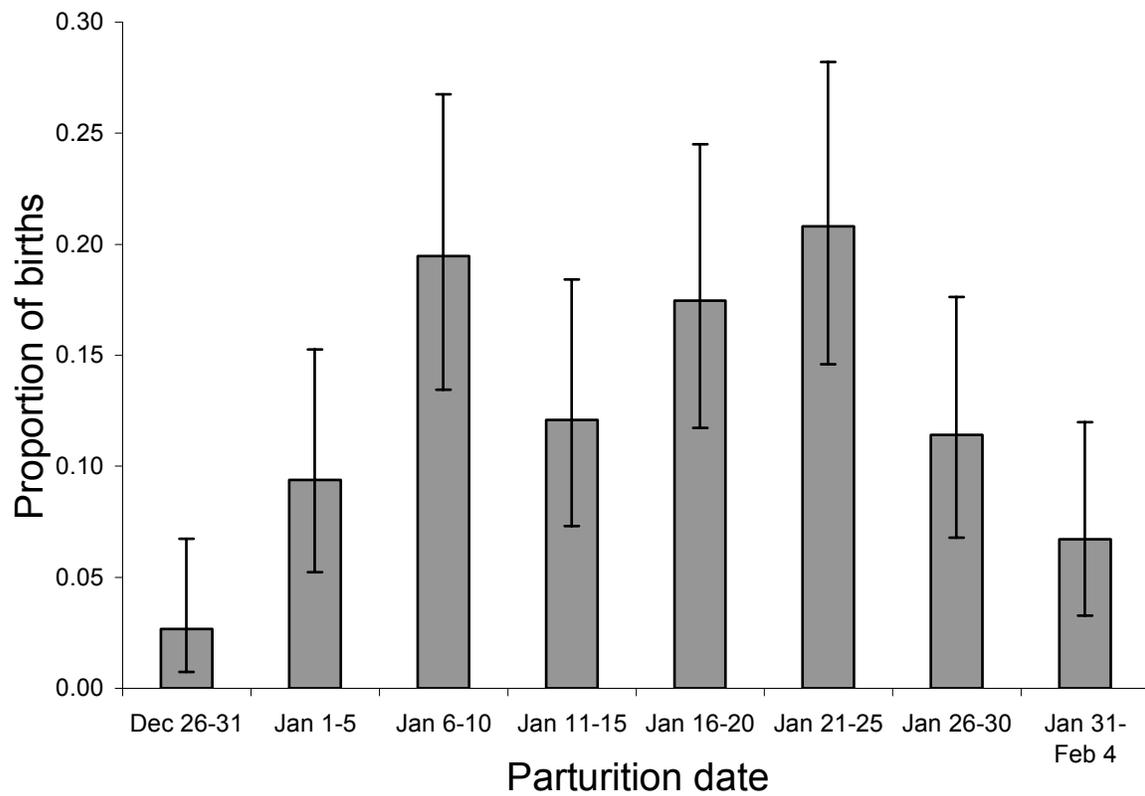
Figure 1.5.  Distribution of estimated parturition dates and 95% confidence intervals from 149 litters of black bear cubs born from 1996–2003 in the Alleghany Mountains of western Virginia, USA.
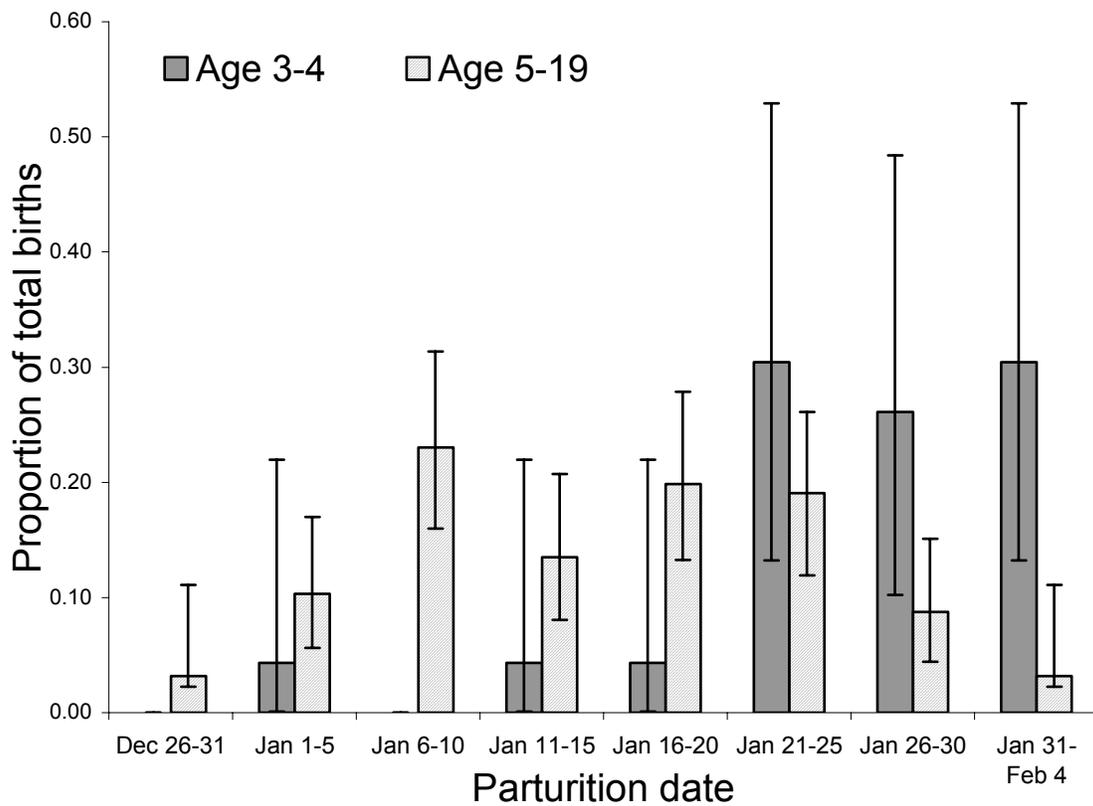
Figure 1.6.  Age-specific proportions and 95% confidence intervals of parturition

dates from 23 litters of black bear cubs born to 3–4-year-old mothers and 126

litters born to ≥5-year-old mothers born from 1996–2003 in the Alleghany

Mountains of Virginia, USA.
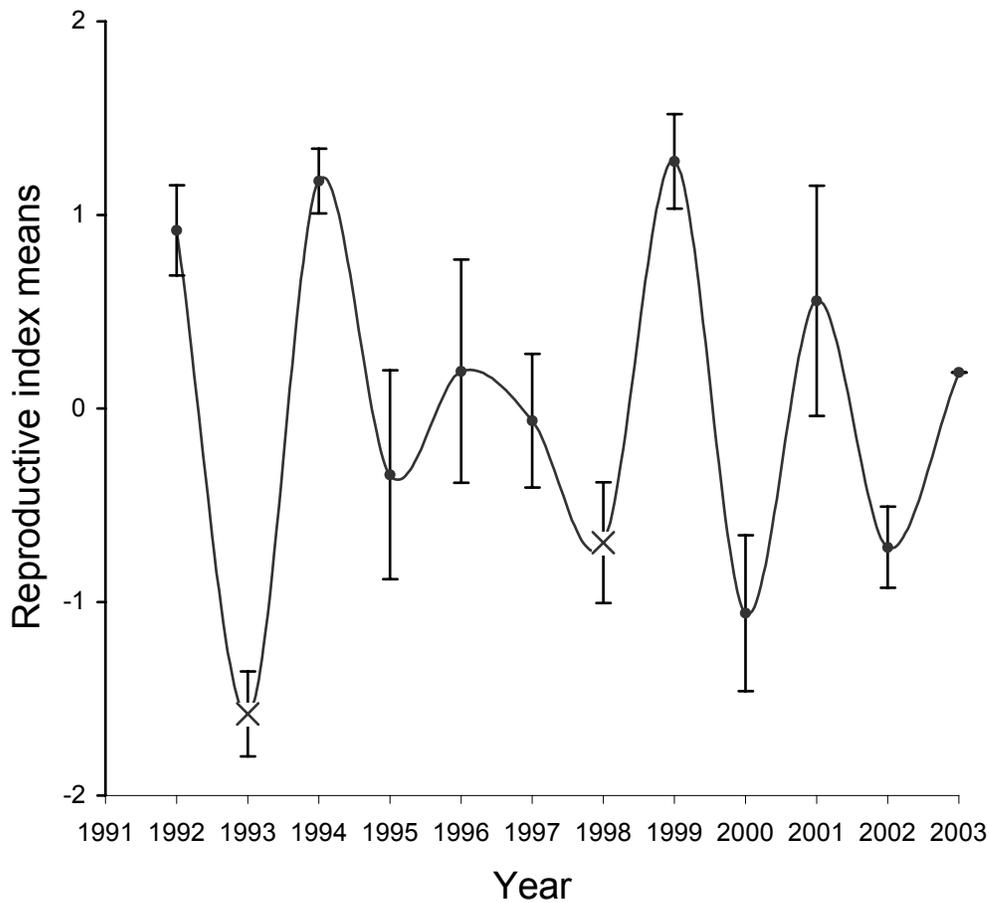
Figure 1.7.  Evidence of synchronized reproduction based on means and 95%
confidence intervals for 5, z-transformed, time-lagged indices (Table 1.4) of
reproduction in western Virginia (USA) black bears, 1992–2003.  Hard mast
failures occurred during 1992 and 1997 accordingly affected 1993 and 1998
reproduction (marked with X).  The 1997 mast (and associated 1998
reproductive) failure apparently reset synchrony from reproductive peaks in even
numbered years from 1992–1996 to peaks in odd numbered years from 1999–
2003.
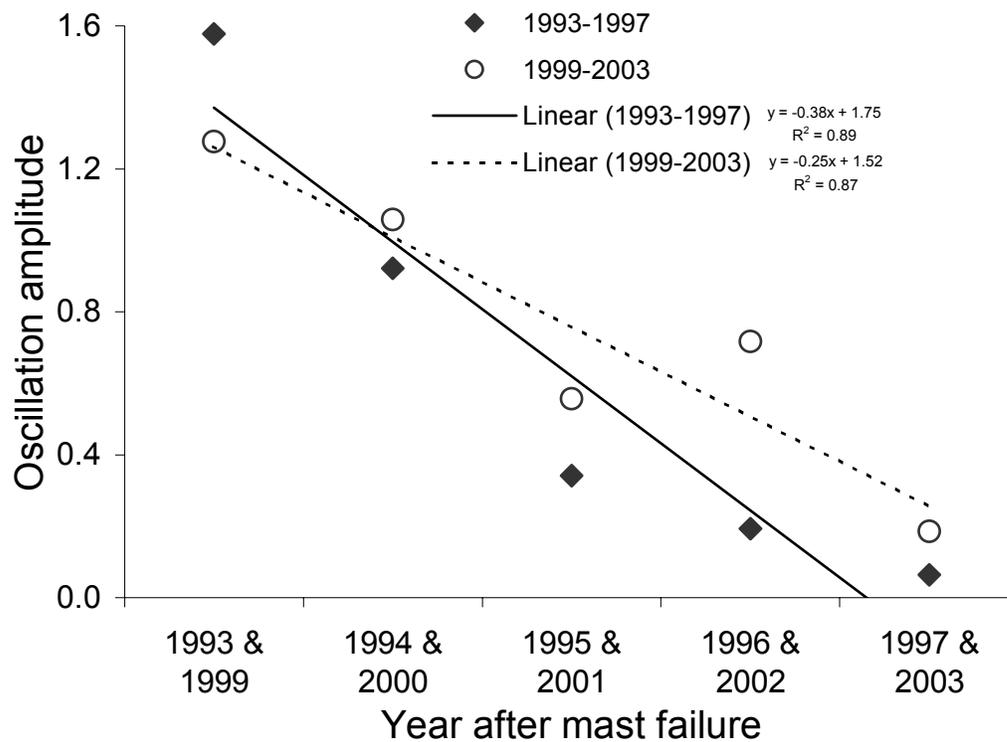
Figure 1.8. Dampening in amplitude of oscillations in reproductive synchrony through time after a mast failure event were evident both prior to and subsequent to the 1997 mast failure and were positively correlated with each other ($P$ = 0.04, $r_s$ = 0.90). A mast failure in 1992 likely resulted in synchrony observed from 1993–1997. Oscillation values are based on absolute values of the mean z-values calculated from Table 1.4.

Table 1.1. Results from analysis of variance (ANOVA) with factorial treatment

arrangement examining differences in parturition date from 1996–2003 from 149

litters of American black bear cubs born in the Alleghany Mountains of western

Virginia, USA

| Source | Degrees of Freedom | Mean Square Error | F | *P* |
|---|---|---|---|---|
| Age class[a] | 1 | 1044.02 | 13.81 | <0.001 |
| Mast failure[b] | 1 | 100.25 | 1.33 | 0.25 |
| Litter size class[c] | 1 | 1.14 | 0.02 | 0.90 |
| Age class*mast failure | 1 | 139.45 | 1.85 | 0.18 |
| Age class*litter size class | 1 | 6.06 | 0.04 | 0.84 |
| Mast failure*litter size class | 1 | 0.05 | 0.00 | 0.98 |
| Age class*mast failure*litter size class | 1 | 18.67 | 0.25 | 0.62 |
| Error | 141 | 75.57 | | |

[a] 3–4-year olds versus ≥5 year olds

[b] 1998 (following mast failure in 1997) versus all other years pooled

[c] 1–2-cub litters versus 3–4-cub litters

Table 1.2.  Litter size frequency distribution, mode, arithmetic mean, and associated standard error from den-site observations of age-class specific reproductive output of parturient black bears from 1995–2003 in western Virginia, USA.

| Female age | n | Litter size | | | | Mode | $\bar{x}$ ± SE |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | | |
| 3 | 14 | 0.57 | 0.36 | 0.07 | 0.00 | 1 | 1.50 ± 0.17 |
| 4 | 20 | 0.15 | 0.70 | 0.15 | 0.00 | 2 | 2.00 ± 0.13 |
| 5 | 30 | 0.07 | 0.37 | 0.53 | 0.03 | 3 | 2.53 ± 0.12 |
| 6–24 | 119 | 0.09 | 0.28 | 0.50 | 0.13 | 3 | 2.65 ± 0.07 |
| Total | 183 | 0.13 | 0.34 | 0.43 | 0.09 | 3 | 2.49 ± 0.06 |

Table 1.3.  Results from analysis of variance (ANOVA) with factorial treatment

arrangement examining differences in litters size from 183 litters of American

black bear cubs born in the Alleghany Mountains of western Virginia, USA

| Source | Degrees of Freedom | Mean Square Error | F | P |
|---|---|---|---|---|
| Age class[a] | 1 | 4.39 | 7.35 | 0.01 |
| Area[b] | 1 | 0.01 | 0.02 | 0.89 |
| Year[c] | 1 | 0.47 | 0.79 | 0.37 |
| Age class*area | 1 | 0.44 | 0.74 | 0.39 |
| Age class*year | 1 | 0.74 | 1.24 | 0.27 |
| Area*year | 1 | 0.01 | 0.02 | 0.89 |
| Age class*area*year | 1 | 0.32 | 0.54 | 0.46 |
| Error | 175 | 0.60 | | |

[a] 3–4-year olds versus ≥5 year olds

[b] Northern versus southern study areas

[c] 1998 (following mast failure in 1997) versus all other years pooled

Table 1.4. Empirically observed parameters and their z-transformed values that were standardized and staggered to represent appropriate reproductive output and demonstrate reproductive synchrony in Figure 1.7.

| Year (time $_t$) | Proportion adult females with cub in den (time $_t$) | | Proportion adult females with cubs in summer (time $_t$) | | Proportion 23-month-olds in harvest (time $_{t-1}$) | | Population reconstruction recruitment index (time $_t$) | | Proportion 2-year-olds in summer trap sample (time $_{t-2}$) | | $\bar{x}$ (time $_t$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Index | Z | Index | Z | Index | Z | Index | Z | Index | Z | Z | S.D. |
| 1992 | | | | | | | 1.42 | 0.80 | 0.37 | 1.04 | 0.92 | 0.17 |
| 1993 | | | | | 0.23 | -1.43 | 0.24 | -1.80 | 0.12 | -1.50 | -1.58 | 0.19 |
| 1994 | | | 0.48 | 1.19 | 0.48 | 1.39 | 1.50 | 0.98 | 0.38 | 1.14 | 1.17 | 0.17 |
| 1995 | | | 0.34 | 0.31 | 0.35 | -0.08 | 0.69 | -0.81 | 0.19 | -0.79 | -0.34 | 0.55 |
| 1996 | | | 0.41 | 0.75 | 0.30 | -0.64 | 1.21 | 0.34 | 0.30 | 0.33 | 0.19 | 0.59 |
| 1997 | 0.68 | 0.19 | 0.18 | -0.70 | 0.35 | -0.08 | 1.03 | -0.06 | 0.30 | 0.33 | -0.06 | 0.39 |
| 1998 | 0.49 | -0.61 | 0.08 | -1.33 | 0.31 | -0.53 | 0.82 | -0.52 | 0.22 | -0.49 | -0.69 | 0.36 |
| 1999 | 0.93 | 1.23 | 0.50 | 1.31 | 0.51 | 1.73 | 1.54 | 1.07 | 0.37 | 1.04 | 1.28 | 0.28 |
| 2000 | 0.27 | -1.53 | 0.12 | -1.07 | 0.31 | -0.53 | | | 0.16 | -1.10 | -1.06 | 0.41 |
| 2001 | 0.91 | 1.15 | 0.35 | 0.37 | 0.37 | 0.15 | | | | | 0.56 | 0.53 |
| 2002 | 0.49 | -0.61 | 0.16 | -0.82 | | | | | | | -0.72 | 0.15 |
| 2003 | 0.68 | 0.19 | | | | | | | | | 0.19 | 0.00 |
| $\bar{x} \pm$ S.D. | 0.64 ± 0.24 | | 0.29 ± 0.16 | | 0.36 ± 0.09 | | 1.06 ± 0.45 | | 0.27 ± 0.10 | | | |

Table 1.5.  Spearman's correlation coefficients between variables (Table 1.4) with ≥5 paired samples used to examine reproductive synchrony in a black bear population in the Alleghany Mountains of western Virginia, USA.

| | Proportion adult females with cubs in summer | Proportion 23-month-olds in harvest | Population reconstruction recruitment index | Proportion 2-year-olds in summer trap sample |
|---|---|---|---|---|
| Proportion adult females with cub in den | $r_s = 0.90$<br>$P = 0.02$<br>$n = 6$ | $r_s = 0.98$<br>$P = 0.01$<br>$n = 5$ | $n = 3$ | $n = 4$ |
| Proportion adult females with cubs in summer | | $r_s = 0.63$<br>$P = 0.10$<br>$n = 8$ | $r_s = 0.83$<br>$P = 0.04$<br>$n = 6$ | $r_s = 0.76$<br>$P = 0.05$<br>$n = 7$ |
| Proportion 23-month-olds in harvest | | | $r_s = 0.72$<br>$P = 0.07$<br>$n = 7$ | $r_s = 0.72$<br>$P = 0.04$<br>$n = 8$ |
| Population reconstruction recruitment index | | | | $r_s = 0.95$<br>$P < 0.001$<br>$n = 8$ |

Table 1.6. Comparison of reproductive parameters calculated from data obtained during den-site observations published in research from across the American black bear's range.

| Region | Study area | Citation | Primiparity | $n$ | $\bar{x}$ litter size |
|---|---|---|---|---|---|
| East | Pennsylvania | (Alt 1989) | 3.2 | 211 | 3.0 |
| East | Arkansas | (White et al. 2001) | | 7 | 2.6 |
| East | Tennessee | (Eiler et al. 1989) | 4.6 | 45 | 2.6 |
| East | Maine | (McLaughlin et al. 1994) | 4–6 (range) | 154 | 2.5 |
| East | Ontario | (Kolenosky 1990) | 5.7 | 18 | 2.5 |
| East | Québec | (Samsom and Hout 1995) | | 15 | 2.5 |
| East | Virginia | This study | 3.8 | 183 | 2.5 |
| East | Massachusetts | (Elowe and Dodge 1989) | 4 | 27 | 2.4 |
| East | Minnesota | (Rogers 1987) | 6.3 | 70 | 2.4 |
| East | Virginia/North Carolina | (Hellgren and Vaughan 1989*a*) | 4 (modal) | 7 | 2.3 |
| East | Virginia | (Kasbohm et al. 1996) | 3–4 (range) | 26 | 2.3 |
| East | South Carolina | (Willey et al. 1996) | 4 | 7 | 2.3 |
| East | Florida | (Dobey et al. 2005) | | 56 | 2.1 |
| East | Arkansas | (Clark and Smith 1994) | 3 (modal) | 57 | 2.1 |
| West | Arizona | (LeCount 1982) | | 13 | 1.9 |
| West | Idaho | (Reynolds and Beecham 1980) | 4–6 | 16 | 1.9 |
| West | Montana | (Kasworm and Thier 1994) | 6 | 20 | 1.8 |
| West | New Mexico | (Costello et al. 2003) | 5.7 | 115 | 1.8 |
| West | Montana | (Jonkel and Cowan 1971) | 7-8 | | 1.7 |
| West | California | (Keay 1995) | 4.1 | | 1.6 |
| West | Washington | (Lindzey and Melsow 1977) | | 10 | 1.6 |
| Mexico | Coahuila, MX | (Doan-Crider and Hellgren 1996) | 4.5 | 12 | 2.8 |
| Alaska | Alaska | (Miller 1994) | 5.9 | 19 | 2.3 |
| Alaska | Alaska | (Schwartz and Franzmann 1991) | 4.6 & 5.8 | 57 | 2.2 &2.3 |

Table 1.7.  Annual variation in median female age and arithmetic mean reproductive output from 183 den-site observations of parturient black bears during 1995–2003 in western Virginia, USA.

| Year | $n$ | Median female age | $\bar{x}$ litter size ± SE |
|------|-----|-------------------|---------------------------|
| 1995 | 13 | 4 | 1.69 ± 0.24 |
| 1996 | 25 | 6 | 2.36 ± 0.16 |
| 1997 | 24 | 7 | 2.29 ± 0.18 |
| 1998 | 21 | 7 | 2.57 ± 0.15 |
| 1999 | 25 | 7 | 2.80 ± 0.15 |
| 2000 | 11 | 10 | 2.64 ± 0.31 |
| 2001 | 25 | 7 | 2.52 ± 0.18 |
| 2002 | 17 | 7 | 2.53 ± 0.17 |
| 2003 | 22 | 8 | 2.73 ± 0.15 |
| Total | 183 | 7 | 2.49 ± 0.06 |

# CHAPTER 2:  SEX AND AGE STRUCTURE

**ABSTACT**

Sex- and age-structures of populations are often incorporated into wildlife management strategies and also are a common subject for ecological theoreticians.  However, determining accurate sex- and age-structure of American black bear (*Ursus americanus*) populations is challenging due to biases in trapping and harvest and difficulty obtaining information from dens containing neonates.  We determined sex for 420 neonatal cubs and found overall sex ratio (1.04M:1F) did not differ from 1M:1F ($\chi^2_1 = 0.15$, $P = 0.70$). However, when 1–3-cub litters (1.12M:1F) were pooled and compared with 4-cub litters (0.70M:1F), there was weak evidence that 1–3-cub litters had different sex ratios than 4-cub litters ($\chi^2_1 = 3.10$, $P = 0.08$).  Further analysis showed that sex ratios did not deviate from expected for 153 1–3-cub but did differ for 17 4-cub litters and that there were more all-female 4-cub litters than expected.  We determined ages for bears handled during 1,426 bear-summers and found sex-specific ages were different ($F_{1,1425} = 108.93$, $P<0.001$) with females (L.S.  $\bar{x} = 4.51$, S.E. ± 0.15, 95% C.I. = 4.22–4.81) older than males (L.S. $\bar{x}$ ± 2.52, S.E. ± 0.12, 95% C.I. = 2.28–2.75).  We determined sex for individuals during 1,494 bear-summers and found males dominated our trapping sample (1.41M:1F; $\chi^2_1 = 42.51$, $P < 0.001$).  Using genetic capture-recapture data, sex ratio based on 3-year mean density estimates was 0.74M:1F.  Expected stable population structure derived from sex- and age-specific survival rates derived from modeling

in Program Riskman was 0.38M:1F.  Comparing proportions derived from our summer trapping with those from our expected stable population structure, it appears a substantial trap-bias existed with young males over-represented and yearling females under-represented in our trapping sample and my derived indices are among the first attempts to index them.  Additionally, these finding have implications for bear research, management, and sex ratio theory.

**INTRODUCTION**

Examining neonatal sex ratios is complicated in black bear research because bears give birth in secluded dens and accessing neonatal cubs to determine the sex ratio soon after birth is time-intensive and potentially hazardous to both bears and researchers (Godfrey et al. 2000).  Further complicating data collection, black bears give birth at ≥2-year intervals (Chapter 1) making multiple years of data collection necessary to draw valid ecological inference (LeCount 1982, Schooley 1994, Pelton and van Manen 1996).

Biological theoreticians have published a vast body of work speculating on the occurrence and potential adaptive value of facultative manipulation of neonatal sex ratios.  Although these theoretical models have proven predictive and accurate for some taxa, success with mammals has been limited (Cockburn et al. 2002).  In recent review of mammalian sex ratio theory, Cockburn et al. (2002) list 11 adaptive hypotheses used to explain mammalian sex ratios.  Equal sex ratios might be the result of simple Mendelian segregation or, assuming equal cost for producing both sexes, stabilizing selection that balances sex ratios

at 1M:1F by favoring producers of the rarer sex when population sex ratio becomes imbalanced (Fisher 1930). The Trivers-Willard hypothesis (Trivers and Willard 1973) suggests that females in good condition that can better equip male offspring to compete should produce sons while females in poor condition should produce daughters. The local resource competition hypothesis suggests if resources are limiting, females should reduce intraspecific competition for resources by producing offspring that are likely to disperse, which, in the case of most mammals, are males (Clark 1978, Silk 1983). Application of this hypothesis suggests males should be produced during times of food scarcity because they are more likely to disperse and thereby reduce competition with their mother and have the opportunity to find better habitats (Verme 1969, Cockburn 1985, Verme 1989). Applicability of sex ratio theory to bear populations is rarely referenced in the bear literature.

Knowledge of sex- and age-structure in the adult population is a key component of management strategies for many hunted species for North American wildlife. For example, management of cervid populations frequently focuses on manipulation of sex and age ratios (McCullough et al. 1990, Clutton-Brock and Lonergan 1994, Clutton-Brock et al. 2002). Researchers and managers studying sexually dimorphic species can use data from count surveys to estimate sex- and, in some cases, age-structure of study populations. However, black bears (*Ursus americanus*) lack of exaggerated secondary sex- and age-revealing traits, such as plumage or antlers; thus, researchers studying sex and age structure cannot reliably determined these parameters via

observational methods.  Observations of trapped or harvested bears to determine sex and age characteristics have been the primary tool used to examine sex and age ratios of black bear populations (Garshelis 1994). However, this method is subject to bias due to differential trapping and harvest vulnerability of different sex and age classes (Bunnell and Tait 1985).  Likely because of these complications, in-depth quantitative assessments of sex and age structure of bear populations have been limited.

In 1994, Virginia Polytechnic Institute and State University and the Virginia Department of Game and Inland Fisheries (VDGIF; among numerous other collaborators) initiated the Cooperative Alleghany Bear Study (CABS) to intensively examine the long-term, broad-scale dynamics of Virginia's hunted black bear population.  This research included den-site visitations to gather reproductive and cub sex ratio data, trapping of subadult and adult black bears, sex-specific density estimation, and sex- and age-specific survival estimation. My objectives in this portion of our research were to use these data to quantify observed sex- and age-structure in our population, identify and attempt to quantify any biases, and finally evaluate the implications of these findings with reference to theory, research, and management.


**STUDY AREAS**

Our research was conducted on 2 study areas in the Alleghany Mountains of western Virginia, USA.  The centers of the 2 study areas were approximately 160 km apart; both were located largely on the George Washington-Jefferson

National Forests.  The northern study area was centered near Reddish Knob at 38° 28' N, 79° 15' W.  It was approximately 840 km$^2$ primarily in Augusta and Rockingham Counties.  The southern study area was 1,544 km$^2$ and was centered near Mountain Lake at 37° 22' N, 80° 31' W.  It was composed primarily of Craig, Giles, and Montgomery Counties.  Elevations on these 2 study areas ranged from 480–1,360 m (Kozak 1970) and common tree species included: eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipfera*), eastern white pine (*P. strobus*), mountain laurel (*Kalmia latifolia*) and scrub oak (*Q. ilicifolia*; Rawinski et al. 1994).  At Mountain Lake, the center of the southern study area, high temperatures ranged from an average high of 24°C in July to an average low of -9°C in the January with total precipitation averaging 125 cm, including 134 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va5828).  The closest weather station to our northern study area was at Dale Enterprises in the lowlands of Rockingham County.  Because it was in the lowlands, weather averages were likely warmer and drier than conditions in the adjacent mountains where our research was conducted.  At Dale Enterprises (38° 45' N, 78° 93' W), temperatures ranged from an average high of 30°C in July to an average low of -5°C in January with total precipitation averaging 90 cm, including 63 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va2208).

Hunting season lengths varied slightly (≤ 7 days) among years. Generally, September was marked by bear-hound training season during which bears could be pursued and treed with hounds, but not harvested. The second week of October through the first week of November was archery-hunting season, during which bears could be harvested using archery equipment. Gun season, during which bears could be killed with firearms, but not with the aid of dogs, was the last week of November. Hound-hunting season, during which bears could be killed using firearms and with the aid of dogs, consisted of the first few days of December through the first Saturday in January. One bear tag / year / hunter was sold with the combined deer, bear, and turkey license. To be legally harvested bears had to weigh ≥45.5 kg live weight or ≥34.1 kg with all internal organs removed. Adult females with cubs could not be legally harvested. Law required that all harvested bears be checked at registered check stations. Checking a bear involved recording any tags, tattoos, and/or transmitters, determining sex of the individual, and removing a premolar for subsequent age determination.

## METHODS

### General

We captured bears with Aldrich spring-loaded foot snares and culvert traps (Johnson and Pelton 1980) from late May through late August 1994–2002. We initiated trapping on our northern study area in 1994 and on our southern study area in 1995. We sedated captured bears with a mixture of ketamine

hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45.5 kg; White et al. 1996) administered via dart pistol, blowpipe, or jab stick.  After bears were sedated, we determined their sex, weighed them, recorded morphometric measurements, and examined females for signs of estrus or lactation.  To determine age, we removed a premolar (Willey 1974), which was sent to Matson's Laboratory (Milltown, Montana, USA) for cementum analysis.   We also tattooed bears' upper lips, and attached individually numbered, plastic, perma-flex, stud-style eartags (National Band and Tag, Newport, Kentucky, USA) to all bears ≥6 months old.  We attached motion-sensitive radio transmitters to bears selected in an attempt to keep our sex ratio of transmittered animals at approximately 1M:3F.  Bears ≥1 year old received collars (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA, Wildlife Materials International, Murphysboro, Illinois, USA) that were equipped with breakaway cotton spacers (Hellgren et al. 1988) or eartag transmitters (Servheen et al. 1981) from ATS.  We administered a tetracycline antibiotic to prevent infection and serve as a permanent biomarker in teeth and bones (Johnson 1964, Garshelis and Visser 1997).  Finally, we administered yohimbine hydrochloride (5mg/ml; 2 ml/45.5 kg) to reverse the xylazine hydrochloride.  Each week, we monitored and attempted to locate bears wearing transmitters.

Biologists from VDGIF conducted surveys in late August to early September to quantify annual hard mast production (Sharp 1958, Coggin and Peery 1973).  Mast surveys involved examination of the same trees annually and

quantifying the mean number of acorns / 10 limbs / tree (Fearer et al. 2002).  I

used mast survey data collected by VDGIF (D. Martin, personal communication)

for the 3 mast survey regions overlapping our study area to examine autumn

hard mast availability.

In the late fall and winter, we used radio telemetry to locate dens of female

bears wearing transmitters.  We returned to and entered (Godfrey et al. 2000)

these dens in January–April to gather reproductive data, change transmitters on

adults, attach transmitters to cubs (Echols 2000, Vashon et al. 2003) and

yearlings, and deploy remote cameras (Bridges et al. 2004).  The Virginia

Polytechnic Institute and State University Animal Care and Use Committee (98-

069-F&W) approved all animal handling protocols.

**Cub sex ratio**

We handled neonatal black bear cubs in their dens from March through

early April each year, 1995–2003.  In all dens where cubs were handled, we

determined sexes of each individual in each litter.  My *a priori* hypothesis was

that the overall sex ratio would not differ from 1M:1F; however, possible sources

of variation included annual differences, differences by adult female age class,

and difference related to litter size.  I tested for year effects, examined sex ratios

for each year, tested for differences in cub sex ratios from young (3–4-year-olds)

versus older (≥5-year-olds) females, and examined sex ratios of 1-, 2-, 3-, and 4-

cub litters.  I then examined whether the expected litter-size-specific sex ratios

differed from observed sex ratios.  I assumed the probability of each cub in a

litter being male (or female) was 0.5 and then constructing expected distributions

of litters for each litter size, 1–4, and compared them with our observations. I tested for statistical differences from the expected 1M:1F sex ratios using $\chi^2$ goodness of fit (GOF) tests.

**Summer capture sex ratios and age structure**

To determine if mean age of summer captures differed by sex, by study area, or if there was a significant interaction between factors, I used analysis of variance (ANOVA) and compared least square means (L.S. $\bar{x}$ ) with associated 95% confidence intervals (C.I.). I used a form of sampling with replacement where individual bears captured each summer (bear-summer) were considered independent from bears captured in previous summers. For example, an individual bear captured 5 times as a 4-year-old in 1996 and once as a 10-year-old in 2002 counted as a single 4-year-old in 1996 and a single 10-year-old in 2002. Because we did not trap on our southern study area in 1994 and we had small sample sizes in most years on our southern study area (particularly for females in 1998, 1999, and 2001), I could not examine age using 3-way interactions among year, sex, and study area. Thus, my ANOVA model examining age included sex, year, and study area and 2-way interactions between sex and years and between sex and study area. I tested to see it there were differences in sex ratios by year and for the sum of all years (1994–2003) with $\chi^2$ GOF tests.

**Genetic capture-recapture relative density**

During our research, we attempted to determine sex-specific black bear population densities. We constructed 50 barbed-wire enclosure hair traps

(Woods et al. 1999) on alternating 1-km$^2$ grid cells on the same 100-km$^2$ grid used for our camera study on the northern study area. These hair traps consisted of approximately 25–30 m of 4-prong barbed wire arranged in 50-cm-high polygons encircling suspended baits. The baits consisted of pastries and molasses centered in the polygon and suspended >3 m high (out of bears' reach) on a rope tied to adjacent trees. Sites were sketched and mapped with barbs numbered sequentially starting with the northern-most tree. For human safety purposes, reflective tape and colored flagging were placed on the wire and signs were placed on the trees that comprised each trap.

We visited each hair-trapping site every 14 days over 2 months (4 intervals / summer) from June–July, 1999–2001. Using a white note card or piece of paper as a backdrop, we examined each barb for entangled hairs. We used tweezers to remove bear hair and placed it in coin envelope labeled with the trap number, barb number, date, and approximate number of hairs in the sample. We then sterilized the tweezers with a propane torch and continued examining barbs. We used rubber gloves during all hair collection procedures. After all bear hairs were collected, we used the propane torch to sterilize each barb to remove any remaining hair or other genetic material in preparation for the next hair-trapping interval. Additionally, we refreshed baits, replaced safety markings, and repaired hair traps as necessary. We froze all hair samples immediately following collection.

I randomly selected 1 sample having ≥ 6 hairs with roots / hair trap / 2-week interval. I sent these samples to Wildlife Genetics International (Nelson,

British Columbia, Canada) where D. Paetkau and J. Wastl performed genetic analyses.  They extracted DNA from hair roots using QIAGEN's DNeasy® (Valencia, California, USA) and standard techniques following manufacturer instructions.  Ten microsatellite markers were tested for variability as potential individual identifiers.  Markers were selected based on level of heterozygosity, with the assumption that an expected heterozygosity of ≥0.73 was necessary for sample sizes of >100 individuals (Paetkau 2003).  Additionally, gender identification based on size polymorphism in the amelogenin gene was conducted for each identified individual (Ennis and Gallagher 1994).

I analyzed our genetic data in Program MARK (White and Burnham 1999) using Pollock's robust design (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997) extended to include Huggins' (Huggins 1989, Huggins 1991) heterogeneity closed capture estimator for population size, which allows for covariates.  The robust design model is a combination of open Jolly-Seber (Jolly 1965, Seber 1965) and closed capture models.  Specific models, their weights, and associated population and density estimates are provided in Chapter 3.

**Stable population structure and capture vulnerability index**

I used Program RISKMAN (Taylor et al. 2001) which uses a life-table approach to model expected stable age structure of the population. Reproductive parameters were based on the proportional distribution of litter sizes, 1–4, produced by females in each age class and also on the proportion of females producing litters every 2 years.  I used reproductive data from den-site

visitations (Chapter 1) to construct litter size proportions (Table 2.1). Because

bears on our study missed few reproductive opportunities, but apparently

experienced mast-induced reproductive failures approximately every 5 years, I

set the proportion of females producing litters every year to 0.8 (1 missed

reproductive opportunity in 5). Based on my mean unbiased (Garshelis et al.

1998) estimate of age at primiparity (3.8 years), I set the proportion of 3-year-old

females producing cubs to 0.2 (20% of 3-year-olds had litters). I used an

expected cub sex ratio of 1M:1F.

I used the survival rates that excluding hunting mortality derived from

known fate analyses as the input parameters for natural survival (Chapter 4).

Natural survival rates were 0.87 for cubs and 0.98 for ≥1-year-old bears (Table

2.2). The harvest data parameters were derived from direct returns (Chapter 4).

Relative vulnerability to harvest was based on the proportion of each age and

sex class harvested annually and was 0.36 for 1–3-year-old males, 0.09 for 1–3-

year-old females, 0.21 for ≥4-year-old males, and 0.08 for ≥4-year-old females

(Table 2.2). I then took the age- and sex-specific direct return numbers and

multiplied them by natural survival rates to get overall survival rates. I then input

these parameters into Program RISKMAN as natural survival. I then set harvest

rate to 0, and using the previously defined reproductive parameters, allowed

Program RISKMAN to run through 25 years to construct an expected stable sex

and age distribution for the population standardized to 1000. I then divided this

population into age and sex grouping including males and females at 1-year-age

steps from 1–9 and ≥10.

A capture vulnerability index was constructed to index trap bias in our sampling and to assess the relative capture vulnerability of each sex and age class. It was based on the proportion of the sex and age class trapped versus the portion available from the calculated stable population distribution. I calculated these indices for males and female from 1–≥10 years old. I pooled data for individuals ≥10 years old because of small or absent sex and age class representation in our trapped sample.

The indices were calculated in 2 ways. For those sex and age classes that were over represented (proportion of trapping sample > proportion available from our stable population structure), capture vulnerability index was calculated as:

(proportion in trapped sample / proportion in stable population structure)-1

For example, if 2-year-old males made up 10% of our trapped sample but only 5% of our stable population structure, their trapping vulnerability index would be (0.10/0.05)-1=1.0 or 100% over-representation.

For those sex and age classes that were under represented (proportion of trapping sample < proportion available from our stable population structure), capture vulnerability index was calculated as:

-(proportion in stable population structure / proportion in trapping sample)+1

For example, if 1-year-old females made up only 5% of our trapped sample but 10% of our stable population structure, their capture vulnerability index would be -(0.10/0.05)+1 = -1.0 or 100% under-representation.

This method is symmetric around 0 so if 4-year-old females made up 5% of our trapping sample and 5% of our stable population structure, their capture vulnerability index would be (0.05/0.05)-1 or -(0.05/0.5)+1, both of which equal 0 and indicate no under- or over-representation.

## RESULTS

### Cub sex ratio

Sex was determined for 420 cubs from 170 litters from 110 females. Overall sex ratio was 1.04M:1F and did not differ from 1M:1F ($\chi^2_1 = 0.15$, $P = 0.70$). There was weak evidence for a year effect ($\chi^2_8 = 12.42$, $P = 0.13$). Annually, 9 den season observations revealed evidence of male predominance in 1996 (2.00M:1F, $\chi^2_1 = 5.33$, $P = 0.02$) and weak evidence of female predominance in 1999 (0.64M:1F, $\chi^2_1 = 3.06$, $P = 0.08$). All other annual sex ratios did not differ from 1M:1F (Table 2.3).

Study area did not affect cub sex ratios ($\chi^2_1 = 0.61$, $P = 0.44$); sex ratio on the northern study area was 0.99M:1F and sex ratios on the southern study area was 1.16M:1F. Sex ratios of cubs from 3-(0.90M:1F), 4-(1.12M:1F), 5-(1.33M:1F), and ≥6-year-old (0.98M:1F) females indicated no age-specific deviation from 1M:1F ($\chi^2_3 = 1.47$, $P = 0.69$). Sex ratios of 1-(1.18M:1F), 2-(1.11M:1F), 3-(1.12M:1F), and 4-cub (0.70M:1F; Figure 2.1) litters did not

indicate litter-size-specific deviation from 1M:1F ($\chi^2_3$ = 3.12, $P$ = 0.37).  However,

when 1–3-cub litters (1.12M:1F) were pooled and compared with 4-cub litters

(0.70M:1F), there was weak evidence ($\chi^2_1$ = 3.10, $P$ = 0.08) that 1–3-cub litters

had different cub sex ratios than 4-cub litters.  Comparing observed versus

expected proportional sex ratios of different litter sizes, distributions of 1-, 2-, and

3-cub litters did not differ from expected proportions ($\chi^2_{1-3}$ = 0.17–8.82, $P$ = 0.19–

0.78; Table 2.4).  However, distribution of 4-cub litters differed from expected ($\chi^2_4$

= 11.67, $P$ = 0.02) and with litters of all-female cubs occurring in 23.53% (95%

C.I. = 6.81–49.90%) of observed litters but only expected to occur in 6.25% of

litters.

**Summer capture sex ratios and age structure**

We determined ages for bears handled during 1,426 bear-summers.

Young males were most heavily represented in our trapping data (Figure 2.2).

Modal age of captured females oscillated from 2-year-olds during even

numbered years and 3-year-olds during odd numbered years until 1998

(following the mast failure of 1997); thereafter, this pattern was reversed (Table

2.5).  The modal age of captured males was 2 years old during most years and

did not show the same annual oscillation observed in the female population

(Table 2.5).  Sex-specific ages were different ($F_{1,1406}$ = 108.93, $P$<0.001; Table

2.6) with females (L.S. $\bar{x}$ = 4.51, S.E. ± 0.15, 95% C.I. = 4.22–4.81) older than

males (L.S. $\bar{x}$ = 2.52, S.E. ± 0.12, 95% C.I. = 2.28–2.75).  Study areas also were

different ($F_{1,1406}$ = 21.46, $P$<0.001; Table 2.6) with bears on the northern study

area older (L.S. $\bar{x}$ = 3.95, S.E. ± 0.09, 95% C.I. = 3.79–4.12) than bears on the

southern study area (L.S. $\bar{x}$ = 3.08, S.E. ± 0.17, 95% C.I. = 2.75–3.41).  There

was weak evidence for a year effect ($F_{8,1406}$ = 1.68, $P = 0.10$; Table 2.6) with age

lowest in 1994 (L.S. $\bar{x}$ = 2.88, S.E. ± 0.30, 95% C.I. = 2.29–3.47) and highest in

1997 (L.S. $\bar{x}$ = 3.98, S.E. ± 0.24, 95% C.I. = 3.52–4.45); all other years (1995,

1996, and 1998–2002) overlapped these confidence intervals.  There was an

interaction between sex and study area ($F_{1,1406}$ = 4.13, $P = 0.04$; Table 2.6) with

females older on the northern study area (L.S. $\bar{x}$ = 5.14, S.E. ± 0.13, 95% C.I. =

4.89–5.40) than on the southern study area (L.S. $\bar{x}$ = 3.88, S.E. ± 0.26, 95% C.I.

= 3.36–4.40) and confidence intervals for ages of males on the northern (L.S. $\bar{x}$ =

2.76, S.E. ± 0.11, 95% C.I. = 2.54–2.98) and southern (L.S. $\bar{x}$ = 2.27, S.E. = 0.21,

95% C.I. = 1.86–2.69) study areas overlapping.   There was little evidence for an

interaction between year and sex ($F_{8,1406}$ = 1.60, $P = 0.12$; Table 2.6) with

females younger in 1994 (L.S. $\bar{x}$ = 3.08, S.E. ± 0.49, 95% C.I. = 2.12–4.05) than

females in 1995, 1997, 1999, and 2002 (L.S. $\bar{x}$ = 4.78–5.28, S.E. ± 0.29–0.38,

95% C.I. = 4.09–4.61) and all other years (1996, 1998, 2000 and 2001)

overlapping these confidence intervals.  Confidence intervals for males

overlapped in all years (L.S. $\bar{x}$ = 2.35–2.69, S.E. ± 0.26–0.34, 95% C.I. = 1.81–

3.35).

 We determined sex for 1,014 individual bears (1.90M:1F; $\chi^2_1$ = 87.4, $P <$

0.001), during 1,494 bear-summers (1.41M:1F; $\chi^2_1$ = 42.51, $P < 0.001$), 1,914

times (1.56M:1F; $\chi^2_1$ = 97.6, $P < 0.001$).  There was evidence year affected sex

ratios ($\chi^2_8$ = 15.74, $P = 0.05$).  Number of individual bears captured annually

ranged from 112 in 1994 to 231 in 2002 with more males than females caught in

every summer (Table 2.7).  Male predominance ranged from 2.20M:1F in 1994 to

1.04M:1F in 2000 and was most pronounced in 1994, 1995, 1996, 1999, and

2001 ($\chi^2_1$ = 4.92–16.69, $P$ = <0.001–0.027; Table 2.7).  There was weak

evidence to suggest sex ratios were affected by study area ($\chi^2_1$ = 2.25, $P$ = 0.13).

The sex ratio of 1,140 bear-summers on the northern study area was 1.35M:1F

($\chi^2_1$ = 24.76, $P$ < 0.001) and the sex ratio of 354 bear-summers captures on the

southern study area was 1.62M:1F ($\chi^2_1$ = 19.93, $P$ < 0.001).  There was evidence

month of trapping affected sex ratio of our trapping sample ($\chi^2_3$ = 8.85, $P$ = 0.03).

Monthly sex ratios were all male dominated ($\chi^2_1$ = 5.23–34.77, $P$ <0.001–0.02)

but were most disproportionate in May and June (Figure 2.3).

**Genetic capture-recapture sex ratio**

We collected 432 black bear hair samples and sent them to Wildlife

Genetics International (Nelson, British Columbia, Canada) for analysis.  They

used 6 microsatellite markers and determined 396 of these samples were

individually identifiable (Chapter 3).  They found 136 individual genotypes, likely

representing 136 individual bears.  Annual density estimates calculated using

Pollock's robust design model for males ranged from 0.36–0.45 bears / km$^2$ and

for females ranged from 0.55–0.59 bears / km$^2$ (Table 2.8).  Sex ratios varied

from 0.65–0.80M:1F with a 3-year (1999–2001) mean of 0.74M:1F (Figure 2.4).

**Stable population structure and capture vulnerability index**

Based on expected sex- and age-specific stable population structure

derived from survival rates based on modeling in Program RISKMAN, there

should be more females than males in each age class (Figure 2.5).  The overall

sex ratio combining age 1–25 years old of the expected stable population structure was 0.38M:1F.

Comparing proportions derived from our summer trapping with proportions expected from our stable age structure to construct capture vulnerability indices, it appears that substantial trap-bias likely existed (Figure 2.6). Yearling females were substantially (400%) under-represented in our trapping. Young (2–5-year-old) males were substantially (97–166%) over-represented in our trapping sample.

## DISCUSSION AND MANAGEMENT IMPLICATIONS

### Cub sex ratio

Sex ratios for neonatal black bear cubs generally have not been found to differ statistically from 1M:1F (Clark and Smith 1994, Miller 1994, Costello et al. 2003). Our results pooling mothers' ages, years, study areas, and litter sizes likewise suggest that sex ratios of cubs did not differ statistically from 1M:1F. These results differ from those from Québec where the sex ratio of 19 litters was male-dominated (Samson and Hout 1995).

I found evidence that large litters (4-cub) contained more females than smaller litters (1–3-cubs) and that all female litters were more common than were expected at this largest litter size (Tables 2.3 and 2.4 and Figure 2.1). Research from Pennsylvania (Alt 1981) and Minnesota (Noyce and Garshelis 1994) suggests litter size could impact sex ratio, especially in large litters. However, these studies indicate an increased proportion of males in large litters.

Though there was evidence for a year effect, we did not document any environmental or ecological reason why sex ratios in 1996 and 1999 might be skewed. The lack of study area effect is not surprising because environmental conditions on the 2 study areas were similar and I had no other reason to believe sex ratios might differ between these 2 areas. One might expect females to improve their physical condition as they grow and mature (from ages ≤4 to ages ≥5) and thus, if condition and size play a role in sex ratio partitioning, produce modified cub sex ratios. However, female age class did not have a significant effect on cub sex ratios.

Although theory-based models have proven predictive and accurate for some taxa, success with mammals has been limited (Cockburn et al. 2002). The equal sex ratios observed in most bear populations may be the result of simple Mendelian segregation or, assuming equal cost for producing both sexes, stabilizing selection that balances sex ratios at 1M:1F by favoring producers of the rarer sex when population sex ratio becomes imbalanced (Fisher 1930).

The Trivers-Willard hypothesis (Trivers and Willard 1973) suggests that in polygynous species, such as bears, more variance in offspring reproductive success results from the condition of male offspring; thus females in good condition that can better equip male offspring to compete should produce sons while females in poor condition should produce daughters.

An alternative hypothesis suggests producing males during times of food scarcity is advantageous because these individuals are more likely to disperse and thereby reduce competition with their mother and have the opportunity to find

better habitats (Verme 1969, Cockburn 1985, Verme 1989).  The local resource competition hypothesis suggests if resources are limiting, females should reduce intraspecific competition for resources by producing offspring that are likely to disperse, which, in the case of most mammals, are males (Clark 1978, Silk 1983).  In sexually dimorphic organisms that develop at different rates while under parental care, cost may not be equal and thus sex ratios may differ from 1M:1F (Willson and Pianka 1963).

My findings suggest that cub sex ratio might be skewed towards females in 4-cub litters when compared with 1–3-cub litters (Tables 2.3 and 2.4 and Figure 2.1).  If the greater proportion of females we observed in large litters is biologically significant, it might be related to a higher cost associated with raising faster-growing (Bridges, unpublished data) male cubs.  Thus, because large 4-cub litters may add stress to females due to the shear number of cubs being raised, these females might reduce cost to themselves by raising more-slowly-growing female cubs.  Alternatively, if 4-cub litters are produced by females in maximum condition and thus are indicative of a relative lack of local resource competition, females may be under less pressure to produce dispersing offspring (males) to minimize intraspecific competition.  Future studies with relatively large samples of regionally maximum litter sizes might help determine which of these theories, if any, is applicable to black bear populations.

**Adult sex ratios and age structure**

Despite acknowledged bias towards males, the most common means of quantifying sex and age ratios in the published literature is based on trapping

data (Garshelis 1994).  Reported sex ratios of adults included: 0.23M:1F in California (Keay 1990), 0.42M:1F in Maine (McLaughlin et al. 1994), 0.68M:1F in Montana (Jonkel and Cowan 1971), 0.95M:1F in Shenandoah National Park in western Virginia, 1.43M:1F in Tennessee (Eiler et al. 1989), 1.45M:F in Arkansas (Clark and Smith 1994), 2.5M:1F in the Dismal Swamp in coastal Virginia (Hellgren and Vaughan 1989).

Our raw trapping data would suggest the vast majority of our population to be young male bears (Figure 2.2).  I suggest that these trapping numbers in isolation offer little valid inference into the sex and age structure of our population.  Because male survival rates, particularly for younger age classes (1–3 years old) were substantially lower than female survival rates (Chapter 4), we would expect our population to contain more females than males.  Unlike trapping data, sex ratios derived from genetic capture-recapture population and density estimates conducted from 1999–2001 indicated a sex ratio of 0.74M:1F (Table 2.8), and likely offer a more realistic estimate than our trapping data.

However, I believe our most realistic estimate was 0.38M:1F and was derived from modeling in Program RISKMAN to build a stable population structure (Figure 2.5).  The substantially lower survival rates of young males versus other sex and age classes (Table 2.2) would suggest the actual population sex ratio to be more disparately female-skewed than even the density estimates suggest.  The capture vulnerability index offers insight into how we sample black bear populations.  These indices indicate yearling females are heavily (400%) under represented in our trapping data while 1–5-year-old males

are substantially over represented.  Causation for these patterns might be related to several aspects of black bear ecology.  Yearling females tended to have very small home ranges on our study area (Lee 2003) and may have been less likely to encounter traps.  Likewise, dispersal patterns of subadult males resulted in large home ranges (Lee 2003) and thus may have made these individuals more likely to encounter traps.

A possible extension of the trapping vulnerability index would be to construct a population multiplier for trapping and/or harvest data.  The underlying principle, that we can construct an estimated stable population structure and then, based on trapping or harvest data, calculate their relative vulnerability, could be extended to a more quantitative multiplier that would allow for sex- and age-specific population estimation.  Calculating variance (which would be necessary) on such a multiplier would involve extensive modeling and simulation and is beyond the scope of my analyses.  However, construction of such a multiplier could be a productive endeavor for future researchers and could be of substantial value to managers as a tool to track their bear populations using harvest data.

Due to the relatively high mortality rate seen in young males, it is not surprising that mean age of females captured was higher than mean age of males captured.  Both the estimated stable population structure (Figure 2.5) and data from our summer trapping data (Figure 2.3) demonstrates this difference. The younger age structure associated with 1994 is puzzling and I do not have a biological explanation for the apparent difference.  Perhaps because it was our

first year of trapping on the study, the trapping skills of our field personal were still in a formative stage and thus they may have had difficulty capturing older and likely more cautious bears. Likewise, evidence of a study area effect on age structure is difficult to explain and I can propose no biological reason why ages of captured bears were younger on our southern study area than on our northern study area.

Managers frequently attempt to manipulate the sex and age ratios of wildlife populations (McCullough et al. 1990, Clutton-Brock and Lonergan 1994, Clutton-Brock et al. 2002). However, for black bears that lack the dramatic secondary sex characteristics seen in many cervids, galliformes, and waterfowl, quantifying population structure generally has relied on admittedly biased (Bunnell and Tait 1985) harvest and trapping data. Understanding and interpreting sex and age structure of black bear populations can be synthesized with other data to propose and subsequently justify management practices. For example, the nearly 1:3 male to female sex ratio that likely was present in our population might lead to concern over whether too many males were being harvested to leave a sufficient number to breed with all available females. However, because bears are polygynous (Garshelis and Hellgren 1994, Schenk and Kovas 1995, Kovach and Powell 2003, Sinclair et al. 2003) and females on our study areas missed few reproductive opportunities (Chapter 1), it appears that sufficient numbers of males were present to breed with all available females and that this skewed sex ratio did not substantially affect reproduction.

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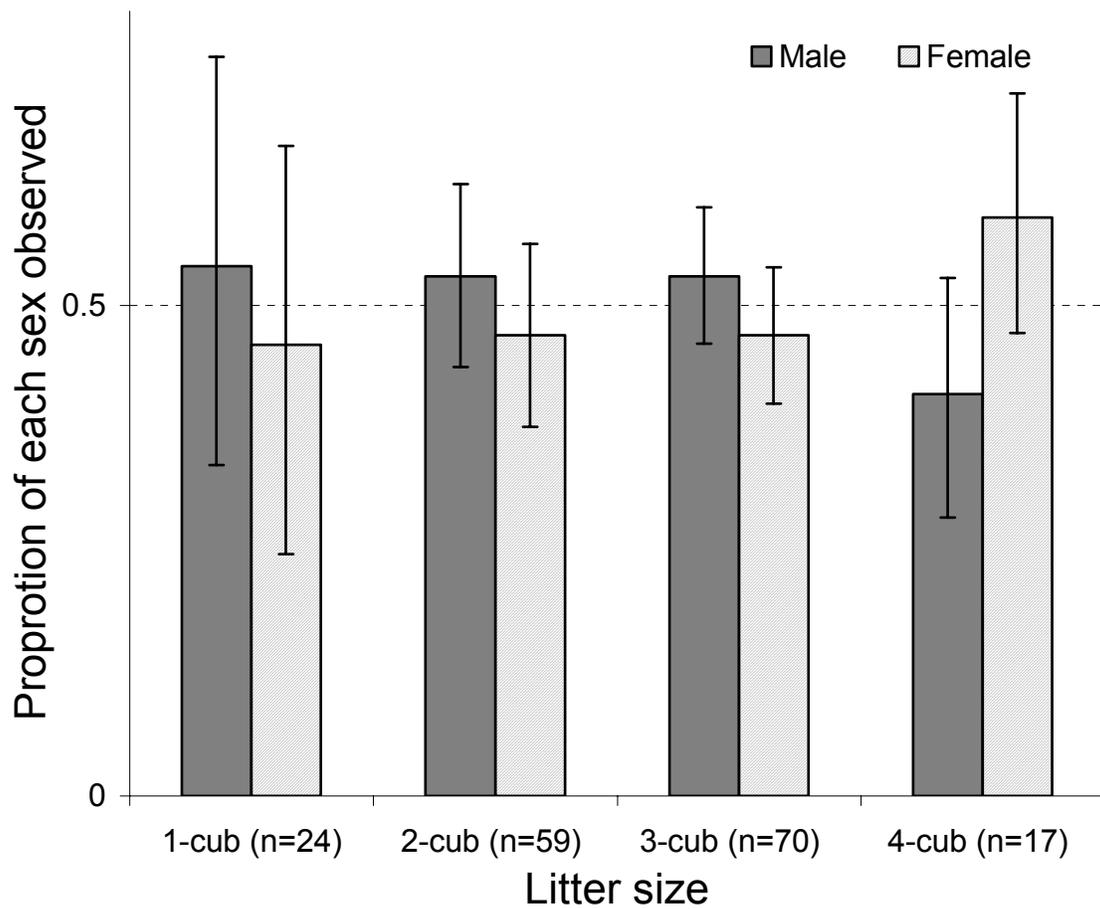
Figure 2.1. Proportions and 95% confidence intervals of black bear cub sex ratios grouped by litter size and derived from den-site observations of 420 cubs from 170 litters from 110 females from 1995–2003, in western Virginia, USA.
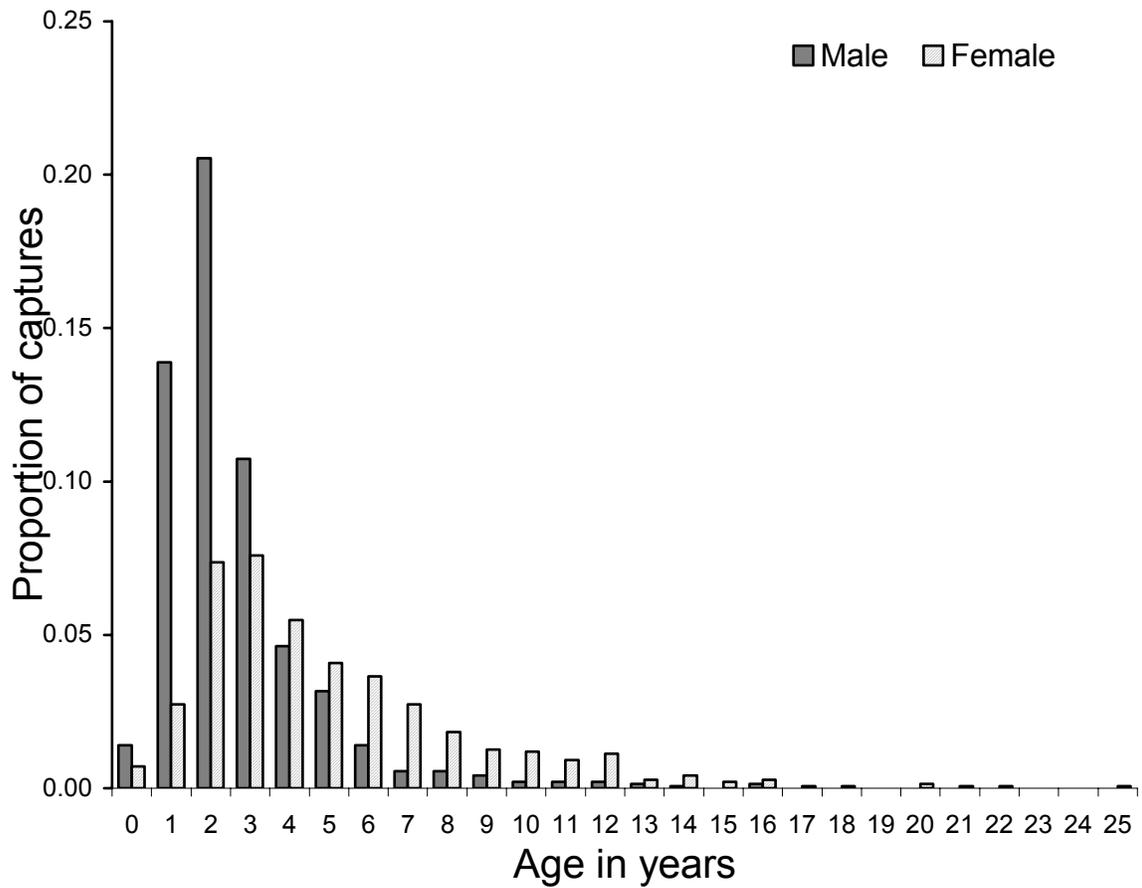
Figure 2.2. Age structure based on 1,426 bear-summers (treating captures from each summer as independent from previous summers) for male and female black bears handled in from 1994–2002 in the Alleghany Mountains of western Virginia, USA.
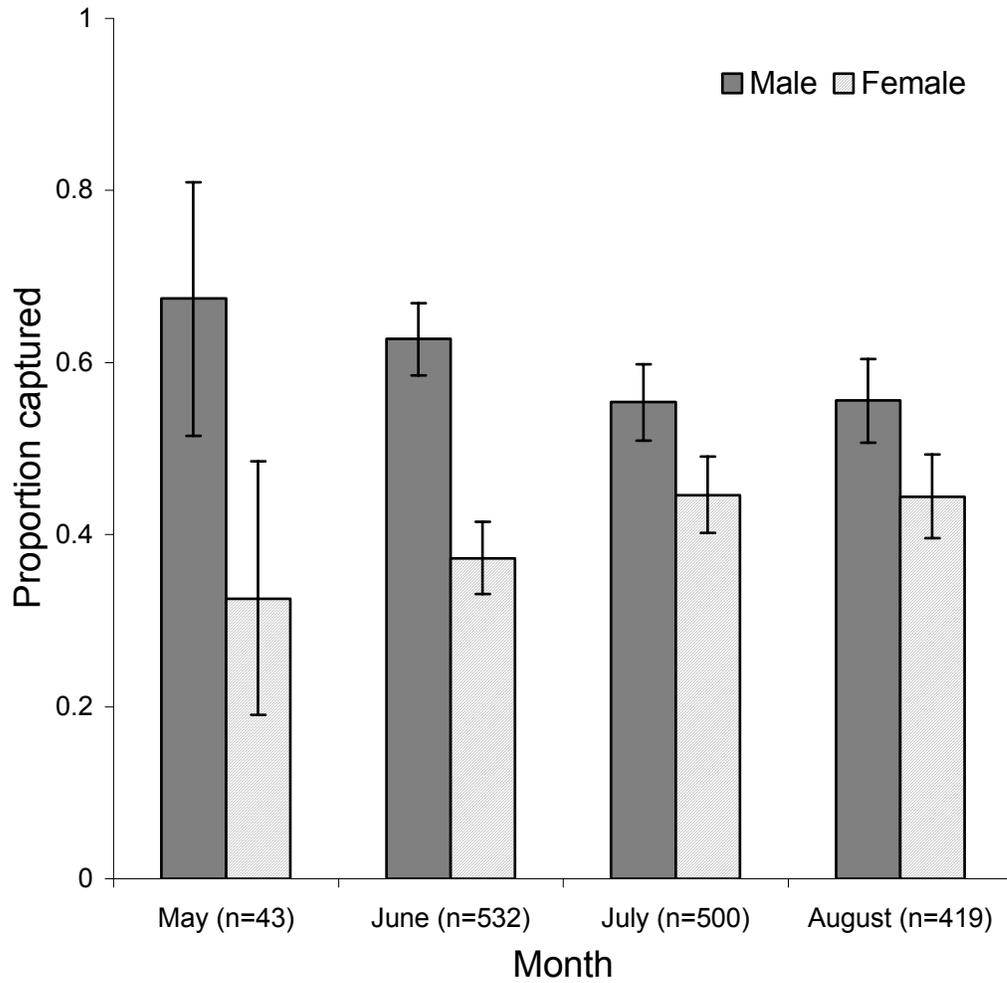
Figure 2.3.  Sex ratio and 95% confidence intervals of trapped black bears

derived from 1,494 bear-summers (treating captures from each summer as

independent from previous summers) from 1994–2002 in Alleghany Mountains of

western Virginia, USA.
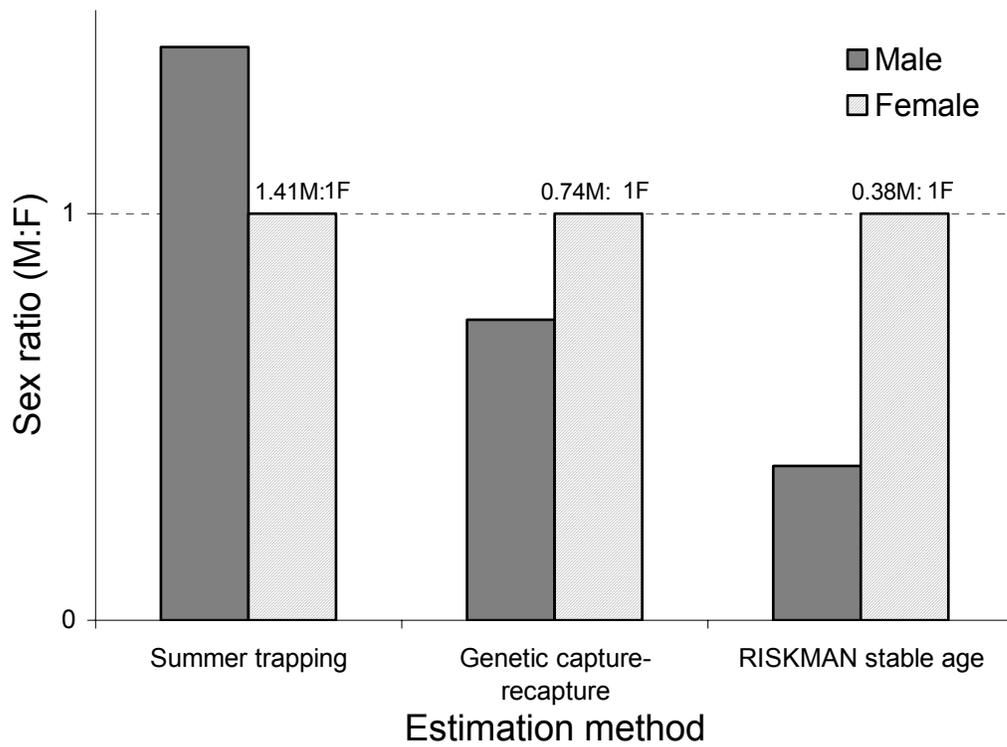
Figure 2.4. Comparison of sex ratios derived from summer trapping data, capture-recapture sex-specific density estimation, and expected stable age distribution derived from modeling in Program RISKMAN and using data collected in the Alleghany Mountains of western Virginia, USA.
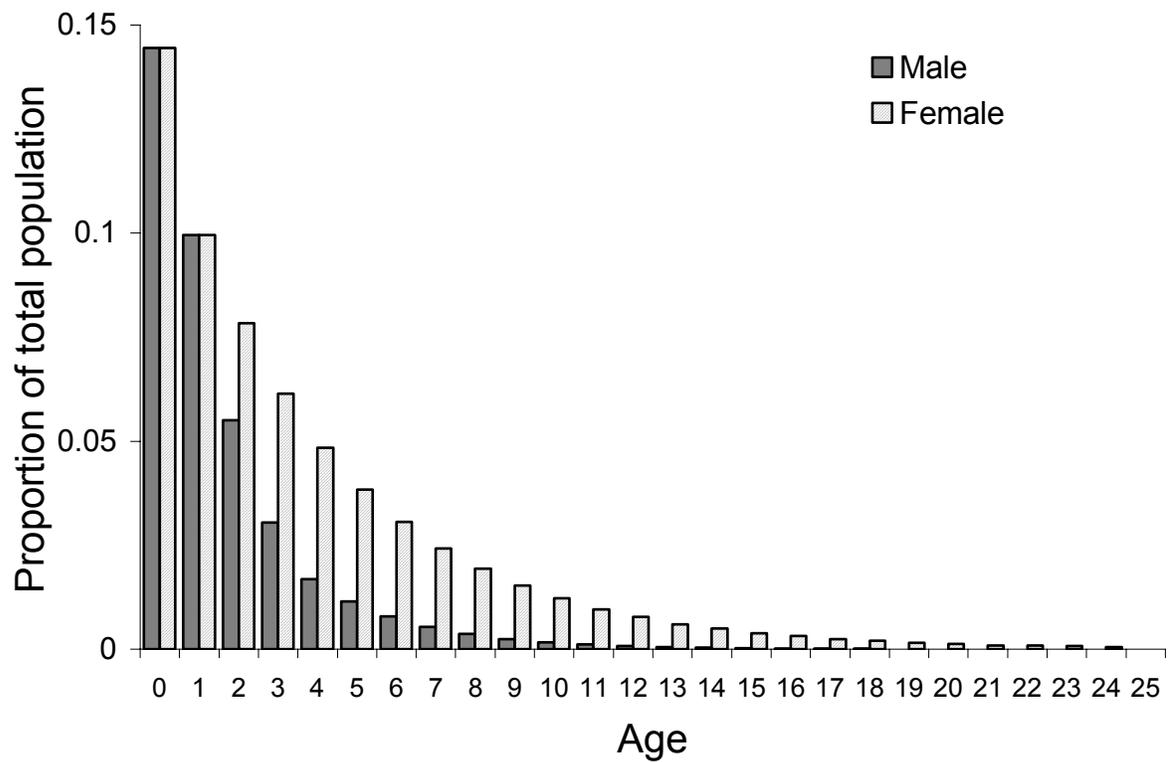
Figure 2.5. Expected stable age structure based on stable age distribution

derived population modeling in Program RSIKMAN using the input parameters

defined in Tables 2.1 and 2.2 and data gathered from 1994–2003 in the

Alleghany Mountains of western Virginia, USA.
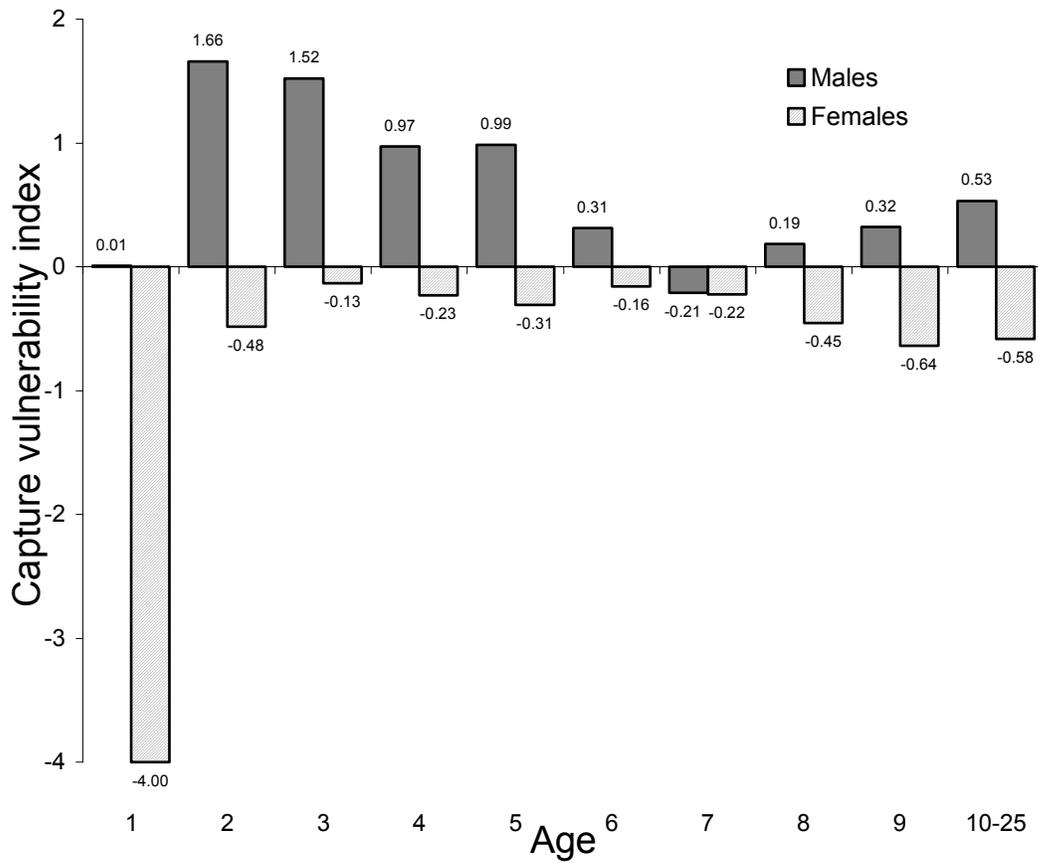
Figure 2.6. Capture vulnerability indices for male and female black bears 1–≥10 years old derived by comparing proportions based on summer trapping (Figure 2.2) with expected stable age structure derived from modeling in program RISKMAN (Figure 2.5) gathered from 1994–2003 in the Alleghany Mountains of western Virginia, USA.

Table 2.1. Model inputs for survival (from known fate analysis of natural survival

rates multiplied by hunting survival rates derived from direct returns of tags)

calculated from data gathered from 1994–2003 in the Alleghany Mountains of

western Virginia, USA and used in a Program RISKMAN model to estimate

stable age distribution.

| Age | Natural survival | |
|---|---|---|
| | Males | Females |
| Cubs (<1-year-old) | 0.87 | 0.87 |
| 1–3 years old | 0.63 | 0.89 |
| ≥4-years old | 0.77 | 0.93 |

Table 2.2.  Model inputs derived from reproductive data gathered from 1994–

2003 in the Alleghany Mountains of western Virginia, USA and used in a

Program RISKMAN model the expected stable age distribution.

| Female age | Probability of producing litter size | | | | $\bar{x}$ litter size | Proportion producing litters |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | |
| 3 | 0.57 | 0.36 | 0.07 | 0.00 | 1.50 | 0.20 |
| 4 | 0.15 | 0.70 | 0.15 | 0.00 | 2.00 | 0.80 |
| 5 | 0.07 | 0.37 | 0.53 | 0.03 | 2.52 | 0.80 |
| 6–24 | 0.09 | 0.28 | 0.50 | 0.13 | 2.67 | 0.80 |

Table 2.3.  Annual sex ratios of 420 neonatal black bear cubs observed from 1995–2003 in western Virginia, USA.   Goodness of fit $\chi^2$ was used to test 1M:1F cub sex ratios.

| Year | Males | Females | Ratio | $\chi^2$ | *P* |
|------|-------|---------|-------|----------|-----|
| 1995 | 12 | 10 | 1.20M:1F | 0.18 | 0.67 |
| 1996 | 32 | 16 | 2.00M:1F | 5.33 | 0.02 |
| 1997 | 23 | 23 | 1.00M:1F | 0.00 | 1.00 |
| 1998 | 23 | 31 | 0.74M:1F | 1.19 | 0.28 |
| 1999 | 25 | 39 | 0.64M:1F | 3.06 | 0.08 |
| 2000 | 18 | 11 | 1.64M:1F | 1.69 | 0.19 |
| 2001 | 32 | 31 | 1.03M:1F | 0.02 | 0.89 |
| 2002 | 17 | 20 | 0.85M:1F | 0.24 | 0.62 |
| 2003 | 32 | 25 | 1.28M:1F | 0.86 | 0.35 |
| Combined | 214 | 206 | 1.04M:1F | 0.15 | 0.70 |

Table 2.4.  Observed versus expected sex ratios of 170 1–4-cub litters of neonatal black bears observed in the den in the Alleghany Mountains of western Virginia, 1995–2003.

| Litter size | Sex ratio | Expected | | Observed | | $\chi^2$ | D.F. | P |
|---|---|---|---|---|---|---|---|---|
| | | # | % | # | % and 95% C.I. | | | |
| 1 | 1M:0F | 12.0000 | 50.00 | 11 | 45.83 (25.55–67.18) | 0.17 | 1 | 0.68 |
| 1 | 0M:1F | 12.0000 | 50.00 | 13 | 54.17 (32.82–74.45) | | | |
| 2 | 2M:0F | 14.7500 | 25.00 | 17 | 28.81 (17.76–42.08) | 0.51 | 2 | 0.78 |
| 2 | 1M:1F | 29.5000 | 50.00 | 28 | 47.46 (34.30–60.88) | | | |
| 2 | 0M:2F | 14.7500 | 25.00 | 14 | 23.73 (13.62–36.60) | | | |
| 3 | 3M:0F | 8.7500 | 12.50 | 11 | 15.71 (8.11–26.38) | 4.82 | 3 | 0.19 |
| 3 | 2M:1F | 26.2500 | 37.50 | 23 | 32.86 (22.09–45.12) | | | |
| 3 | 1M:2F | 26.2500 | 37.50 | 32 | 45.71 (33.74–58.06) | | | |
| 3 | 0M:3F | 8.7500 | 12.50 | 4 | 5.71 (1.58–13.99) | | | |
| 4 | 4M:0F | 1.0625 | 6.25 | 0 | 0.00 (0.00–16.16) | 11.67 | 4 | 0.02 |
| 4 | 3M:1F | 3.1875 | 18.75 | 3 | 17.65 (3.80–43.43) | | | |
| 4 | 2M:2F | 8.5000 | 50.00 | 5 | 29.41 (10.31–55.96) | | | |
| 4 | 1M:3F | 3.1875 | 18.75 | 5 | 29.41 (10.31–55.96) | | | |
| 4 | 0M:4F | 1.0625 | 6.25 | 4 | 23.53 (6.81–49.90) | | | |

Bridges

Table 2.5.  Annual age distributions based on 1,426 bear-summers (treating captures from each summer as independent from previous summers) for male and female black bears handled on 2 study areas in western Virginia, USA.

| | Female bear ages | | | | Male bear ages | | | |
|------|-----|-------|------|-------------|-----|-------|------|-------------|
| Year | $n$ | Range | Mode | $\bar{x}$ ± S.E. | $n$ | Range | Mode | $\bar{x}$ ± S.E. |
| 1994 | 35  | 1–11  | 2 | 3.7 ± 0.37 | 75  | 1–12  | 2 | 2.9 ± 0.23 |
| 1995 | 55  | 0–16  | 3 | 5.3 ± 0.53 | 105 | 0–12  | 1 | 2.7 ± 0.22 |
| 1996 | 59  | 0–17  | 2 | 4.9 ± 0.43 | 85  | 0–13  | 2 | 2.6 ± 0.22 |
| 1997 | 72  | 1–20  | 3 | 5.7 ± 0.46 | 86  | 0–14  | 2 | 2.8 ± 0.24 |
| 1998 | 62  | 0–12  | 4 | 4.4 ± 0.33 | 73  | 0–9   | 2 | 2.6 ± 0.16 |
| 1999 | 70  | 0–20  | 2 | 5.2 ± 0.48 | 97  | 0–16  | 2 | 2.6 ± 0.21 |
| 2000 | 71  | 1–21  | 3 | 5.1 ± 0.43 | 74  | 1–16  | 2 | 2.6 ± 0.28 |
| 2001 | 81  | 0–22  | 2 | 4.8 ± 0.40 | 120 | 0–12  | 2 | 2.5 ± 0.18 |
| 2002 | 101 | 0–25  | 3 | 5.2 ± 0.41 | 120 | 0–13  | 1 | 2.6 ± 0.18 |
| Total | 571 | 0–25 | 3 | 5.0 ± 0.15 | 835 | 0–16  | 2 | 2.6 ± 0.07 |

Table 2.6.  Results from analysis of variance (ANOVA) with factorial treatment

arrangement examining annual, study area, and sex-specific differences in ages

of 1,426 bear-summers (treating captures from each summer as independent

from previous summers), 1994–2003 on 2 study areas in Alleghany Mountains of

western Virginia, USA

| Source | Degrees of Freedom | Mean Square Error | F | *P* |
|---|---|---|---|---|
| Sex | 1 | 845.35 | 108.93 | <0.001 |
| Area | 1 | 166.54 | 21.46 | <0.001 |
| Year | 8 | 13.06 | 1.68 | 0.10 |
| Sex*area | 1 | 32.03 | 4.13 | 0.04 |
| Sex*year | 8 | 12.39 | 1.60 | 0.12 |
| Error | 1406 | 7.76 | | |

Table 2.7. Sex ratio of black bears trapped during late spring and summer, 1994–2002, in the Alleghany Mountains of western Virginia, USA. Goodness of fit $\chi^2$ was used to test 1M:1F sex ratios.

| Year | n | M:1.0F | $\chi^2$ | P |
|---|---|---|---|---|
| 1994 | 112 | 2.20 | 15.75 | <0.001 |
| 1995 | 162 | 1.95 | 16.69 | <0.001 |
| 1996 | 155 | 1.54 | 7.03 | 0.008 |
| 1997 | 154 | 1.11 | 0.42 | 0.517 |
| 1998 | 143 | 1.27 | 2.02 | 0.155 |
| 1999 | 171 | 1.41 | 4.92 | 0.027 |
| 2000 | 157 | 1.04 | 0.06 | 0.807 |
| 2001 | 209 | 1.46 | 7.28 | 0.007 |
| 2002 | 231 | 1.29 | 3.64 | 0.056 |
| Total | 1,494 | 1.41 | 42.51 | <0.001 |

Table 2.8. Comparison of sex-specific estimates of black bear density / km$^2$ and sex ratios from genetic capture-recapture data analyzed with a robust design model in Program MARK. Data were collected 1999–2001 on a 100-km$^2$ grid in Rockingham County Virginia, USA.

| Year | Genetic mark-recapture | | |
| --- | --- | --- | --- |
| | Bears/km$^2$ (95% C.I.) | | Sex ratio |
| | Male | Female | M:F |
| 1999 | 0.36 (0.28–0.45) | 0.55 (0.44–0.73) | 0.65M:1F |
| 2000 | 0.44 (0.35–0.47) | 0.55 (0.42–0.80) | 0.80M:1F |
| 2001 | 0.45 (0.36–0.49) | 0.59 (0.46–0.89) | 0.76M:1F |
| $\bar{x}$ (1999–2001) | 0.42 (0.33–0.47) | 0.56 (0.44–0.81) | 0.74M:1F |

# CHAPTER 3:  POPULATION SIZE AND DENSITY

**ABSTRACT**

Quantifying population size and subsequently estimating density for black bears (*Ursus americanus*) is challenging because their generally secretive nature and forested habitats preclude visual count methodologies.  We used 2 techniques, photography-based capture-recapture and genetic-based capture-recapture to estimate population size and associated density on 2 study areas in the Alleghany Mountains of western Virginia, USA.  Annual density estimates (N / 100km$^2$) derived from photography-based capture-recapture data analyzed with Bowden's estimator in Program NOREMARK ranged from 0.78 (95% C.I. = 0.51–1.21) bears / km$^2$ in 1999 to 1.32 (95% C.I. = 1.08–1.62) bears / km$^2$ in 2002 on our northern study area.  On our southern study area (approximately 160 km to the southwest of our northern study area) density was estimated at 0.78 (95% C.I. = 0.62–1.00) bears / km$^2$ in 2002.  Estimated population growth rate (λ) derived from the photography-based capture-recapture estimates was 1.05 (95% C.I. = 0.88–1.24) from 1998–2002.  Using genetic capture-recapture data analyzed with a robust design model in Program MARK, sex-specific density estimates for males ranged from 0.36 (95% C.I. = 0.28–0.45) in 1999 to 0.45 (95% C.I. = 0.36–0.49) in 2001.  For females, density estimates ranged from 0.55 in 1999 and 2000 (95% C.I. ≤ 0.28–0.47) to 0.59  (95% C.I. = 0.46–0.89) in 2001.  Combining sex-specific estimates, density estimates ranged from 0.91 (95% C.I. = 0.72–1.18) bears / km$^2$ in 1999 to 1.04 (95% C.I. = 0.64–1.37) in 2001.

Population growth rates from 1999–2001 were positive for males (λ = 1.12, 95%

C.I. = 1.01–1.24), females (λ = 1.04, 95% C.I. = 1.00–1.08) and both sexes

combined (λ = 1.07, 95% C.I. = 1.05–1.09).  These finding suggest a relatively (to

previously published findings) dense population of black bears that seems to be

growing through time.  Taking only the first 3 years estimates or the last 3 years

estimates from our photography-based capture-recapture our data gave very

different λ values than the full 5 years.  This finding underscores the importance

of long-term data to draw valid inference from bear population dynamics studies.

Additionally, there I found possible (though not definitive) evidence of density

dependence, suggesting the study population may be approaching carrying

capacity.


**INTRODUCTION**

Populations of American black bears (*Ursus americanus*), like much of

North America's wildlife, experienced large-scale decline or extirpation in the

early 1900's.  In recent years, populations of black bears generally have

rebounded and in some places been repatriated (Smith and Clark 1994, Clark et

al. 2002).  Black bears are now most abundant of the world's 8 bear species and

the most frequently encountered large carnivore in North America (Servheen

1990).  However, because they dwell in forested habitats and do not lend

themselves to visual counts, examining population trends through population and

density estimation may require longer time frames (LeCount 1982, Schooley

1994, Pelton and van Manen 1996) than funding limitations often allow.

Until the 1990's, the predominant method of population and density estimation for bears found in the published literature was based on physical capture-recapture analysis (Garshelis 1994). Density estimates for black bears in the published literature range from 0.08 bears / km$^2$ in a recently-repatriated population in Arkansas (Clark and Smith 1994) to 1.3 bears / km$^2$ on an island off the coast of Washington (Lindzey et al. 1986). In more typical (not recently repatriated or island-bound) populations in eastern North America, reported densities included 0.2 bears / km$^2$ in Maine (McLaughlin et al. 1994, McLaughlin 1998), 0.29 bears / km$^2$ in Tennessee (McLean and Pelton 1994), 0.59 bears / km$^2$ in the Dismal Swamp in coastal Virginia (Hellgren 1988, Hellgren and Vaughan 1989), and 0.86 bears / km$^2$ in Shenandoah National Park in western Virginia (Carney 1985). In the 1990's, researchers began using photography-based capture-recapture (Mace et al. 1994, Bowman et al. 1996, Martorello et al. 2001) and genetics-based capture-recapture (Woods et al. 1999, Mowat and Strobeck 2000, Boulanger et al. 2002) as alternative methodologies to estimate population sizes and quantify bear densities.

Prior to this study, black bear research in Virginia focused on unhunted populations in the Shenandoah National Park in western Virginia (Carney 1985, Kasbohm et al. 1996) and the Great Dismal Swamp in coastal Virginia (Hellgren and Vaughan 1989). In the Alleghany Mountains that run along the western border of the state, bear hunting is a long-standing tradition. Over the past 3 decades, harvest levels rose from roughly 200 / year to nearly 1,000 / year (Martin and Steffen 2000). Because relationships between harvest, hunters, and

population density are confounded when catch / unit effort is unknown (Burton et al. 1994) harvest data may not be an effective means of monitoring bear population status (Noyce and Garshelis 1997), and may not be reliable to detect early stages of declines (Harris and Metzgar 1987).  Thus, management decisions based solely on harvest data and without knowledge of underlying parameters and their influences may not be biologically sound (Lubow et al. 1996).

In response to the need to better understand and manage this apparently growing population, in 1994 the Virginia Polytechnic Institute and State University and the Virginia Department of Game and Inland Fisheries (VDGIF; among numerous other collaborators) initiated the Cooperative Alleghany Bear Study (CABS) to intensively examine the long-term, broad-scale dynamics of Virginia's hunted black bear population.  Our objective in this portion of our research was to estimate density and population growth rate of the black bear population in western Virginia's Alleghany Mountains and compare results from photographic-based and genetic-based capture-based methodologies.

**STUDY AREAS**

Our research was conducted on 2 study areas in the Alleghany Mountains of western Virginia, USA.  The centers of the 2 study areas were approximately 160 km apart; both were located largely on the George Washington-Jefferson National Forests.  The northern study area was centered near Reddish Knob at 38° 28' N, 79° 15' W.  It was approximately 840 km$^2$ primarily in Augusta and

Rockingham Counties.  The southern study area was 1,544 km$^2$ and was centered near Mountain Lake at 37° 22' N, 80° 31' W.  It was composed primarily of Craig, Giles, and Montgomery Counties.  Elevations on these 2 study areas ranged from 480–1,360 m (Kozak 1970) and common tree species included: eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*)*,* beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipfera*), eastern white pine (*P. strobus*), mountain laurel (*Kalmia latifolia*) and scrub oak (*Q. ilicifolia*; Rawinski et al. 1994).  At Mountain Lake, the center of the southern study area, high temperatures ranged from an average high of 24°C in July to an average low of -9°C in the January with total precipitation averaging 125 cm, including 134 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va5828). The closest weather station to our northern study area was at Dale Enterprises in the lowlands of Rockingham County.  Because it was in the lowlands, weather averages were likely warmer and drier than conditions in the adjacent mountains where our research was conducted.  At Dale Enterprises (38°45' N, 78°93' W), temperatures ranged from an average high of 30°C in July to an average low of -5°C in January with total precipitation averaging 90 cm, including 63 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va2208).

Hunting season lengths varied slightly (≤ 7 days) among years.  Generally, September was marked by bear-hound training season during which bears could be pursued and treed with hounds, but not harvested.  The second week of

October through the first week of November was archery-hunting season, during which bears could be harvested using archery equipment. Gun season, during which bears could be killed with firearms, but not with the aid of dogs, was the last week of November. Hound-hunting season, during which bears could be killed using firearms and with the aid of dogs, consisted of the first few days of December through the first Saturday in January. One bear tag / year / hunter was sold with the combined deer, bear, and turkey license. To be legally harvested bears had to weigh ≥45.5 kg live weight or ≥34.1 kg with all internal organs removed. Adult females with cubs could not be legally harvested. Law required that all harvested bears be checked at registered check stations. Checking a bear involved recording any tags, tattoos, and/or transmitters, determining sex of the individual, and removing a premolar for subsequent age determination.

## METHODS

### General

We captured bears with Aldrich spring-loaded foot snares and culvert traps (Johnson and Pelton 1980) from late May through late August 1994–2002. We initiated trapping on our northern study area in 1994 and on our southern study area in 1995. We sedated captured bears with a mixture of ketamine hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45.5 kg; White et al. 1996) administered via dart pistol, blowpipe, or jab stick. After bears were sedated, we determined their sex, weighed them, recorded morphometric

measurements, and examined females for signs of estrus or lactation. To determine age, we removed a premolar (Willey 1974), which was sent to Matson's Laboratory (Milltown, Montana, USA) for cementum annuli analysis. We also tattooed bears' upper lips, and attached individually numbered, plastic, perma-flex, stud-style eartags (National Band and Tag, Newport, Kentucky, USA) to all bears ≥6 months old. We attached motion-sensitive radio transmitters to bears selected in an attempt to keep our sex ratio of transmittered animals at approximately 1M:3F. Bears ≥1 year old received collars (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA, Wildlife Materials International, Murphysboro, Illinois, USA) that were equipped with breakaway cotton spacers (Hellgren et al. 1988) or eartag transmitters (Servheen et al. 1981) from ATS. We administered a tetracycline antibiotic to prevent infection and serve as a permanent biomarker in teeth and bones (Johnson 1964, Garshelis and Visser 1997). Finally, we administered yohimbine hydrochloride (5mg/ml; 2 ml/45.5 kg) to reverse the xylazine hydrochloride. Each week, we monitored and attempted to locate bears wearing transmitters.

Biologists from VDGIF conducted surveys in late August to early September to quantify annual hard mast production (Sharp 1958, Coggin and Peery 1973). Mast surveys involved examination of the same trees annually and quantifying the mean number of acorns / 10 limbs / tree (Fearer et al. 2002). I used mast survey data collected by VDGIF (D. Martin, personal communication)

for the 3 mast survey regions overlapping our study area to examine autumn hard mast availability.

In the late fall and winter, we used radio telemetry to locate dens of female bears wearing transmitters.  We returned to and entered (Godfrey et al. 2000) these dens in January–April to gather reproductive data, change transmitters on adults, attach transmitters to cubs (Echols 2000, Vashon et al. 2003) and yearlings, and deploy remote cameras (Bridges et al. 2004*a*).  The Virginia Polytechnic Institute and State University Animal Care and Use Committee (98-069-F&W) approved all animal handling protocols.

**Photographic capture-recapture**

Our camera surveys were conducted on 2 100-km$^2$ grids.  We outlined 1 grid on our northern study area in Rockingham County and 1 grid on our southern study area in Giles County, Virginia, USA.  Fifty camera sites were placed near the center of alternating 1-km$^2$ cells on our 100-km$^2$ grids.  On our northern study area, we conducted 2 (summer and autumn) camera surveys each year from 1999–2001 and only summer surveys in 1998 and 2002.  On our southern study area, we conducted a summer survey in 2002.  Each individual survey lasted approximately 2 weeks.  Summer surveys were conducted between July 29 and August 31.  Autumn surveys were conducted between October 1 and October 27.  From 1998–2002, we used fishing-line-triggered single-expose systems (Martorello et al. 2001) and CamTrakker$^®$ (CamTrak South, Inc., Watkinsville, Ga.) cameras with infrared censors to trigger the camera, multiple picture capability, adjustable delays between photographs, and

photographic stamps identifying the date and time each picture was taken.  In 2001 and 2002, we replaced the single-exposure fishing-line-triggered systems with DeerCam® (Non Typical, Inc., Park Falls, Wi.) infrared-triggered, multi-exposure camera systems similar to the CamTrakkers.

For multi-exposure systems, we set a 10-minute delay between photographs to allow multiple bears to be photographed in short periods of time while minimizing the incidence of multiple shots of the same bear during 1 visitation.  We used 24- or 36- exposure 400ASA film in all cameras.  Baits were used to attract bears to camera sites.  We used fencing staples to nail baits 2–3 m off the ground on large trees.  We attached cameras to smaller trees with wire (CamTrakker) or drawstrings (DeerCam) and locked them in place with security cables.  We positioned cameras parallel to and facing the bait 1–3 m off the ground (depending on slope).  We placed baits 2–4 m from the cameras and aligned them from north to south (or vice versa) to avoid morning and evening glare.  We checked cameras and rebaited every 2–4 days.  Baits consisted of donuts placed in red mylar produce bags and soaked in molasses.  We poured extra molasses on bait trees around the bait bag to act as a scent lure and encourage additional investigation and photograph opportunities after donuts were consumed.

We captured bears in the northern 100-km$^2$ camera survey area during late May– early August from 1998–2002 and on the southern study area during late May– early August in 2002.  We fitted captured bears with color-coded

individual-specific streamers attached to colored eartags (Martorello et al. 2001).

Streamers were replaced on bears recaptured in subsequent summers.

I estimated density using the Bowden's estimator (Bowden and Kufeld 1995) in program NOREMARK (White 1996).  Bowden's estimator is a modification of the Minta-Mangel model (Minta and Mangel 1989) using bootstrapping and log-transformation to yield an unbiased estimator and confidence interval (White 1996).  Assumptions of Bowdens' estimator were 1) random sampling without replacement, 2) resights are recorded without error, 3) sighting effort allows for "many" individuals to be resighted ≥1 times, 4) number of unmarked animal sightings is recorded without error, 5) marking status does not influence sight/resightability and 6) population closure.

I considered a maximum of 1 observation / bear / site / 24-hour period to be independent and usable for analyses.  Bears appearing unmarked or those marked in previous years, but not handled and marked with streamers immediately prior to the annual survey(s) were considered unmarked.  Bears handled immediately prior to the camera survey, but who were not identifiable in photographs due to streamer loss or obstruction were entered as marked, but unidentifiable.  Two independent observers evaluated each photograph and in the event of disagreement, a third, impartial observer broke the tie.  Estimates represent maximum density because we did not have sufficient numbers of telemetry-based locations to make adjustments for violations of geographic closure during trapping periods (White and Shenk 2001).   I calculated λ and

associated 95% confidence intervals using exponential regression (Caughley 1977, Sauer 1990).

**Genetic capture-recapture**

We constructed 50 barbed-wire enclosure hair traps (Woods et al. 1999) on alternating 1-km$^2$ grid cells on the same 100-km$^2$ grid used for our camera study on the northern study area. These hair traps consisted of approximately 25–30 m of 4-prong barbed wire arranged in 50-cm-high polygons encircling suspended baits. The baits consisted of pastries and molasses centered in the polygon and suspended >3 m high (out of bears' reach) on a rope tied to adjacent trees. Sites were sketched and mapped with barbs numbered sequentially starting with the northern-most tree. For human safety purposes, reflective tape and colored flagging were placed on the wire and signs were placed on the trees that comprised each trap.

We visited each hair-trapping site every 14 days over 2 months (4 intervals / summer) from June–July, 1999–2001. Using a white note card or piece of paper as a backdrop, we examined each barb for entangled hairs. We used tweezers to remove bear hair and placed it in coin envelope labeled with the trap number, barb number, date, and approximate number of hairs in the sample. We then sterilized the tweezers with a propane torch and continued examining barbs. We used rubber gloves during all hair collection procedures. After all bear hairs were collected, we used the propane torch to sterilize each barb to remove any remaining hair or other genetic material in preparation for the next hair-trapping interval. Additionally, we refreshed baits, replaced safety

markings, and repaired hair traps as necessary.  We froze all hair samples immediately following collection.

I randomly selected 1 sample having ≥ 6 hairs with roots / hair trap / 2-week interval.  I sent these samples to Wildlife Genetics International (Nelson, British Columbia, Canada) where D. Paetkau and J. Wastl performed genetic analyses.  They extracted DNA from hair roots using QIAGEN's DNeasy$^®$ (Valencia, California, USA) and standard techniques following manufacturer instructions.  Ten microsatellite markers were tested for variability as potential individual identifiers.  Markers were selected based on level of heterozygosity, with the assumption that an expected heterozygosity of ≥0.73 was necessary for sample sizes of >100 individuals (Paetkau 2003).  Additionally, gender identification based on size polymorphism in the amelogenin gene was conducted for each identified individual (Ennis and Gallagher 1994).

I analyzed our genetic data in Program MARK (White and Burnham 1999) using Pollock's robust design (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997) extended to include Huggins' (Huggins 1989, Huggins 1991) heterogeneity closed capture estimator for population size, which allows for covariates.  The robust design model is a combination of open Jolly-Seber (Jolly 1965, Seber 1965) and closed capture models.  It divides sampling into primary intervals where the population is open (births, deaths, immigration, and emigration are allowed) and shorter secondary intervals where the population is assumed to be closed (no births, deaths, immigration, or emigration) (Kendall et al. 1995, Kendall et al. 1997, Kendall 1999).  There are 4

primary assumptions: 1) Population closure within secondary sampling intervals, 2) population can be open between primary intervals, 3) temporary emigration if occurring within primary intervals is assumed to be random, Markovian, or based on temporary trap response and 4) survival rate between primary periods is assumed to be the same for all individuals, regardless of marking status or availability to capture.

I treated each 2-month sampling season as a primary interval and each of the 4 2-week sampling intervals within each primary interval as the secondary intervals. I explored models pooling sexes as well as sex-specific models that compared constant, time-specific, and/or sex-specific (Table 3.1) rates of survival using *a priori* models that included survival (S), emigration ($\gamma''$), immigration ($\gamma'$), initial capture probability ($p_i$) / session and recapture probabilities ($c_i$ ; p in MARK) / session (Tables 3.2 and 3.3). Models were selected using an information-theoretic approach (Burnham and Anderson 2002) based on Akaike's Information Criterion (Akaike 1973; discussed in more depth in Chapter 4) bias adjusted to $AIC_c$ for small samples size (Sugiura 1978). I calculated population growth rate ($\lambda$) using exponential regression (Caughley 1977, Sauer 1990).

## RESULTS

### Photographic capture-recapture

We marked 42–78 individual bears / year during late May– early August, 1998–2002 on our northwestern study area and 42 bears on our southwestern study area in 2002 (Table 3.4). We collected 103–403 photographs of bears /

year during the August resight period, 1998–2002.  From these photographs 14–59 marked individuals were identified each August.  October surveys conducted 1999–2001 resulted in 114–245 photographs of bears, from which we identified 15–22 individuals.  As we improved our camera alignment techniques, the percentage of photographs that were unidentifiable as either marked or unmarked declined from 29% and 37% in 1998 and 1999 respectively, to 10% and 4% in 2001 and 2002, respectively.

Using Bowden's estimator (Bowden and Kufeld 1995) in NOREMARK (White 1996), I estimated density on our northern study site ranged from 0.78 (95% 0.51–1.21) bears / km$^2$ in 1999 to 1.32 (95% C.I. = 1.08–1.62) bears / km$^2$ in 2002 to (Figure 3.1).  I estimated density in the southwest at 0.78 (95% C.I. = 0.62–1.00) bears / km$^2$ in 2002.  October surveys in the northern area were similar, though characterized by larger confidence intervals (Table 3.4).  Estimated population growth rate (λ) derived from the camera survey was 1.05 (95% C.I. = 0.88–1.24, $r^2$ = 0.09, $P$ = 0.63) from 1998–2002 (Table 3.5).

**Genetic capture-recapture**

We collected 3,013 hair samples, from which we randomly selected 1 sample / hair trap / sampling interval.  Geneticists at Wildlife Genetics International analyzed these 432 samples and selected 6 microsatellite markers.  Mean expected heterozygosity was 0.80 and thus surpassed the recommended threshold of 0.73 (Paetkau 2003).  Additionally, because expected and observed levels of heterozygosity corresponded closely, frequency of allelic dropout or null alleles was likely low.  Analyses yielded 396 (91%) individually identifiable

samples, 7 (2%) mixed (from multiple individuals characterized by >2 alleles / marker) samples, and 29 (7%) failed (failed to produce reliable data from ≥3 samples) samples.  The 396 usable samples were then genotyped and error checked (Paetkau 2003).  Only 7 samples were found to have errors (3 were human errors and 4 were amplification errors) in genotyping during the error-checking phase yielding a per-locus detection error rate of 7/2,592 (6 markers × 432 samples) or 0.3%.  We found 136 individual genotypes, likely representing 136 individual bears.  Examination of the probability of 0MM-pairs (identical multilocus genotypes) revealed 6 2MM-pairs and 3 1MM-pairs and thus a relatively high proportion of closely related individuals.  Based on a 10% error rate for 1MM-pairs and 1% error rate for 2MM-pairs (Paetkau 2003) there is a ≤ 9% chance that the 136 genotypes documented actually came from 137 individuals.

For analyses pooling sexes (to be comparable with the pooled sex structure of the photography-based estimates), the model most heavily supported by the data had time-dependent initial capture and recapture probabilities (Table 3.2).  This model carried a model weight ($\omega_i$) of 0.72 and differed from the second most highly supported model by 1.94.  I used model averaging (which takes an average of all models based on their respective model weights) of derived parameters to estimate $N_t$.  Associated density estimates (N/100 km$^2$) ranged from 0.91 (95% C.I. = 0.57–1.25) bears / km$^2$ in 1999 to 1.08 (95% C.I. = 0.69–1.47) bears / km$^2$ in 2001 (Table 3.5).  Population growth rate ($\lambda$) from

1999–2001 was positive and estimated at 1.09 (95% C.I. = 1.07–1.11, $r^2$ = 0.98, $P$ = 0.08; Table 3.5).

The most highly selected model for estimating sex-specific population size had sex-dependent survival and emigration parameters and time-dependent immigration, initial capture, and recapture probabilities (Table 3.3). This model carried a weight ($\omega_i$) of 0.99 and differed from the second most supported model by 10.71 and thus no model averaging was necessary. Sex was a primary component in the highest ranked models, indicating sex-specific differences contributed substantially to these models. Sex-specific density estimates (N/100km$^2$) for males ranged from 0.36 (95% C.I. = 0.28–0.45) in 1999 to 0.45 (95% C.I. = 0.36–0.49) in 2001 (Table 3.6). For females, density estimates ranged from 0.55 in 1999 and 2000 (95% C.I. ≤ 0.28–0.47) to 0.59 (95% C.I. = 0.46–0.89) in 2001 (Table 3.6). Combining sex-specific estimates, confidence intervals were narrower than for analyses that did not consider sex. These combined density estimates climbed from 0.91 (95% C.I. = 0.72–1.18) bears / km$^2$ in 1999 to 1.04 (95% C.I. = 0.64–1.37) in 2001. Population growth rates from 1999–2001 were positive for males ($\lambda$ = 1.12, 95% C.I. = 1.01–1.24, $r^2$ = 0.82, $P$ = 0.28), females ($\lambda$ = 1.04, 95% C.I. = 1.00–1.08, $r^2$ = 0.75, $P$ = 0.33) and both sexes combined ($\lambda$ = 1.07, 95% C.I. = 1.05–1.09, $r^2$ = 0.98, $P$ = 0.10; Tables 3.5 and 3.6).

## DISCUSSION AND MANAGEMENT IMPLICATIONS

Our data met most of the assumptions of Bowden's estimator (Bowden and Kufeld 1995) for the photographic capture-recapture estimates. The first assumption of random sampling without replacement were likely the most heavily violated as we have determined that our trapping and marking data were biased towards young males and were not equally representative of the entire population (Chapter 2). Thus, the estimates may be overly reflective of the subadult male population. This overrepresentation may have exaggerated the dip in density observed in 1999 and 2000 because a small cohort produced in the winter of 1998 (Chapter 1) was moving through the population in 1999 and 2000. The second assumption, that resights are recorded without error, likely was not severely violated. My protocol was to evaluate each photograph with 2 independent observers. In cases where they disagreed on the identification of an individual, we used a third, impartial observer to break the tie and thus, error should have been minimal. The third assumption, that sighting effort allows for "many" individuals to be resighted ≥1 times, was likely met as our 50 camera sites presented many opportunities for photographic resight and "many" pictures of marked individuals were provided (Table 3.4). Regarding the fourth assumption, that number of unmarked animal sightings is recorded without error, we saw very little evidence of streamer loss within sampling intervals and thus unmarked individuals were likely documented with relatively little error. The fifth assumption that marking status does not influence sight/resightability was likely

met because bear are large and relatively easy to observe in photographs and thus determining if a bear was present in a picture was dependent on marking or streamers.  Also, because a different and non-invasive recapture technique was used (photography), bears that might have become trap shy after their initial capture and marking should not have been underrepresented in our recapture sample.  The final assumption of population closure is difficult to evaluate due to small numbers of radio telemetry locations, especially on subadult males.  Because this precluded adjustments (White and Shenk 2001) for violations of this assumption, these estimates should be considered maximum densities.  However, because our marking period and resight period occurred in relatively short succession, it is unlikely this assumption was severely violated for our summer samples.  The autumn surveys likely had more severe violation of the closure assumption and accordingly yielded inflated estimates of population size with larger confidence intervals (Table 3.4).  In general, the lack of closure in the autumn surveys made them less reliable as population estimators and we gained little by including them in our study.

There are 4 primary assumptions of the robust design model (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1995, Kendall et al. 1997) used to analyze genetic capture-recapture data.  The first assumption, that population was closed within secondary sampling intervals, was largely met.  Births did not occur during summer (Chapter 1) and survival rates in summer were nearly 1.0 (Chapter 4).  Immigration and emigration within secondary intervals likely occurred, but should have been limited during the 8-week intervals.  Because the

second assumption allows the population to be open during primary intervals, the births, deaths, immigration, and emigration that certainly occurred between intervals is allowable.  However, the third assumption, that temporary emigration if occurring within primary intervals was assumed to be random, Markovian, or based on temporary trap response, was likely violated because young males likely did not have equal emigration probabilities to other sex and age classes (Lee 2003) and there is no reason to believe visiting a hair trap induced subsequent temporary emigration.  This might have made fewer of these individuals available for recapture and thus could have biased estimates high for males.  However, by controlling for sex-specific immigration, emigration, and recapture probabilities in our models, this bias should not have substantially affected results.  Finally, the fourth assumption that survival rate between primary periods is assumed to be the same for all individuals was likely violated because young males had substantially lower annual survival rates than annual survival rates calculated for other age and sex classes (Chapter 4).  However, because sex-specific survival was incorporated into the models, this should not have substantially biased estimates.

Because we marked a substantial portion of the population for our photographic capture-recapture method (>80% of the photographs in 2001 and 2002 were of marked bears) and conducted our camera survey immediately following marking (reducing the effects of immigration and emigration) the estimates should generally be valid.  However, because we trapped a disproportionate number of young male bears, our estimates may have been

unduly representative of this sex and age class.  Additionally, these estimates

should be corrected for immigration and emigration by using telemetry data from

marked individuals (White and Shenk 2001).  However, our limited amount of

telemetry data did not permit this correction and therefore, these estimates

represent a maximum density.

The genetic capture-recapture data analyzed in a robust design model

took into account immigration and emigration and thus the derived estimates may

be more accurate.  Also, the sex ratio of our genetic samples was not as male-

skewed as the sex ratios of our trapping sample and thus was likely more

representative of true population structure (Chapter 2).  Additionally, this method

allowed for the sex-specific population estimates we could not calculate using

photographic techniques.  Finally, because genetic techniques did not require

handling bears, risk to bears and cost and time associated with trapping were

reduced.  For these reasons, I recommend that researchers use genetic capture-

recapture techniques only 1 population and density estimation method is

employed.

I attempted to use physical capture-recapture techniques to estimate

population size and associated density.  Two problems precluded use of this

technique.  First, we did not have sufficient numbers of recaptures for models in

Program MARK to estimate population size.  This was true even for our heavily-

trapped 100-km$^2$ study grid.  Additionally, we did not consistently sample the

same area in the same year (for closed estimators) or between years (for open

estimators) and therefore recapture probabilities were not equal for all

individuals.  If recapture probabilities were biased due to inconsistent trapping effort, capture-recapture methods would result in biased estimates (B. Kendall, USGS, personal communication).  Therefore, I was not able to use our physical capture-recapture data for population estimation.

Compared with other published research from across the black bear's range, my maximum density estimates indicate bears on our study area existed at 1 of the highest densities ever documented.  Garshelis (1994) found that most employed physical capture-recapture estimators, and that the only density estimates higher than ours were from Long Island, Washington, where density was estimated at 1.30 bears / km$^2$ (Lindzey et al. 1986).  The second most dense population documented in his review was from Shenandoah National Park where density was estimated at 0.86 bears / km$^2$ (Carney 1985).  In comparison with more recent studies employing similar techniques (photographic or genetic capture-recapture estimates), our estimates were higher than any found in the literature.  For example, genetic capture-recapture in Louisiana resulted in an overall density estimate of 0.36 bears / km$^2$ (Boersen et al. 2003).  In Florida, genetic capture-recapture densities on 2 study areas were 0.12 and 0.14 bears / km$^2$ (Dobey et al. 2005).  In Alaska, density estimates using photographic capture-recapture in conjunction with radio telemetry yielded density estimates ranging from 0.09–0.29 black bears / km$^2$ (Miller et al. 1997).  In Wyoming, photographic capture-recapture yielded an estimate of 0.03 bears / km$^2$ (Grogan and Lindzey 1999).  In Arkansas, photographic capture-recapture density estimates ranged from 0.34–0.74 black bears / km$^2$ (Bowman et al. 1996).

However, Bowman et al. (1996) did not actually mark bears with an individual-specific tagging system and instead claimed to be able to identify individuals based on natural morphometric characteristics.  Because black bears lack clearly defining coat patterns and thus cannot be definitively identified without an artificial marking system (Bridges et al. 2004b) I question the validity of their technique and accordingly the accuracy of their density estimates.

These results illustrate the importance of long-term data in attempting to examine density and population growth.  Conclusions regarding population growth would have differed dramatically if only the first 3 years or only the last 3 years of photographic capture-recapture population estimation had been conducted (Figure 3.2).   These results support the conclusion that in black bear research, valid inference may require long-term research (Schooley 1994, Pelton and van Manen 1996).

No research has definitively documented density dependence as a population regulation mechanism for black bears (Garshelis 1994).  It has been hypothesized that as density increases towards K, cub survival rates would drop due to resource limitation and intraspecific aggression from adult males (Garshelis 1994).  Consistent cub survival rates found on our 2 study areas and through time (Chapter 4) have implications for density dependence.  Though we only had paired density estimates for 1 year (2002), the density estimate for our southern study area was lower than for our northern study area.  However, with the caveat that carry capacity might be different on our 2 study areas, estimated cub survival rates were not appreciably different (Chapter 4).   Likewise, though

it appears density was generally increasing through time on our northern study area, cub survival rates remained relatively high and consistent (Chapter 4).

Another possible mechanism of density dependence is intraspecific predation (Garshelis 1994). This mortality source was documented only twice in our research, and both instances occurred immediately following den work, making these observations suspect.

The annual harvest of bears that occurred on our study areas would likely dampening any density-dependent effects. Additionally, likely due to relatively high mortality rates in young males (Chapter 4), our population contained relatively few of the adult males that other studies suggested might be associated with density-dependent intraspecific killings (Kemp 1972, Kemp 1976, Young and Ruff 1982). Thus, this mechanism may have been effectively removed from our population.

Despite these limitations, measurements of parameters from our population suggest possible effects of density dependence. The apparent reproductive failure documented following the mast failure (Chapter 1) might suggest density dependence if intraspecific competition for food limited nutritional acquisition. Thus, a resource-limitation, density-dependent response may have occurred. However, we cannot definitely evaluate the role of intra- versus interspecific competition for food or whether mast failure acted as a catastrophic event and affected the population independently of density. In conclusion, results suggest density-dependence and associated resource limitation may play a role in this high-density population; however, this relationship is not conclusive.

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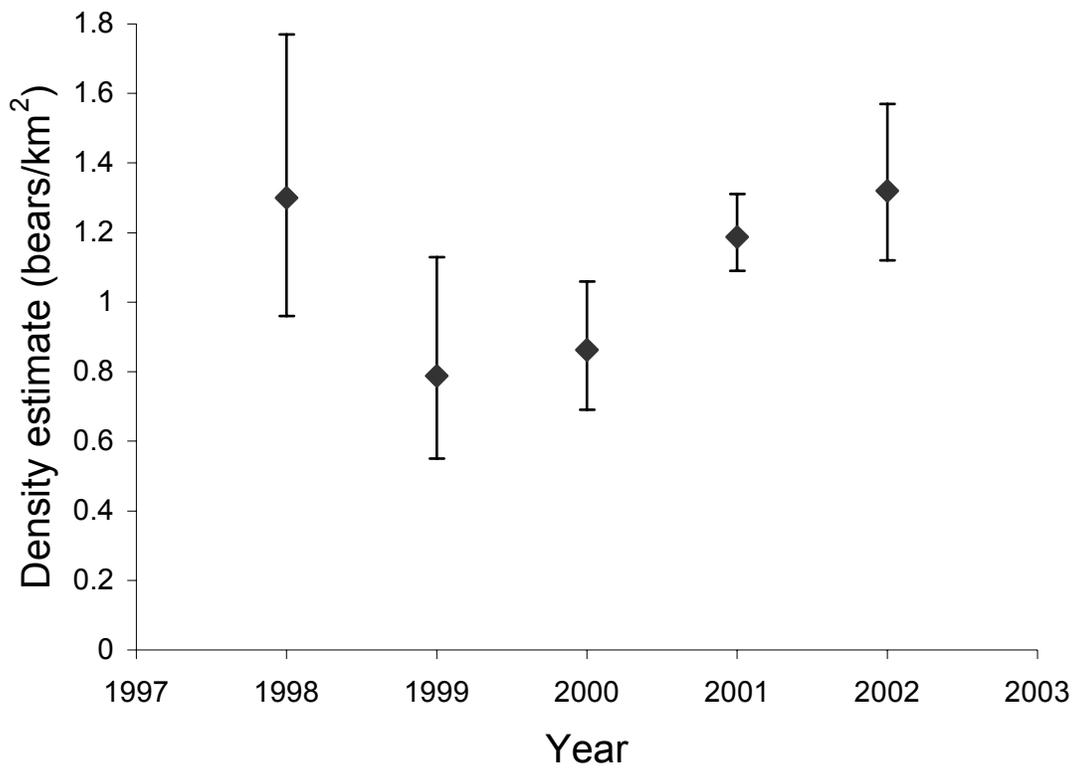
Figure 3.1. Estimated black bear density based on capture and subsequent photographic resight calculated using Bowden's estimator. Data were collected on a 100-km$^2$ grid in Rockingham County, Virginia, USA for summers, 1998–2002.
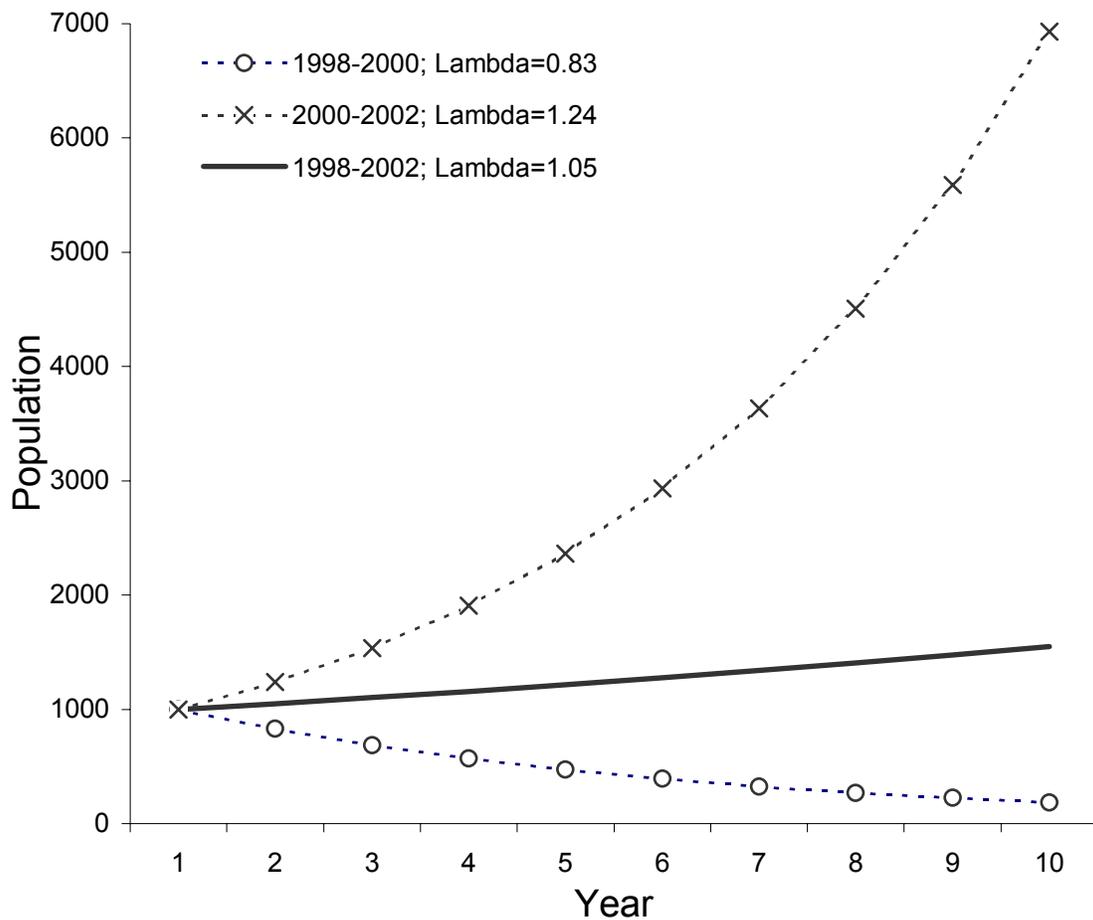
Figure 3.2. Differential population trajectories over 10 years based on a hypothetical starting population of 1000 bears and lambdas derived from exponential regression after taking 2 3-year blocks (the first 3 years and the last 3 years) and comparing them with the full 5-year data set of population estimates. Population estimates were obtained using Bowden's estimator of photography-based capture-recapture data gathered from 1998-2002 in Rockingham County in the Alleghany Mountains of western Virginia, USA.

Table 3.1. Variables used in the development of robust design models (Tables 3.2 and 3.3) used to estimate population size and associated density from genetic capture-recapture data gathered from American black bears on a 100-km$^2$ grid from 1999–2001, in Rockingham County, Virginia, USA.

| Variable | Description |
|----------|-------------|
| . | Neither time nor age variation were included |
| Time' | Variation based on primary time steps (between years) |
| Time'' | Variation based on secondary time steps (between sampling occasions within years) |
| Sex | Variation due to sex (male or female) was included |

Table 3.2. Model selection from robust design analysis genetic capture-recapture data pooled by sex and gathered during summers 1999–2001 from black bears in Rockingham County, Virginia, USA. Parameters include: actual survival rate (S), emigration (γ"), immigration (γ'), initial capture probability ($p_i$) and recapture probability (p); variables are described in Table 3.1.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(.) γ"(.) γ'(.) $p_i$ (Time") p (Time")} | 0.00 | 0.72 | 1.00 | 11 |
| {S(Time') γ"(.) γ'(.) $p_i$ (Time") p (Time")} | 1.94 | 0.27 | 0.38 | 12 |
| {S(.) γ"(.) γ'(.) $p_i$ (.) p (.)} | 9.52 | 0.01 | 0.09 | 5 |
| {S(Time') γ"(Time') γ'(Time') $p_i$ (.) p (.)} | 11.60 | 0.00 | 0.00 | 6 |
| {S(.) γ"(Time') γ'(Time') $p_i$ (.) p (.)} | 11.60 | 0.00 | 0.00 | 6 |

Table 3.3.  Model selection from robust design analysis of sex-specific genetic capture-recapture data gathered during summers 1999–2001 from black bears in Rockingham County, Virginia, USA.  Parameters include:  actual survival rate (S), emigration (γ''), immigration (γ'), initial capture probability ($p_i$) and recapture probability (p); variables are described in Table 3.1.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Sex) γ''(Sex) γ'(Time') pi (Time'') p (Time'')} | 0.0 | 0.99 | 1.00 | 12 |
| {S(Sex) γ''(Sex) γ'(Sex) pi (.) p (.)} | 10.7 | 0.00 | 0.00 | 7 |
| {S(Sex) γ''(Sex) γ'(Sex) pi (Sex) p (Sex)} | 12.0 | 0.00 | 0.00 | 10 |
| {S(Sex*Time') γ''(Sex*Time') γ'(Sex*Time') pi (Sex*Time'') pi (Sex*Time'')} | 18.9 | 0.00 | 0.00 | 23 |
| {S(Time) γ''(Time') γ'(Time') pi (Time'') p (Time'')} | 23.2 | 0.00 | 0.00 | 12 |
| {S(.) γ''(.) γ'(.) pi (.) p (.)} | 30.8 | 0.00 | 0.00 | 5 |

Table 3.4.  Inputs, population estimates and density estimates for black bears based on Bowden's estimator of capture-resight data from trapping and camera surveys conducted on 2 100-km$^2$ grids on the northern (Augusts, 1998–2002 and October 1999–2001) and southern (August 2002) study areas of the Cooperative Alleghany Bear Study, Virginia, USA.  Data inputs include number of bears marked ($n$), total number of photographs of bears in which we could not determine marking status ($Y_{unknown}$), total number of resights of marked bears ($Y_{marked}$), and total number of unmarked bears photographed ($Y_{unmarked}$).

| Sampling Session | $n$ | $Y_{unknown}$ | $Y_{unmakred}$ | $Y_{marked}$ | $N$-hat | Density (bears/km$^2$) | 95% C.I. |
|---|---|---|---|---|---|---|---|
| North, August | | | | | | | |
| 1998 | 50 | 9 | 68 | 31 | 130 | 1.30 | 0.90–1.88 |
| 1999 | 42 | 14 | 51 | 38 | 78 | 0.78 | 0.51–1.21 |
| 2000 | 44 | 13 | 92 | 81 | 86 | 0.86 | 0.66–1.10 |
| 2001 | 78 | 20 | 118 | 200 | 119 | 1.19 | 1.07–1.34 |
| 2002 | 73 | 8 | 185 | 214 | 132 | 1.32 | 1.08–1.62 |
| North, October | | | | | | | |
| 1999 | 42 | 8 | 40 | 24 | 92 | 0.92 | 0.68–1.25 |
| 2000 | 44 | 13 | 78 | 40 | 105 | 1.05 | 0.73–1.51 |
| 2001 | 78 | 9 | 93 | 65 | 171 | 1.71 | 1.26–2.34 |
| South, August | | | | | | | |
| 2002 | 42 | 4 | 59 | 62 | 78 | 0.78 | 0.62–1.00 |

Table 3.5.  Comparative black bear density / $km^2$ and associated λ values from Bowden's estimator for capture-resight (1998–2002), Burnham's robust design using Huggins heterogeneity model for genetic capture-recapture (1999-2001) for summers (June–August) in Rockingham County Virginia, USA.

| | Density with 95% confidence intervals | | | | | |
|---|---|---|---|---|---|---|
| | Photographic capture-resight | | Genetic capture-recapture | | | |
| Year | Sexes combined | | Sexes combined | | Sex-specific | |
| 1998 | 1.30 | 0.90–1.88 | | | | |
| 1999 | 0.78 | 0.51–1.21 | 0.91 | 0.57–1.25 | 0.91 | 0.72–1.18 |
| 2000 | 0.86 | 0.66–1.10 | 1.01 | 0.70–1.32 | 0.99 | 0.77–1.27 |
| 2001 | 1.19 | 1.07–1.34 | 1.08 | 0.69–1.47 | 1.04 | 0.64–1.37 |
| 2002 | 1.32 | 1.08–1.62 | | | | |
| $\bar{x}$ Density | | | | | | |
| 1999–2001 | 0.94 | 0.75–1.22 | 1.00 | 0.65–1.35 | 0.98 | 0.71–1.27 |
| 1998–2002 | 1.09 | 0.84–1.43 | | | | |
| Λ | | | | | | |
| 1999–2001 | 1.24 | 1.09–1.40 | 1.09 | 1.07–1.11 | 1.07 | 1.05–1.09 |
| 1998–2002 | 1.05 | 0.88–1.24 | | | | |

Table 3.6. Comparison of sex-specific estimates of black bear density / km$^2$ with 95% confidence intervals and associated λ values derived from genetic capture-recapture data analyzed with a robust design model.  Data were collected 1998–2002 on a 100-km$^2$ grid in Rockingham County Virginia, USA.

| | Density with 95% confidence intervals | | | |
| | Female | | Male | |
| Year | | | | |
| 1999 | 0.55 | 0.44–0.73 | 0.36 | 0.28–0.45 |
| 2000 | 0.55 | 0.42–0.80 | 0.44 | 0.35–0.47 |
| 2001 | 0.59 | 0.46–0.89 | 0.45 | 0.36–0.49 |
| $\bar{x}$ Density | | | | |
| 1999–2001 | 0.56 | 0.44–0.81 | 0.42 | 0.33–0.47 |
| $\Lambda$ | | | | |
| 1999–2001 | 1.04 | 1.00–1.08 | 1.12 | 1.01–1.24 |

# CHAPTER 4: SURVIVAL RATES

**ABSTRACT**

Survival is a primary component of individual fitness and adult female survival is a primary influence in bear population dynamics. Accordingly, quantifying survival rates is important for research and management of bear populations. I quantified survival rates and examined associated influences for black bears (*Ursus americanus*) in the Alleghany Mountains of western Virginia, 1994-2003. We monitored 131 (65M:66F) 1–11-month-old cubs for 629 months and, using a known fate model in Program MARK, found overall annual cub survival was 0.87 (95% C.I. = 0.82–0.90). We followed 399 (154M:245F) individual ≥1-year-old black bears though 6,109 bear-months. Known fate analysis indicated young (1–3-year-old) males had lower annual survival rates (0.57, 95% C.I. = 0.45–0.69) than older (≥ 4-year-old) males (0.89, 95% C.I. = 0.74–0.96). Female survival was relatively constant across ages and estimated at 0.91 (95% C.I. = 0.88–0.93). Mortality rates were low in all months except hunting season and highest during hound hunting season in December. Without hunting mortality, estimated survival rates for all bears was 0.98 (95% C.I. = 0.97–0.99). We tagged and released 1,041 (668M:373F) bears and tags were returned for 488 (386M:102F) bears. Male bear survival in 1997 (during a mast failure) was 0.67 (95% C.I. = 0.51–80) and was 0.49 in all other (95% C.I. = 0.42–0.56). Male bears wearing transmitters had annual survival rates of 0.62 (95% C.I. = 0.51–0.73) and those not wearing transmitters had annual survival

rates of 0.48 (95% C.I. = 0.38–0.53), suggesting there may have been a bias against harvesting males wearing transmitters.   With all ages, years, and transmitter status combined, annual male survival was 0.52 (95% C.I. = 0.45–0.58) and female survival was 0.89 (95% C.I. = 0.85–0.92).  Using data from 211 (122M:89F) individual bears tagged in 264 bear-summers on a 100-km$^2$ grid and from 94 tags returned from these bears, I estimated annual sex-specific survival to be 0.57 (95% C.I. = 0.48–0.65) for males and 0.88 (95% C.I. = 0.82–0.92) for females.  Based on direct returns of tags from 1,491 bear-summers (870M:621F) harvest rates were different ($\chi^2_3$ = 83.10, $P$ < 0.001) for 4 sex and age classes.  One–3-year-old males and females were harvested at rates of 0.36 (95% C.I. = 0.32–0.39) and 0.09 (95% C.I. = 0.06–0.14), respectively.  Harvest rates for ≥ 4-year-old males and females were 0.21 (95% C.I. = 0.15–0.28) and 0.08 (95% C.I. = 0.05–0.11), respectively.  In overview, survival rates for females from cubs through adulthood were approximately 90% while for males survival varied by method of estimation and, more importantly, by age class.  These results are generally consistent with previous research and indicate high survival rates for females and relatively low survival rates for young males.

**INTRODUCTION**

Survival is a primary component of individual fitness (Gaillard and Yoccozb 2003) and black bear population dynamics are largely governed by adult female survival rates (Bunnell and Tait 1980, Freedman et al. 2003).

Consequently, accurately quantifying survival rates is a common objective in bear research and is important for bear management.

Anthropogenic sources are the dominant form of mortality in adult black bears in North America (Bunnell and Tait 1981).  In harvested populations, legal hunting accounts for 34–100% of documented deaths (Bunnell and Tait 1985).  Natural predators of black bears in western North America include brown bears (*Ursus arctos*; Miller 1985, Mattson et al. 1992, Smith and Follmann 1993) and wolves (*Canis lupus*; Horejsi et al. 1983).  However, in eastern North America, sympatric large carnivores are absent or have been extirpated.  Thus, eastern black bears have few interspecific natural predators and intraspecific predation (or cannibalism) accounts for the few predation-related sources of mortality (Bunnell and Tait 1981, Garshelis 1994).

Previous black bear research in Virginia has focused on unhunted populations in Shenandoah National Park in western Virginia (Carney 1985, Kasbohm et al. 1996) and the Great Dismal Swamp in coastal Virginia (Hellgren and Vaughan 1989).  In the Alleghany Mountains that run along the western border of the state, bear hunting is a long-standing tradition.  Over the past 3 decades, harvest levels rose from roughly 200 / year to nearly 1,000 / year (Martin and Steffen 2000).  Because relationships between harvest, hunters, and population density are confounded when catch / unit effort is unknown (Burton et al. 1994) harvest data may not be an effective means of monitoring bear population status (Noyce and Garshelis 1997), and may not be reliable to detect early stages of declines (Harris and Metzgar 1987).  Thus, management

decisions based solely on harvest data and without knowledge of underlying parameters and their influences may not be biologically sound (Lubow et al. 1996).

In response to the need to better understand and manage the population of black bears in western Virginia, in 1994 the Virginia Polytechnic Institute and State University and the Virginia Department of Game and Inland Fisheries (VDGIF; among numerous other collaborators) initiated the Cooperative Alleghany Bear Study (CABS) to intensively examine the long-term, broad-scale dynamics of Virginia's hunted black bear population. My objective in this portion the study was to examine and quantify the age- and sex-specific survival rates and associated influences for black bears in western Virginia's Alleghany Mountains.

**STUDY AREAS**

Our research was conducted on 2 study areas in the Alleghany Mountains of western Virginia, USA. The centers of the 2 study areas were approximately 160 km apart; both were located largely on the George Washington-Jefferson National Forests. The northern study area was centered near Reddish Knob at 38° 28' N, 79° 15' W. It was approximately 840 km$^2$ primarily in Augusta and Rockingham Counties. The southern study area was 1,544 km$^2$ and was centered near Mountain Lake at 37° 22' N, 80° 31' W. It was composed primarily of Craig, Giles, and Montgomery Counties. Elevations on these 2 study areas ranged from 480–1,360 m (Kozak 1970) and common tree species included:

eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipfera*), eastern white pine (*P. strobus*), mountain laurel (*Kalmia latifolia*) and scrub oak (*Q. ilicifolia*; Rawinski et al. 1994). At Mountain Lake, the center of the southern study area, high temperatures ranged from an average high of 24°C in July to an average low of -9°C in the January with total precipitation averaging 125 cm, including 134 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va5828). The closest weather station to our northern study area was at Dale Enterprises in the lowlands of Rockingham County. Because it was in the lowlands, weather averages were likely warmer and drier than conditions in the adjacent mountains where our research was conducted. At Dale Enterprises (38° 45' N, 78° 93' W), temperatures ranged from an average high of 30°C in July to an average low of -5°C in January with total precipitation averaging 90 cm, including 63 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va2208).

Hunting season lengths varied slightly (≤ 7 days) among years. Generally, September was marked by bear-hound training season during which bears could be pursued and treed with hounds, but not harvested. The second week of October through the first week of November was archery-hunting season, during which bears could be harvested using archery equipment. Gun season, during which bears could be killed with firearms, but not with the aid of dogs, was the last week of November. Hound-hunting season, during which bears could be

killed using firearms and with the aid of dogs, consisted of the first few days of December through the first Saturday in January. One bear tag / year / hunter was sold with the combined deer, bear, and turkey license. To be legally harvested bears had to weigh ≥45.5 kg live weight or ≥34.1 kg with all internal organs removed. Adult females with cubs could not be legally harvested. Law required that all harvested bears be checked at registered check stations. Checking a bear involved recording any tags, tattoos, and/or transmitters, determining sex of the individual, and removing a premolar for subsequent age determination.

## METHODS

### General

We captured bears with Aldrich spring-loaded foot snares and culvert traps (Johnson and Pelton 1980) from late May through late August 1994–2002. We initiated trapping on our northern study area in 1994 and on our southern study area in 1995. We sedated captured bears with a mixture of ketamine hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45.5 kg; White et al. 1996) administered via dart pistol, blowpipe, or jab stick. After bears were sedated, we determined their sex, weighed them, recorded morphometric measurements, and examined females for signs of estrus or lactation. To determine age, we removed a premolar (Willey 1974), which was sent to Matson's Laboratory (Milltown, Montana, USA) for cementum annuli analysis. We also tattooed bears' upper lips, and attached individually numbered, plastic,

perma-flex, stud-style eartags (National Band and Tag, Newport, Kentucky, USA) to all bears ≥6 months old.  We attached motion-sensitive radio transmitters to bears selected in an attempt to keep our sex ratio of transmittered animals at approximately 1M:3F.  Bears ≥1 year old received collars (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada; Telonics, Mesa, Arizona, USA, Wildlife Materials International, Murphysboro, Illinois, USA) that were equipped with breakaway cotton spacers (Hellgren et al. 1988) or eartag transmitters (Servheen et al. 1981) from ATS.  We administered a tetracycline antibiotic to prevent infection and serve as a permanent biomarker in teeth and bones (Johnson 1964, Garshelis and Visser 1997).  Finally, we administered yohimbine hydrochloride (5mg/ml; 2 ml/45.5 kg) to reverse the xylazine hydrochloride.  Each week, we monitored and attempted to locate bears wearing transmitters.

Biologists from VDGIF conducted surveys in late August to early September to quantify annual hard mast production (Sharp 1958, Coggin and Peery 1973).  Mast surveys involved examination of the same trees annually and quantifying the mean number of acorns / 10 limbs / tree (Fearer et al. 2002).  I used mast survey data collected by VDGIF (D. Martin, personal communication) for the 3 mast survey regions overlapping our study area to examine autumn hard mast availability.

In the late fall and winter, we used radio telemetry to locate dens of female bears wearing transmitters.  We returned to and entered (Godfrey et al. 2000) these dens in January–April to gather reproductive data, change transmitters on

adults, attach transmitters to cubs (Echols 2000, Vashon et al. 2003) and yearlings, and deploy remote cameras (Bridges et al. 2004). The Virginia Polytechnic Institute and State University Animal Care and Use Committee (98-069-F&W) approved all animal handling protocols.

**Survival Analyses**

To examine survival rates of black bears in western Virginia, I used 4 types of analyses. Data for these analyses involved radio telemetry (known fate models), tag return (tag return models), tag return combined with physical capture-recapture (combined models), and direct returns of tags (tags returned during the year they were deployed). I compared models built *a prior* and based on what I perceived to be likely influences on survival rates. I used an information-theoretic approach to model selection (Burnham and Anderson 2002) based on Akaike's Information Criterion (AIC; Akaike 1973) and associated model weighting and support for models as calculated in Program MARK (White and Burnham 1999). AIC should be bias-adjusted to $AIC_c$ (Sugiura 1978) if sample sizes are small (Burnham and Anderson 2002) and Program MARK automatically makes this adjustment. Included in each model set was a "global" model in which all other tested models were nested. To evaluate model fit, I used the overdispersion parameter $c$. Many of the models-types available in Program MARK do not have valid goodness of fit procedures and estimating a median $\hat{c}$ variance inflation factor is currently the most accepted method to determine if overdispersion is present in model sets (White 2002). Accordingly, I used median $\hat{c}$ calculated from the global model to evaluate variance inflation

and overdispersion.  A  ĉ ≠ 1.0 indicates lack of fit and a ĉ > 1.0  indicates

overdispersion.  When median ĉ > 1.0, AIC should be converted into quasi-

likelihood AIC (QAIC).  Thus, after calculating median ĉ for the global model, I

adjusted AIC to QAIC as appropriate.  Theoretically, a ĉ <1.0 indicates

underdispersion, but no corrections are currently available and it is

recommended that ĉ values from 0–1 be ignored (White 2002).

The model with the lowest AIC was considered the most parsimonious

model best supported by the data.  I calculated $\Delta_i$ by subtracting the AIC for each

model $i$ from the model with the smallest AIC value.  I considered models with $\Delta_i$

≤ 2.0 to have substantial support (Burnham and Anderson 2002).   When $\Delta_i$ ≤ 2.0

between the most highly supported model and the second most highly supported

model, I used model averaging to estimate common parameters of interest.

Model averaging derives average parameter estimates for common parameters

based on proportional weight of each respective model tested during analysis

(Burnham and Anderson 2002).

**Known fate – cubs**

We handled neonatal black bear cubs in their dens from March– early

April each year, 1995–2003.  We attached transmitters (Advanced Telemetry

Systems, Isanti, Minnesota, USA) to selected (the first cubs handled each year

fitting weight criteria until our annual transmitter supply was exhausted) cubs

weighing ≥1.6 kg.  Transmitter types included expandable cub collars (Vashon et

al. 2003) or implanted transmitters (Echols 2000, Echols et al. 2004).

Transmitters were motion sensitive and emitted a mortality signal if no movement was detected for ≥4 hours.

We monitored cubs ≥1 time every 7 days until the transmitters were dropped or the cub died. I censored (White and Garrott 1990) cubs not heard for >60 days. Censor dates (White and Shenk 2001) were calculated as the time an individual was last heard prior to its >60-day absence. I estimated transmitter drop dates and mortality dates as the midpoint between the last active signal and the first mortality signal. For mortalities, we collected remains and attempted to determine cause of death via field necropsy or, if decomposition was not severe, by taking the dead individual to the Department of Biomedical Sciences and Pathobiology of the Virginia-Maryland Regional College of Veterinary Medicine. Cub mortalities likely resulting from research activities, such as maternal abandonment, were not included in analyses.

I calculated survival rates using the know fate survival estimator in Program MARK (White and Burnham 1999). This model employs a model similar to the non-parametric Kaplan-Meier (Kaplan and Meier 1958) survival estimator as modified (Pollock et al. 1989$a$, Pollock et al. 1989$b$) to allow for right censoring and staggered entry (left censoring) and is advantageous in providing continuous-time survival estimates. The assumptions of this model were: 1) animals are randomly sampled, 2) individual survival rates are independent of each other, 3) radio tagging does not influence survival and 4) censoring is independent of animal's fate (Pollock et al. 1989$a$, Pollock et al. 1989$b$).

Based on *a priori* knowledge of cub survival, I built models incorporating several possible influential factors. I pooled data from both transmitter types (cub collars and implants) because we excluded cubs dying immediately as a result of implant surgery and because there was no evidence of transmitter type affecting survival (Echols 2000). I hypothesized that cub survival might be time dependent with influences including sex of the individual cub, litter size, mother's age, and study area. Accordingly, I coded for attribute groups including: male cubs, females cubs, cubs from large litters (≥3 cubs), cubs from small litters (≤2 cubs), cubs from young mothers (3–4 years old), cubs from older mothers (≥ 5 years old), cubs from our northern study area, and cubs from our southern study area (Table 4.1.). Additionally, I calculated monthly cub survival estimates for 10 occasions from March through December and examined whether models supported pooling time intervals into emergence (March–May) and post-emergence (June–December) blocks.

**Known fate – subadults and adults**

We attached motion-sensitive eartag or collar-mounted transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA; Lotek Wireless Inc., Newmarket, Ontario, Canada; Telonics Inc., Mesa, Arizona, USA) to ≥1-year-old bears during summer trapping (1994–2002) and winter den work (1995–2002). We attempted to monitor each individual ≥1 time / week. We used receivers equipped with H-style, and/or omnidirectional-style antennas to monitor transmitters. We conducted monthly aerial telemetry to locate and monitor individuals that we could not find from the ground. All transmitters were

equipped with motion-sensitive mortality sensors which emitted a mortality signal if no activity was documented for >30 minutes. Individuals whose status could not be determined for >60 days were censored from analyses and the last recorded signal documented was used as the censor date. I estimated transmitter drop dates and mortality dates as the midpoint between the last active signal and the first mortality signal. For mortalities, we performed field necropsies and collected remains in an attempt to determine cause of death. When feasible (bear could be removed from the field and decomposition was not extensive), dead individuals were taken to the Department of Biomedical Sciences and Pathobiology of the Virginia-Maryland Regional College of Veterinary Medicine for more in-depth necropsy.

I used these data to explore month-, sex-, study area-, and age-specific survival rates. Because of small (and frequently absent) annual representation from these attribute groups, I pooled data across years. I used the known fates model in Program MARK (White and Burnham 1999) for analyses. This model employs a binomial equivalent to Kaplan-Meier (Kaplan and Meier 1958) modified (Pollock et al. 1989*a*, Pollock et al. 1989*b*) to allow for right censoring and staggered entry (left censoring). However, because of its binomial individual encounter history input structure, it also allows for examination of covariates such as sex and age. Model assumptions are the same as described for known fate cub survival.

I constructed *a priori* models representing biologically plausible representation of the system and influences. I hypothesized that survival might

differ by season, with hunting season (October–December) and particularly hound-hunting season (December) having higher mortality rates and accordingly lower survival rates. Because hunting season carried over into the first few (≤6) days of January, I considered bears killed during these days as December mortalities of the previous calendar year. I also believed survival rates might be study area-, sex-, and/or age-class specific (Table 4.2). I then quantified natural survival rates by censoring all hunting mortalities and, alternatively, hunting survival rates by censoring all natural mortalities. Model selection (Burnham and Anderson 2002) was used to determine which model(s) were best supported by the data.

**Tag return**

We marked bears throughout our 2 study areas with individual-specific eartags, lip tattoos, and, in some cases, transmitters. We marked bears on our northern study area during summers from 1994–2002 and on our southern study area from 1995–2002. Hunters were legally required to check all harvested bears at registered check stations where sex, tag number, and tattoo number were recorded. VDGIF offered a $25 reward for the return of eartags and we offered a $50 reward for the return of transmitters, which allowed us to crosscheck data from check stations.

I used a combination of direct (during the year of marking) and indirect (during subsequent years) recovery of these tags to estimate sex- and year-specific survival rates. I used the tag return (dead recoveries) model in Program MARK (White and Burnham 1999) that employs an equivalent to the Brownie

model (Brownie et al. 1985) which allows the recovery process to be separated from the survival process (Seber 1970, Anderson et al. 1985, Catchpole et al. 1995). I used individual encounter histories rather than the traditional recovery matrix, which allowed me to estimate sex-specific survival rates.

This model is based on 6 primary assumptions: 1) the marked sample is representative of the population as a whole, 2) no mark loss or miss-readings, 3) age and sex of sampled animals are correctly determined, 4) year of tag return is correctly recorded and tabulated, 5) survival rates are not effected by tagging, and 6) fates of banded individuals are independent of each other (Brownie et al. 1985, Williams et al. 2002).

I constructed *a priori* models representing possible relationships between survival and likely influences. I hypothesized that survival might differ by study area, sex, year, or if an individual was or was not wearing a radio transmitter (Table 4.3). I then used model selection (Burnham and Anderson 2002) to determine which model(s) were best supported by the data.

**Combined model**

We intensively trapped a 100-km$^2$ grid on our northern study area during summers, 1998–2002. I combined this open mark-recapture data with tag return data for individuals trapped within this grid to estimate annual and sex-specific survival using Burnham's combined model (Burnham 1993) in Program MARK (White and Burnham 1999). The assumptions of the combined model (Burnham 1993), were the same as for the tag return model with the addition of assumptions implicit to Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965,

Seber 1965).  These additional assumption include: 1) each marked animal present in the population has an equal probability of recapture, 2) each marked animal has the same probability of surviving until the next sampling period, 3) no marks are lost between sampling intervals or misread or incorrectly recorded during handling, 4) sampling periods are instantaneous (or very short), 5) emigration is permanent and 6) fates of individuals with respect to survival or recapture probability are independent.

I constructed *a prior* models representing possible relationships between survival and likely influences.  These models were similar to those from tag return analyses, with the exception of study area, which could not be examined because these data were gathered only on our northern study site.  The models tested examined effects of sex, time, and wearing a transmitter on survival of ≥1-year-old bears.  Model variables used in Burnham's combined model analysis of subadult and adult survival are described in Table 4.4.

**Direct returns**

I calculated simple annual hunting mortality rates based on the proportion of tags placed on individual bears during summers that were returned during the fall and winter of that same year (direct returns).  These estimates were derived primarily for use as relative vulnerability inputs for harvest modeling (Chapter 5).  Because annual samples of females trapped and/or harvested were small when divided by sex and age class (i.e., 0–1 tagged individuals and/or returned individuals in several years), I pooled years and study areas to quantify harvest rates for sex- and age-class combinations (1–3-year-old versus ≥4-year-old

males and females). I then examined annual variation in harvest rates by pooling age classes and study areas and examining total harvest, and sex-specific harvest rates. I tested for differences in sex, age class, and annual harvest rates with goodness of fit (GOF) $\chi^2$ tests.

**RESULTS**

**Known fate – cubs**

We monitored 131 (65M:66F) 1–11-month-old cubs for 629 months. We documented 11 (7M:4F) mortalities. Causes of mortalities included intraspecific predation (6), unknown (2), interspecific predation (1), poaching (1), and snake bite (1). Ten of 11 mortalities occurred from March–July and 1 occurred in October as reflected in the monthly survival rates in Figure 4.1. No cub mortalities were documented in 1998, following the mast failure of 1997.

The median $\hat{c}$ variance inflation factor for the global cub survival model was <1.0 and thus quasi-likelihood AIC$_c$ adjustment was not necessary. The 2 models considered highly supported by the data were both time-specific (Table 4.5). The model most highly supported by the data ($\omega_i = 0.62$) was constant for sex, mother's age, litter size, study area. It estimated 2 parameters: 10-month survival based on March–May survival rates (0.78, 95% C.I. = 0.69–0.84) and 10-month survival based on June–December survival rates (0.91, 95% C.I. = 0.83–0.95). The second most highly supported model ($\omega_i = 0.29$, $\Delta_i = 1.54$) had survival varying by month. Monthly estimates of cub survival varied from 0.96 (95% C.I. = 0.93–0.98) to 1.0 (Figure 4.1.). None of the models including cub sex, study area, mother's age, or litter size were selected or received substantial

weight (Table 4.5) and confidence intervals for survival rates based on these possibly influential factors overlapped (Figure 4.2). Model averaging indicated overall cub survival from March–December was 0.87 (95% C.I. = 0.82–0.90; Table 4.6).

**Known fate – subadults and adults**

We followed 399 (154M:245F) individual ≥ 1-year-old black bears through 6,109 bear-months. We documented 98 non-research-related mortalities of transmittered individuals. Only 7 of the mortalities occurred outside of the hunting season (January–September). Three were unknown, 2 were due to intraspecific predation, 1 hung herself after catching her head in the opening of a hollow tree and 1 was poached. During hunting season, harvest accounted for 85 known mortalities, nuisance complaints accounted for 2 mortalities, vehicular collision accounted for 1 mortality, and 3 were unknown. Based on these empirical data, legal harvest accounted for ≥87% of known mortalities.

Examination of *a prior* models with Program MARK indicated ĉ for the global model was < 1.0 indicating quasi-likelihood adjustment should not be performed. One model was strongly supported ($\omega_i$ = 1.00; Table 4.7.) and it included 3 time intervals (January–September, October–November, December) and an interaction term that grouped all age classes for females, but divided them into 1–3-year-olds and ≥4 years old for males. Based on this model, annual survival was 0.57 (95% C.I. = 0.45–0.69) for 1–3-year-old males, 0.89 (95% C.I. = 0.74–0.96) for ≥ 4-year-old males, and 0.91 (95% C.I. = 0.88–0.93) for all females (Table 4.8). Mortality rates were higher during hunting season

(October–December) and highest during hound hunting season in December (Figure 4.3).

When non-hunting mortalities were censored to examine survival with hunting as the only source of mortality, model selection was similar (Table 4.9.) The most highly selected model ($\omega_i$ = 1.00; Table 4.9.) estimated annual hunting survival was 0.58 (95% C.I. = 0.46–0.70) for 1–3-year-old males, 0.92 (95% C.I. = 0.80–0.97) for ≥ 4-year-old males and 0.92 for all females (95% C.I. = 0.89–0.94; Table 4.8).

When all hunting mortalities were censored to examine natural survival rates, 3 models had $\Delta_i$ <2.0. The most highly supported model ($\omega_i$ = 0.46; Table 4.10.) indicated no differences by sex, study area, age or time and yielded an annual survival rate of 0.98 (95% C.I. = 0.96–0.99). The second most highly supported model ($\omega_i$ = 0.23, $\Delta_i$ = 1.39) included study area and gave estimates of 0.99 (95% C.I. = 0.97–0.99) for the northern area and 0.98 (95% C.I. = 0.93–0.99) for the southern study area. The third most highly supported model ($\omega_i$ = 0.19, $\Delta_i$ = 1.73) included sex and gave estimates of 0.99 (95% C.I. = 0.93–0.99) for males and 0.98 (95% C.I. = 0.96–0.99) for females.

**Tag return**

We tagged and released 1,041 bears (668M:373F) during 1994–2002. Tags were returned for 488 (386M:102F) bears during 1994–2002. Median $\hat{c}$ indicated mild over dispersion with an estimated value of 2.1. Thus, I adjusted for $\hat{c}$ = 2.1 and used calculated $QAIC_c$ for model selection. Three models were considered highly supported by the data ($\Delta_i$ <2.0; Table 4.11). The most highly

supported model ($\omega_i$ = 0.43) indicated female survival rate was 0.89 (95% C.I. = 0.85–0.92) and was constant across years, for female bears wearing transmitters versus those not wearing transmitters, and on both study areas. This model included different survival for males in 1997 (0.67, 95% C.I. = 0.51–0.80) versus all other years (0.49, 95% C.I. = 0.42–0.56). The second most highly selected model ($\omega_i$ = 0.23, $\Delta_i$ = 1.31) included different survival rates for females wearing transmitters (0.88, 95% C.I. = 0.80–0.93), females not wearing transmitters (0.89, 95% C.I. = 0.84–0.93), males wearing transmitters (0.62, 95% C.I. = 0.51–0.73), and males not wearing transmitters (0.48, 95% C.I. = 0.40–0.55). The third model selected ($\omega_i$ = 0.19, $\Delta_i$ =1.70) included differential survival for males in 1997 (0.49, 95% C.I. = 0.42–0.56) versus all other years (0.67, 95% C.I. = 0.51–0.80) and also included differential survival for females in 1997 (0.86, 95% C.I. = 0.72–0.94) versus all other years (0.89, 95% C.I. = 0.85–0.93). Study area was not included in any of the highly supported models.

**Combined model**

I used data from 211 (122M:89F) individual bears handled in 264 bear-summers and from 94 tag returns to estimate annual sex-specific survival. There was no evidence of lack of fit ($\hat{c}$ < 1.0) so adjustment was not necessary. The most highly supported model ($\omega_i$ = 0.87; Table 4.12) separated sexes but combined fidelity and initial capture probabilities, while recovery likelihood was set to 1.0 for bears wearing transmitters. The combined model yielded estimates consistent with other techniques. Annual survival was estimated to be 0.57 (95% C.I. = 0.48–0.65) for males and 0.88 (95% C.I. = 0.82–0.92) for females.

**Direct returns**

We placed tags on bears during 1,491 bear-summers (870M:621F). Pooling all data, total harvest rate was 0.22 (95% C.I. = 0.20–0.24). There was no evidence of year effect (1994–2002) on total harvest rate ($\chi^2_8$ = 5.44, $P$ = 0.71) or harvest rate of males ($\chi^2_8$ = 6.90, $P$ = 0.55) or females ($\chi^2_8$ = 10.97, $P$ = 0.21). There was no evidence ($\chi^2_1$ = 0.74, $P$ = 0.39) total harvest rate during 1997 (0.19, 95% C.I. = 0.13–0.26) was different from total harvest rates during all other years combined (0.23, 95% C.I. = 0.20–0.25). Likewise, there was no evidence ($\chi^2_1$ = 1.74, $P$ = 0.19) that female harvest differed in 1997 (0.12, 95% C.I. = 0.06–0.22) versus all other years combined (0.07, 95% C.I. = 0.05–0.10) or that male harvest rate differed ($\chi^2_1$ = 1.57, $P$ = 0.21) in 1997 (0.24, 95% C.I. = 0.15–0.35) versus all other years (0.33, 95% C.I. = 0.30–0.57).

There was strong evidence of differences between harvest rates of sex- and age-classes (1–3-year-old versus ≥4-year-old males and females; $\chi^2_3$ = 83.10, $P$ < 0.001). Age class affected male harvest rates ($\chi^2_1$ = 7.11, $P$ = 0.01) with 1–3-year-old males harvested at a higher rate (0.36, 95% C.I. = 0.32–0.39; Table 4.13) than ≥ 4-year-old males (0.21; C.I. = 0.15–0.28). Age class did not affect female harvest rate ($\chi^2_1$ = 0.30, $P$ = 0.58) and the 1–3-year-old female harvest rate (0.09, 95% C.I. = 0.06–0.13) and the ≥ 4-year-old female harvest rate (0.08, 95% C.I. = 0.05–0.11) were similar. Harvest rates for males and females (all ages combined) were different ($\chi^2_1$ = 74.13, $P$ < 0.001) with males (0.32, 95% C.I. = 0.29–0.35) harvested at a higher rate than females (0.09, 95% C.I. = 0.06–0.11).

**DISCUSSION AND MANAGEMENT IMPLICATIONS**

**Cub survival**

Cub survival has been difficult to calculate due to small sample sizes and ineffective marking techniques.  Generally, my cub survival estimate of 0.87 was higher than those calculated in much of the previously published research.   For example, annual survival estimates were 0.54 in Alaska (Miller 1994), 0.48 in Arizona (LeCount 1982), and 0.81 in Mexico (Doan-Crider and Hellgren 1996). Survival in Massachusetts was 0.59 for all cubs (≤ 1 year) with males having significantly lower survival than females (Elowe and Dodge 1989).  In North Carolina, annual estimates ranged from 0.21–0.50 with an upper limit of 0.71, but these numbers were based on a total sample size of 15 cubs (Powell et al. 1996).  Annual cub survival estimates on 2 study areas in Arkansas were 0.40 and 0.65 (Clark and Smith 1994).  In Shenandoah National Park, annual cub survival was 0.73 with higher mortality in larger litters and no evidence that mast-crop failure reduced survival (Kasbohm et al. 1996).  Cub survival in the Great Dismal Swamp could not be determined, but was estimated at 0.75 based on reduction of litter size from birth to subsequent observation 6–12 months later (Hellgren and Vaughan 1989).  The highest cub survival estimate that I found in reviewing the literature was 0.91 in Alaska (Schwartz and Franzmann 1991). Our estimates, which are not truly annual (they are 10-month), were higher than any of the previously listed estimates with the exception of this Alaskan study.

Regarding the assumption of the Kaplan-Meier (Kaplan and Meier 1958, Pollock et al. 1989*a*, Pollock et al. 1989*b*) equivalent known fate model in

Program MARK, the first assumption that animals are randomly sampled might have been violated because we could place transmitters only on larger cubs (>1.6 kg).  To reach 1.6 kg by March, these cubs may have been born earlier and to older mothers (Chapter 1).  However, because we saw no difference in cub survival related to mother's age, violation of this assumption likely had a negligible effect on overall survival rate estimation.  The second assumption, that individual survival rates are independent of each other, also likely was violated.  This is because we frequently (though not exclusively) attached transmitters to entire litters and the fate of each cub in that litter was likely linked to the fate of the entire litter.  However, because little mortality was documented and few involve the entire litter, this likely did not substantially bias estimates.  The third assumption, that radio tagging does not influence survival, likely was met.  Although we documented multiple instances where the expandable collars did not expand correctly, we documented no instances where this lack of expansion killed <1-year-old bears.  However, it could be argued that attaching transmitters to any animal has some effect on its survival.  Finally, the assumption that censoring was independent of individuals' fate was difficult to evaluate.  If poachers (killing cubs is illegal in Virginia) killed a collared cub, they may have disabled the cub's transmitter, thus censored bears may not have been totally independent of their fate.  Thus, if poaching was a larger problem than we believe it was, survival rates might be biased high.

Recruitment into the adult population was apparently negatively affected by the mast crop failure in 1997 (Chapter 1).  A logical hypothesis is that this

reduction in recruitment operated through reduced cub survival the following year because mothers were in poorer physical condition from the previous autumn's mast failure.  However, we documented no cub mortalities (survival was equal to 1.0) the year following the mast failure.  Thus, it appears that survival rates of >6-week-old cubs were not negatively affected by previous year autumn mast failure.  In experiments with pregnant captive bears at the Virginia Tech Center for Ursid Research, nutritionally stressed females lost their litter almost immediately following birth (likely due to reduced lactation; M. Vaughan, Virginia Tech, personal communication).  Because we collared only cubs >1.6 kg (who were >6 weeks old) we could not document survival during the first 6 weeks of life.  Thus, reduced cub survival may have occurred following the mast failure, but it may have occurred prior to our den visitations and thus gone unreported.  In the future, cameras and video recording systems placed in dens might be able to better document survival immediately following birth (Bridges et al. 2004).

Cub survival rates were consistent across attribute groups and model selection supported only time-dependent variation in survival (Table 4.5).  The poor support from model selection and strongly overlapping confidence intervals for various attribute groups suggest cub sex, study area, and mother's age had little effect on cub survival rates.

Bears on our study area most frequently had their first litter at 3 years of age (Chapter 1).  However, because of the small sample we had for collared cubs from 3-year-old mothers, pooling survival rates for cubs produced by 3- and 4-year-old females was necessary for analyses.  It is possible that females

producing cubs at 3 years old lost litters at higher rates than those producing cubs at ≥4 years old, but these differences could not be tested due to requisite age-class pooling for known fate analyses.

It has been hypothesized that individuals that reproduce at an early age experience lower offspring survival than those reproducing later, however, this observation has not been consistently supported (Festa-Bianchet et al. 1995). For bears, survival of cubs is difficult to calculate and large samples of primiparous females may be necessary to elucidate differences based on the mothers' experience or age. Even with our relatively large sample size, no clear relationship between cub survival and female age was established. Speculatively, it might be possible that younger females increased their cubs' survival rates by having smaller litters than older female (Chapter 1). This relationship would assume it is less challenging to raise a small litter than a large litter and might offer explanation for both the smaller litters observed in young females (Chapter 1) and the apparently high survival rates of those offspring. Researchers attempting to explore this possible relationship should consider targeting young females for research to determine if, within this age class, survival rates differed for small versus large litters.

Historically, the most common method of calculating cub survival was based on the assumption that cubs present in the den as neonates, but not present in the den with their mother the following year, died naturally during the year (Hellgren 1988, Garshelis 1994). This form of estimation may, however, result in substantial underestimates of natural cub survival and Bunnell and Tait

(1981:82) considered it "an inappropriate method of estimating cub mortality."

We found 13 yearlings that denned successfully alone (separated from their

mother) and thus would have been considered dead using traditional

methodologies.  Additionally, based on our observations, I believe researcher-

induced den abandonment (Hellgren and Vaughan 1989, Godfrey 1996) is

underreported in most studies.  Litters lost due to researcher-induced but

undocumented den abandonment would be assumed to have died naturally, thus

lowering cub survival estimates.  These 2 issues may have influenced

(negatively) the previously reported estimates of cub survival and may be

partially responsible for the disparity between my estimates and lower estimates

found in the published literature.

**Subadult and adult survival**

Annual survival rates for females were consistent across estimation

techniques.  Known fate, tag return, Burnham's combined, and direct returns

yielded annual female survival rates of 0.91, 0.89, 0.88 and 0.91, respectively.

Female survival rates were consistent across age classes from cubs through

adulthood (Figure 4.7) and model selection and associated survival estimates

from tag returns and Burnham's combined model indicated females wearing

transmitters did not experience different survival rates than females without

transmitters.  A relative lack of heterogeneity through time, age classes, and

whether they wore transmitters, likely lead to the consistent survival rates

observed.  In a simplified approximation, we can say that roughly 9 out of 10 of

female bears (regardless of age) in our study areas survive each year.

For males, results were less consistent with known fate, tag return, Burnham's combined, and direct returns yielding estimates of 0.69, 0.52, 0.57, and 0.68, respectively. Unlike females, however, known fate model selection indicated that male age classes should be divided and that young males (1–3-year-olds) survived at lower rates (0.57) than older males (≥4-year-olds; 0.89). A similar, though less dramatic pattern was evident using direct returns, where young male survival was estimated at 0.64 and older male survival was estimated at 0.79. Further complicating male survival estimation, wearing a radio transmitter may have affected male survival rates. Based on tag return models, males may have survived at higher rates (0.62) when wearing transmitters than they did when not wearing transmitters (0.48). However, confidence intervals for these estimates slightly overlapped. Klenzendorf (2002) reported a transmitter bias in our data. Thus, the less consistent estimates among models for pooled males likely resulted from the effects of age and transmitter bias.

As I expected, based on the low incidence of natural mortality observed in our study, the natural survival rate was high (0.98). Although model selection indicated support for models sex and study area (Table 4.10) the differences in survival estimates for these attribute groups was negligible (0.97–0.99). Similarly, when natural mortalities were removed, model selection was consistent with model selection based on harvest mortality from the complete data set (Table 4.7 and 4.9) and survival rates were nearly identical.

My findings were generally similar to those from other black bear studies (Table 4.13). In unhunted populations in the southwest, annual survival was

0.98 in Arizona (LeCount 1982), and 0.94 in Mexico (Doan-Crider and Hellgren 1996).  In unhunted populations in Arkansas, annual adult female survival was 0.98 (Clark and Smith 1994).  These results are very similar to my estimated non-hunting survival rates of 0.98.  In North Carolina, adult survival was estimated at 0.83 for all bears (Powell et al. 1996) and 0.82 for adult females and 0.89 for adult males (Beringer et al. 1998).  The survival rates of adult females on our study areas were likewise similar to those from adult females in the Shenandoah National Park in western Virginia (Kasbohm et al. 1996) both in areas affected and unaffected by a gypsy moth infestation (0.89 and 0.94).  CABS results were similar to estimates from the Great Dismal Swamp in coastal Virginia, where annual survival was calculated at 0.87 for females, 0.59 for males and 0.77 overall (Hellgren and Vaughan 1989).  Our female survival was higher than that reported from a hunted population in Montana, where annual adult female survival was 0.79 (Kasworm and Thier 1994).  Our survival rates were substantially higher for subadult males than those from a hunted population in North Carolina, where annual survival was estimated at only 0.27.   However, researchers in the Great Dismal Swamp documented no mortalities for 11 subadults (< 3 years of age) over 1,780 radio days, indicating subadult survival was likely lower on our study area than in their research.

As was the case in the majority of reports regarding the proportion of mortality resulting from hunting in harvested populations (Bunnell and Tait 1985), I found few bears on our study area died of natural causes and that natural, non-hunting survival rates for ≥1-year-old males approached 1.0.  Only 3 of 98 (3%)

deaths of transmittered animals were definitively the result of non-anthropogenic causes. Understanding this relationship is of special importance because black bears are long-lived and reproduce slowly and a population may take years to recover from excessive harvest (Miller 1990). In a Canadian brown bear population, 77–85% of mortalities were human-related with males more vulnerable to harvest than females (McClellan et al. 1999). Hunting was the primary source of adult male black bear mortality in Montana (Kasworm and Thier 1994). In Pennsylvania, hunting accounted for 70–84% of annual mortality while vehicle collisions accounted for 7–20% of mortalities (Lindzey et al. 1983). In years without a bear season, vehicle collisions accounted for approximately 65% of annual mortalities. Vehicle collisions were rare in our study. In a hunted population in Minnesota, adult female and adult male survival rates were estimated at 0.81 and 0.73, respectively (Rogers 1976). Similarly, in Ontario, Canada, hunted female and male black bears had annual survival rates of 0.88 and 0.77, respectively (Kolenosky 1986). Based on telemetry records from 15 studies, Garshelis (1994) found adult male survival varied from 0.59 (Carney 1985, Hellgren and Vaughan 1989) to 1.0 (Lindzey et al. 1986).

As demonstrated, male and female bears frequently exhibit different survival rates, especially when subject to harvest. Bunnell and Tait (1985) examined multiple hunted populations and concluded that females are generally less heavily harvested and thus their survival rates were, on average, 0.09 higher than survival rates for males. My results indicate that in addition to commonly reported sex-related differences, it also is important to consider age structure.

As previously described, survival rates for male bears are frequently reported to be lower than for female bears.  However, I found that this difference is most evident for subadults (1–3-year-olds).  Based on known fate analysis, adult males (0.89), though likely biased high by a selection against harvesting individuals wearing transmitters (Figure 4.5), had similar survival rates to adult females (0.91).

Regarding the assumption of the Kaplan-Meier (Kaplan and Meier 1958, Pollock et al. 1989a, Pollock et al. 1989b) equivalent known-fates model in Program MARK, the first assumption that animals are randomly sampled was violated due to apparent trap bias towards young males (Chapter 2).  However, because sex and age (the covariates linked to trapping bias) were accounted in the selected models and specific survival parameters were reported for each sex and age class, this violation was likely accounted for sufficiently (Williams et al. 2002).   The second assumption, that individual survival rates are independent of each other, was likely not violated because black bears are generally solitary (Pelton 1982) and thus individual fates can be assumed to be largely independent of each other.  The third assumption, that radio tagging does not influence survival, was likely violated as my analyses of tag return and combined capture-recapture and tag return survival estimates indicate wearing a transmitter may have affected survival for males.  Likewise, an earlier analysis of our data found a bias against harvesting bears wearing transmitters (Klenzendorf 2002). If hunters refrained from harvesting bears wearing transmitters, survival rates would be overestimated.  Finally, the assumption that censoring was

independent of animals' fate is difficult to evaluate.  If someone killed a bear

illegally, they may have disabled any transmitters it might have been wearing,

thus censored bears may not have been totally independent of their fate.

Violation of this assumption in this manner would lead to overestimation of

survival rates.

Regarding the 6 primary assumptions of the tag-return model (Brownie et

al. 1985, Williams et al. 2002), the first assumption that the marked sample is

representative of the population as a whole was likely violated due to trapping

bias in our marked sample (Chapter 2).  I was able to model and thus account for

the sex component, but not the age component of this bias.  The second

assumption of no mark loss was likely met because we marked bears with 2

eartags, a permanent lip tattoo, and frequently with transmitters; thus, complete

mark loss was rare.  Additionally, to double-check tag numbers recorded at

check stations, VDGIF offered a $25 reward for returned eartags and thus

misreading marks was also unlikely.  The third assumption, that sex and age of

sampled animals is recorded correctly, was likely not violated because sex

determination was made by professional biologist who were handling

anesthetized bears.  Additionally, age determination via cementum annuli

analysis (Stoneberg and Jonkel 1966, Willey 1974) has been determined to be

accurate to within acceptable levels (Smith et al. 1994, Keay 1995, Harshyne et

al. 1998). The fourth assumption, that year of tag return is correctly recorded and

tabulated was likely met as these records were meticulously recorded by VDGIF.

The fifth assumption, that survival rates are not affected by tagging, was likely

met for individuals not wearing transmitters because tags were small, and in some cases black, and thus likely played little role in decisions by hunters regarding harvesting individual bears.  For males wearing transmitters, this assumption may have been violated and would result in inflated survival estimates.  Finally, the sixth assumption that fates of tagged individuals were independent was likely met due to the solitary nature of black bears (Pelton 1982).

The assumptions of the combined model (Burnham 1993), were the same as for the band return model with the addition of assumptions implicit to Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965).   The first assumption, that each marked animal present in the population has an equal probability of recapture, likely was violated due to trapping biases (Chapter 2). The second assumption, that each marked animal has the same probability of surviving until the next sampling period was likewise violated as young males had a lower probability of surviving between sampling intervals.  As was the case for the tag return model, I was able to model and thus control for the sex but not the age component of violations of the first and second assumption.  The third assumption, that no marks are lost between sampling intervals or misread or incorrectly recorded during handling was likely met as losing 2 eartags and a lip tattoo was unlikely and I believe our biologists rarely misreported marking data. Regarding the fourth assumption that sampling periods were instantaneous or very short, our sampling periods were 10–12 weeks long as opposed to the 40– 42 weeks between sampling periods, and were therefore relatively short.  The

fifth assumption, that emigration is permanent, was, based on our telemetry data (Lee 2003, Olfenbuttel 2005), likely violated.  However, this violation was likely mild and had little effect because most individuals that emigrated were subadult males who likely emigrated permanently (Lee 2003).  Finally, the sixth assumption, that the fates of individuals are independent with respect to survival or recapture probability, was likely met.

Determining which estimate was most valuable is difficult and depends on study objectives.  Known fate analyses allowed me to examine temporal variation in survival, examine cause-specific mortality, and determine fine-scale age relationships in survival rates.  However, the possible bias against harvesting males wearing transmitters was problematic and could have resulted in overestimates of male survival rates.  Tag return data were less subject to transmitter-related bias and allowed me to examine whether this source of bias was present in known fate analysis.  However, it was contingent on hunters killing, recovering and checking their bears at check stations and then returning the tags to VDGIF.  Additionally, natural sources of mortality, though I found them to be minimal in our study, cannot be documented reliably using tag return.  Finally, this model type is not well suited to modeling age-specific survival rates, which I found to be an important component, particularly for males.  The model combining mark-recapture and tag return suffers from the same problems as the tag return model.  Additionally, results from combined model are subject to unequal capture and recapture probabilities and permanent emigration from the study area.  Furthermore, this method requires high levels of trapping intensity to

gain sufficient numbers of recaptures and thus may not be well suited for use on an area larger than our 100-km$^2$ grid.  While nuisance parameters in the tag recovery and return are factored into tag return estimates, they nevertheless build noise into survival estimates.  These results suggest that multiple measures of survival and associated ability to evaluate bias is important for research examining bear survival rates.  However, if only 1 method was selected, I believe the advantages of the known fate model (continuous-time estimation, natural mortality documentation, and age-specific survival estimation) outweigh its disadvantages (the possible bias against harvesting males wearing transmitters during our study).

Black bears, with their large body size, iteroparous reproduction, small litter sizes, and long natural life span, are a classic example of a *K*-selected species (MacArthur and Wilson 1967, Pianka 1970).  The classic survival curves (Deevey 1947) of *K*-selected species are generally Type I or II (Pianka 1970).  However, the survival curve for male black bears based on known fate telemetry data is closer to Type III in shape.  I believe this is because density dependence, from which *K*-selected (carrying capacity) species received their grouping, may not have played a substantial role in regulating this system (Chapter 3).  Additionally, in *r*-selected species, who's survival curves should theoretically look more similar to those derived for males bears on our study areas, mortality is supposed to be the result of "catastrophic, non-directed, density-independent" (Pianka 1970:593) factors.  I suggest that the reason male survival curves resemble *r*-selected, Type III curves is because they experienced relatively high

levels of hunting mortality that functioned as annual, catastrophic, and relatively

density-independent sources of mortality.  For females, who experienced

substantially lower harvest rates than males, survival curves resemble the Type II

curves we might expect from this *K*-selected species.

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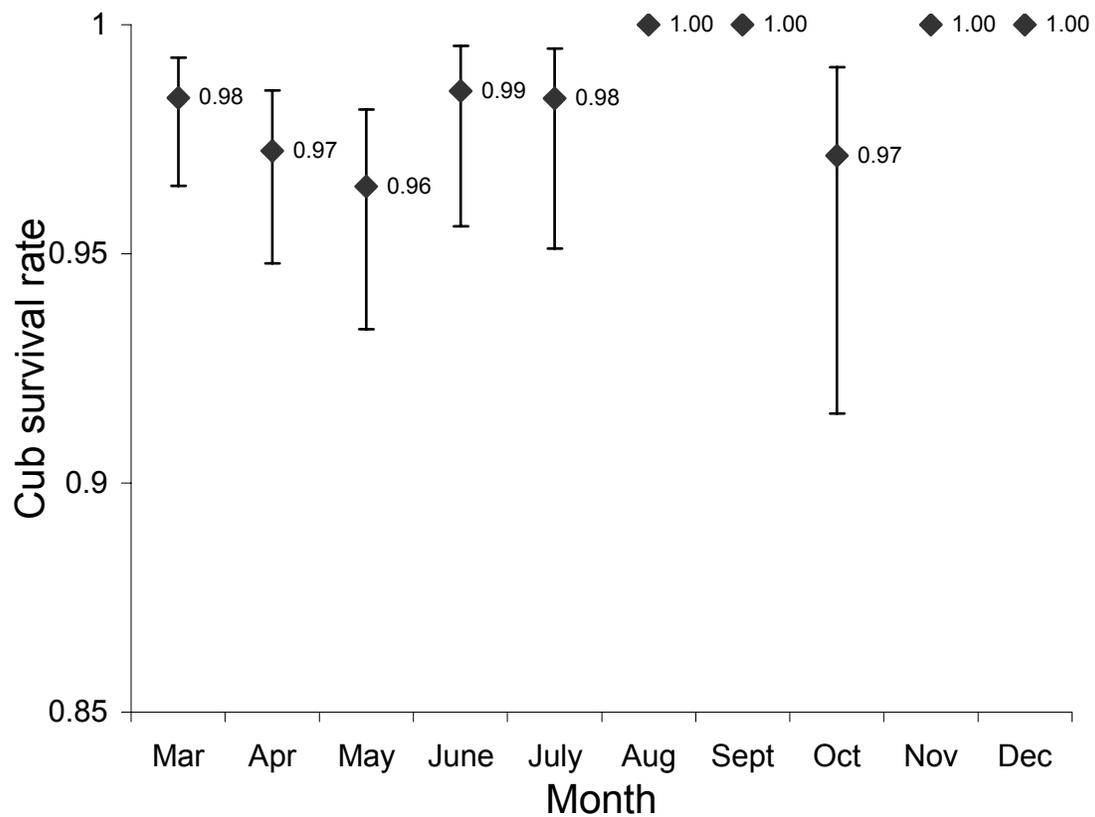
Figure 4.1. Estimated monthly (March–December) known fate survival rates and associated 95% confidence intervals for 131 (66M:65F) black bear cubs followed over 629 radio months from 1996–2002 in the Alleghany Mountains of western Virginia, USA.
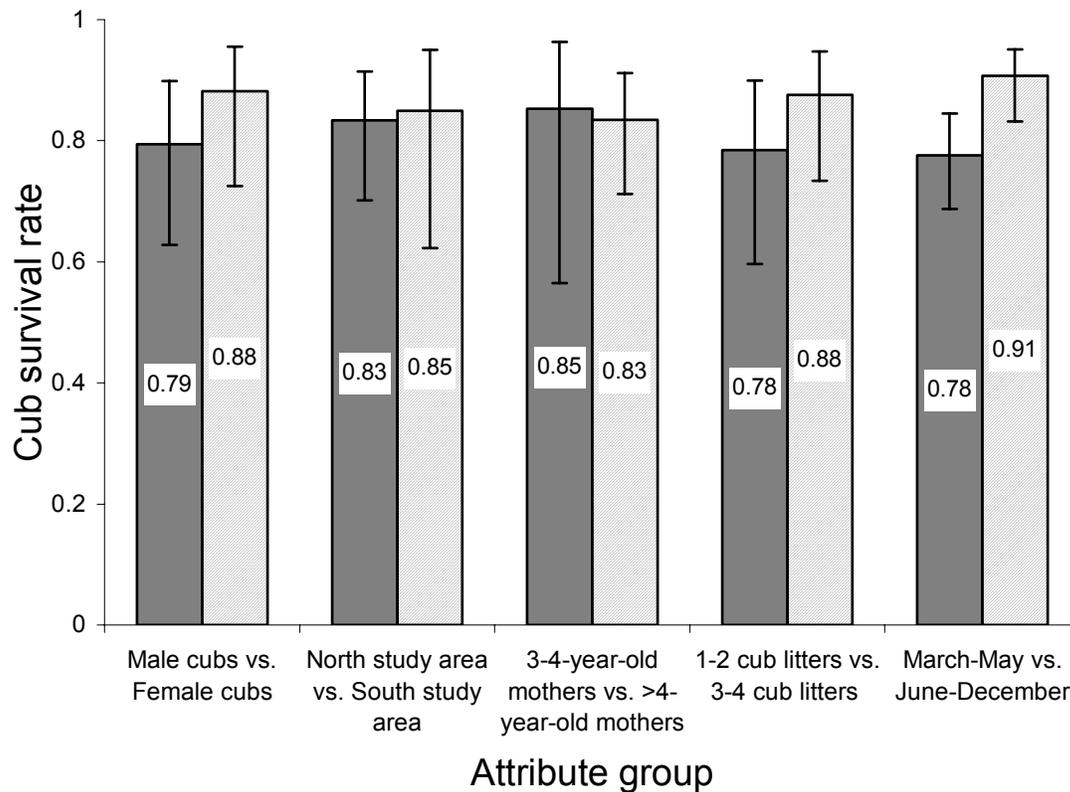
Figure 4.2. Estimated 10-month (March–December) survival rates of black bear cubs by attribute group derived from know-fate data from 131 (66M:65F) cubs followed over 629 radio months from 1996–2002 in the Alleghany Mountains of western Virginia, USA. March–May and June–December estimates are not survival rates during these intervals, but are survival rates that would be expected over 10-months if survival rates observed during these intervals (March–May versus June–December) were constant throughout the 10-month interval.
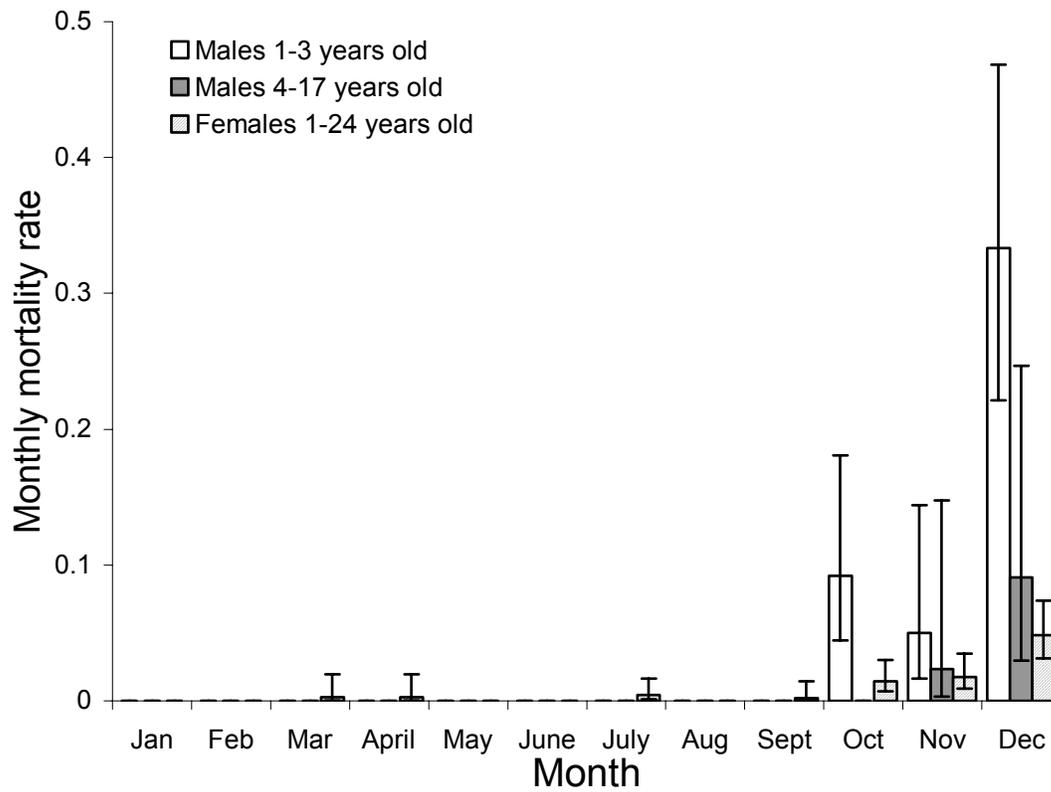
Figure 4.3. Sex- and age- (males) specific mortality rates for black bears based on known fate data collected from 399 individuals (154M:254F) tracked during 979 bear-years from 1994–2003 in the Alleghany Mountains of western Virginia, USA.
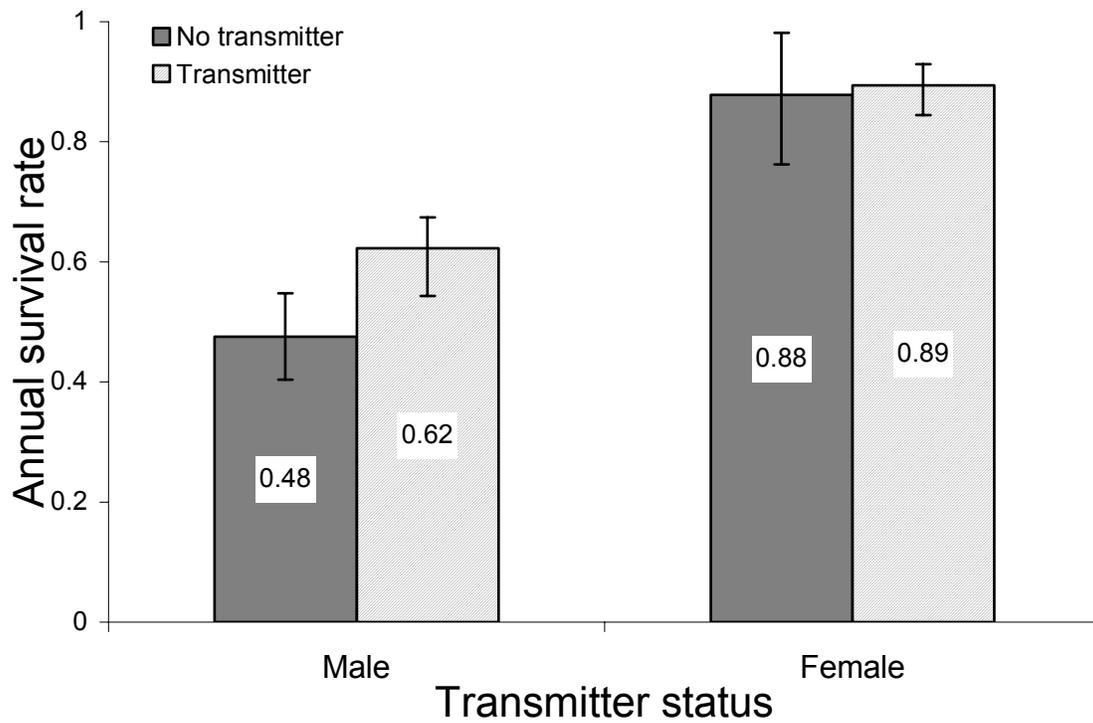
Figure 4.4. Sex-specific annual survival rates of black bears wearing transmitters versus bears not wearing transmitters based on tag-return data from 1,041 bears and 488 returned tags in the Alleghany Mountains of western Virginia, 1994–2002.
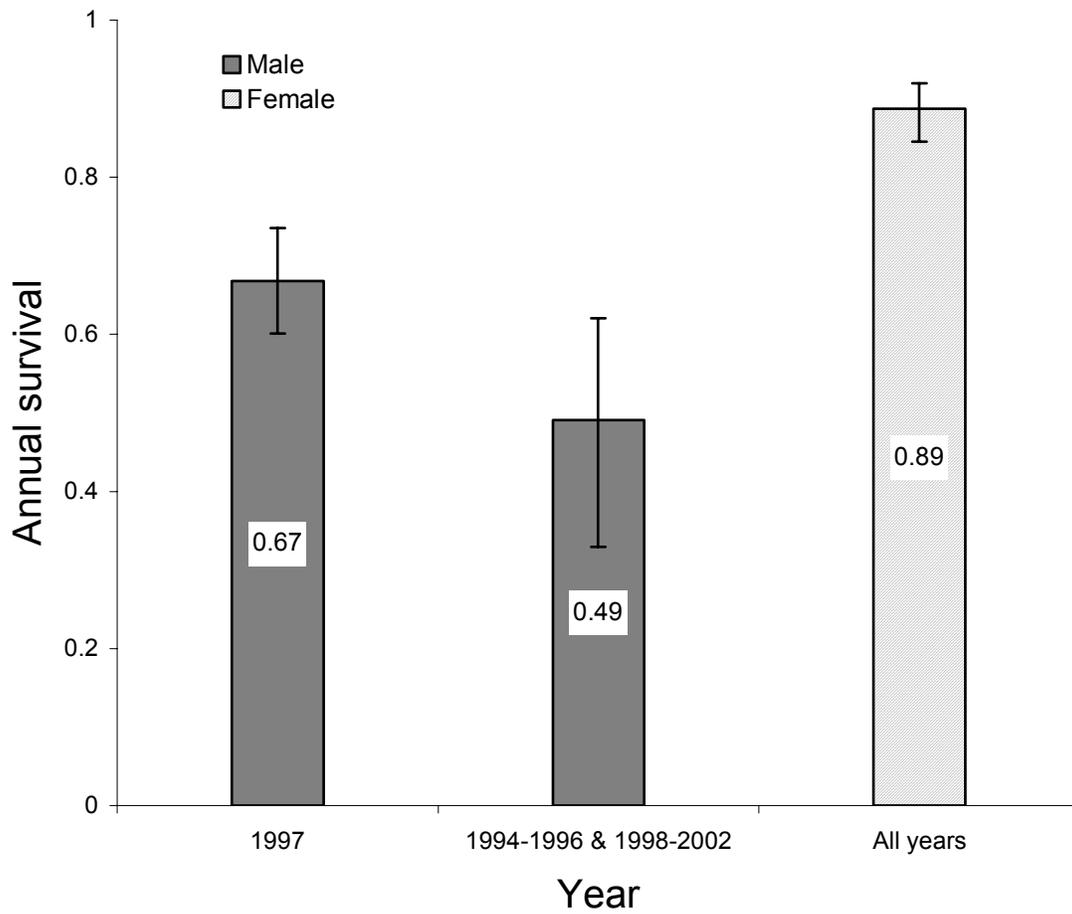
Figure 4.5. Black bear survival rates based on 1,041 marked black bears and 488 returned tags in the Alleghany Mountains of western Virginia, USA, yielded a best-supported model that had survival constant through years for females but differing in 1997 (following the mast failure) for males.
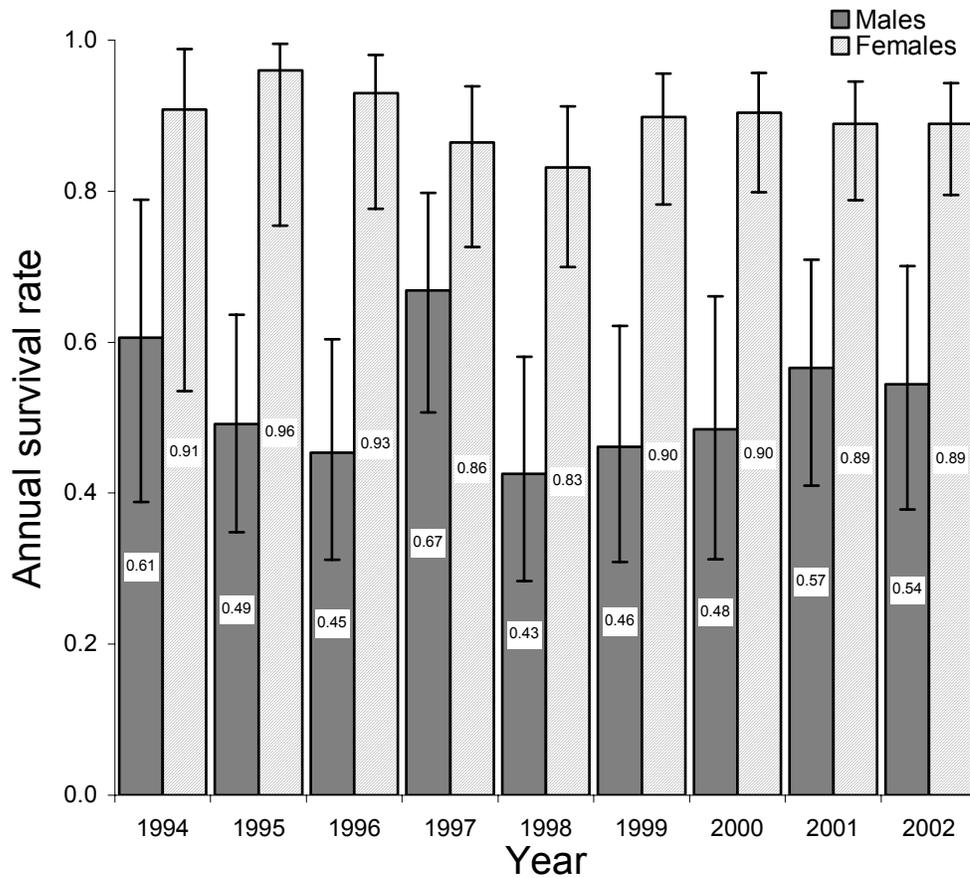
Figure 4.6.  Sex-specific annual survival rates based on 1,041 marked black bears and 488 returned tags collected in the Alleghany Mountains of western Virginia, 1994–2002.
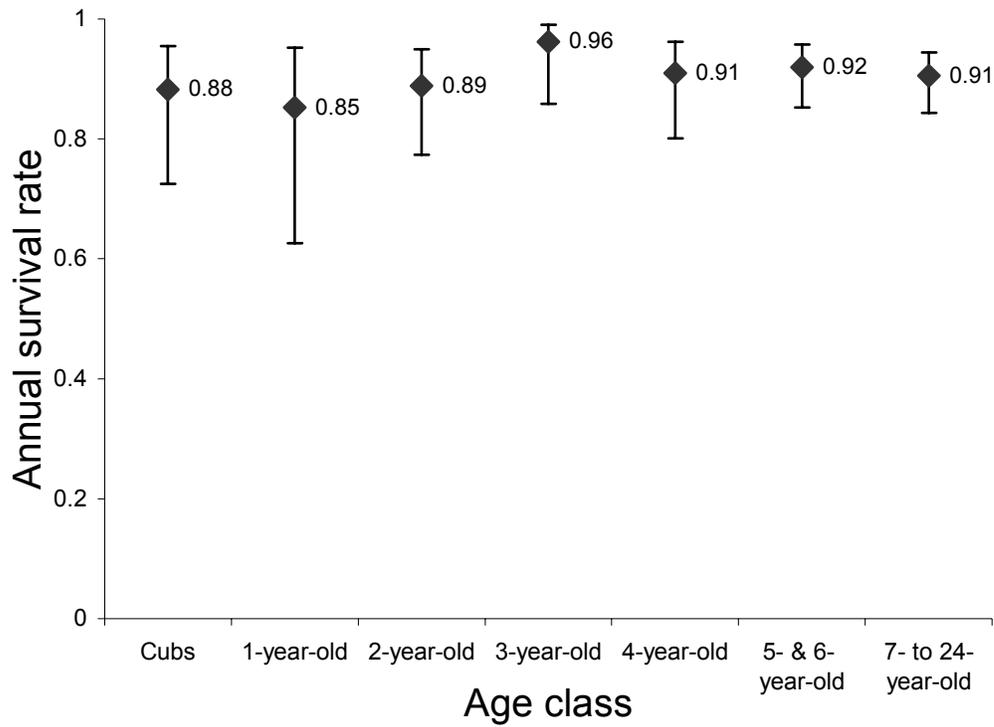
Figure 4.7.  Female black bear survival in all age classes from know-fate data collected from 65 female cubs and 254 females ≥1 year old during 1994–2003 in the Alleghany Mountains of western Virginia, USA.
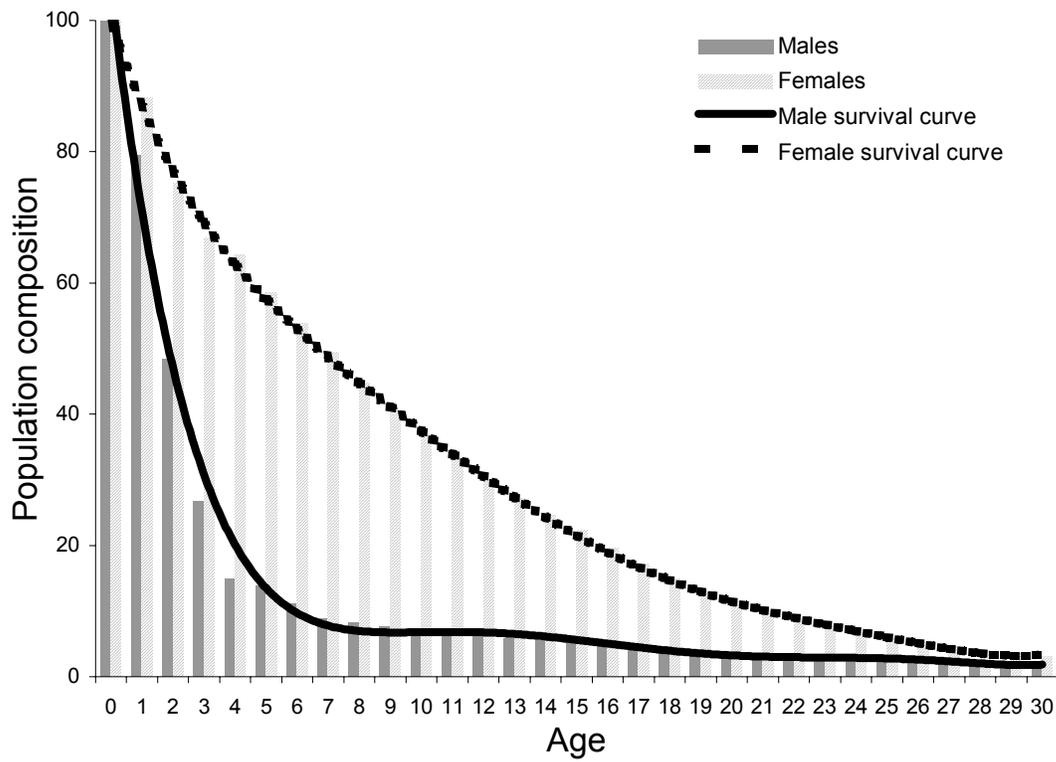
Figure 4.8.  Sex and age specific population composition and survival curves

based on know-fate data from 399 bears (154M:254F) collected from 1994–2003

in the Alleghany Mountains of western Virginia, USA.

Table 4.1. Variables used to development *a priori* models to investigate known fate survival rates (S) of ≤1-year-old American black bear cubs in the Alleghany Mountains of western Virginia, 1995–2003.

| Variable | Description |
| --- | --- |
| Female Age | Age of the adult female that bore the litter: 3–4 years old or ≥5 years old. |
| Litter Size | Size of the litter the cub was born into: 1–2 or 3–4. |
| Sex | Individual cub was male or female |
| $Time_2$ | Time steps pooled into 2 blocks:  March–May (pre den emergence) and June–December (post den emergence). |
| $Time_{10}$ | Time steps divided into 10 blocks: March, April, May, June, July, August, September, October, November and December. |

Table 4.2. Description of variables used in the development of *a priori* models used to investigate known fate survival rates of ≥1-year-old American black bears in the Alleghany Mountains of western Virginia, 1994–2003.

| Variable | Description |
| --- | --- |
| $Age_6$ | Age classifications grouped for 1-, 2-, 3-, 4-, 5–6, and ≥7-year-olds |
| $Age_2$ | Age classifications grouped for 1–3 (subadults) and ≥4-year-olds (adults) |
| $Age_{sex3}$ | Age classifications grouped for 1–3 (subadults) males, ≥4-year-olds (adults) males and 1–24-year-old females |
| Sex | Individual bear was male or female |
| Study Area | Individuals lived on our northern or southern study area |
| $Time_{12}$ | Annual survival rates based on 12 monthly time steps, January–December |
| $Time_3$ | Annual survival rates based on 3 time steps, January–September (non-hunting season), October–November (archery and general firearms), and December (hound hunting) |

Table 4.3.  Variables used to develop *a priori* models used to investigate tage

return survival rates of ≥1-year-old American black bears from 1994–2002 on 2

study areas in the Alleghany Mountains, of western Virginia, USA.

| Variable | Description |
|---|---|
| Sex | Individual bear was male or female |
| $Sex_{1997}$ | Interaction between sex and year: males in 1997, males in all other years, females in 1997, and females in all other years |
| $Male_{1997}$ | Interaction between sex and year for males but not females: males in 1997, males in all other years, and females in all years |
| Study Area | Individual lived on our northern or southern study area |
| Time | Annual time steps, 1994–2002 |
| Trans | Individual bear was equipped with a radio transmitter |
| $Trans_1$ | Recovery probability was constant for bears not wearing transmitters and fixed at 1.0 for bears wearing transmitters |

Table 4.4. Description of variables used in the development of *a priori* models used to investigate combined capture-recapture and tag return survival rates of ≥1-year-old American black bears on a 100-km$^2$ grid from 1998–2002 in Rockingham County, Virginia, USA.

| Variable | Description |
| --- | --- |
| Sex | Individual bear was male or female |
| Time | Annual time steps, 1998–2002 |
| Trans | Equipped with a radio transmitter |
| $Trans_1$ | Recovery probability was constant for bears not wearing transmitters and fixed at 1.0 for bears wearing transmitters |

Table 4.5. Model selection for know fate data gathered to quantify actual survival rate (S) for black bear cubs during 1995–2002 in the Alleghany Mountains of western Virginia, USA.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Time$_2$)} | 0.00 | 0.62 | 1.00 | 2 |
| {S(Time$_{10}$)} | 1.54 | 0.29 | 0.46 | 10 |
| {S(.)} | 4.76 | 0.06 | 0.09 | 1 |
| {S(Litter Size)} | 5.77 | 0.01 | 0.02 | 2 |
| {S(Sex)} | 5.79 | 0.01 | 0.02 | 2 |
| {S(Female Age)} | 6.74 | 0.01 | 0.01 | 2 |
| {S(Female Age*Litter Size*Sex)} | 16.84 | 0.00 | 0.00 | 8 |
| {S(Female Age*Litter Size*Sex*Time$_{10}$)} | 122.55 | 0.00 | 0.00 | 80 |

Table 4.6.  Annual survival rates for based known fate, tag return, combined capture and tag return, and direct return survival models.  Parameters are based on the most highly supported model in each analysis (known fate, tag return, and combined capture and tag return) in which model selection was employed to rank competing model.  Data for survival analyses of black bears were gathered in the Alleghany Mountains of Virginia, USA.

| Sex | Age class (years) | Model | Years | Annual survival rate | 95% C.I. |
|---|---|---|---|---|---|
| Both | <1 (cubs) | Known fate | 1994–2003 | 0.87 | 0.82–0.90 |
| Male | 1–3 | Known fate | 1994–2003 | 0.57 | 0.45–0.69 |
| Male | 1–3 | Direct returns | 1994–2002 | 0.64 | 0.61–0.68 |
| Male | 4–17 | Known fate | 1994–2003 | 0.89 | 0.74–0.96 |
| Male | 4–17 | Direct returns | 1994–2002 | 0.79 | 0.72–0.85 |
| Male | 1–17 | Direct returns | 1994–2002 | 0.68 | 0.65–0.71 |
| Male | 1–17 | Combined | 1998–2002 | 0.57 | 0.48–0.65 |
| Male | 1–17 | Tag return | 1994–1996 & 1998–2002 | 0.49 | 0.42–0.56 |
| Male | 1–17 | Tag return | 1997 | 0.67 | 0.51–0.80 |
| Female | 1–3 | Direct returns | 1994–2002 | 0.91 | 0.87–0.94 |
| Female | 4–24 | Direct returns | 1994–2002 | 0.92 | 0.89–0.95 |
| Female | 1–24 | Direct returns | 1994–2002 | 0.91 | 0.89–0.94 |
| Female | 1–24 | Known fate | 1994–2003 | 0.91 | 0.88–0.93 |
| Female | 1–24 | Tag return | 1994–2002 | 0.89 | 0.85–0.92 |
| Female | 1–24 | Combined | 1998–2002 | 0.88 | 0.82–0.92 |

Table 4.7. Model selection to estimate survival rates (S) from known fate black bear survival data gathered during 1994–2002 in the Alleghany Mountains of western Virginia, USA.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Age$_{sex3}$*Time$_3$)} | 0.00 | 1.00 | 1.00 | 9 |
| {S(Time$_3$)} | 37.54 | 0.00 | 0.00 | 3 |
| {S(Age$_6$*Sex*Time$_3$)} | 38.42 | 0.00 | 0.00 | 36 |
| {S(Time$_{12}$)} | 47.58 | 0.00 | 0.00 | 12 |
| {S(Age$_{sex3}$)} | 171.46 | 0.00 | 0.00 | 3 |
| {S(Age$_6$*Sex)} | 181.42 | 0.00 | 0.00 | 12 |
| {S(Sex)} | 182.56 | 0.00 | 0.00 | 2 |
| {S(Age$_6$)} | 193.36 | 0.00 | 0.00 | 6 |
| {S(Age$_6$*Sex*Study Area)} | 197.86 | 0.00 | 0.00 | 24 |
| {S(.)} | 205.72 | 0.00 | 0.00 | 1 |
| {S(Area)} | 207.25 | 0.00 | 0.00 | 2 |
| {S(Age$_6$*Sex*Time$_{12}$)} | 227.66 | 0.00 | 0.00 | 144 |
| {S(Age$_6$*Sex*Study Area*Time$_{12}$)} | 507.36 | 0.00 | 0.00 | 288 |

Table 4.8. Monthly and annual survival rates for the most highly selected model based on known fate data and exploring survival rates for subadult and adult black bears gathered from 1994–2003 in the Alleghany Mountains of Virginia, USA.

| Mortality source | Sex | Age class (years) | January–September | October–November | December | Annual |
|---|---|---|---|---|---|---|
| All | Male | 1–3 | 1.00 (>0.99–1.00) | 0.93 (0.87–0.96) | 0.67 (0.53–0.78) | 0.57 (0.45–0.69) |
| All | Male | 4–17 | 1.00 (>0.99–1.00) | 0.99 (0.92–1.00) | 0.91 (0.75–0.97) | 0.89 (0.74–0.96) |
| All | Female | 1–24 | 1.00 (>0.99–1.00) | 0.98 (0.97–0.99) | 0.95 (0.93–0.97) | 0.91 (0.88–0.93) |
| | | | | | | |
| Hunting | Male | 1–3 | 1.00 (>0.99–1.00) | 0.93 (0.88–0.97) | 0.67 (0.55–0.80) | 0.58 (0.46–0.70) |
| Hunting | Male | 4–17 | 1.00 (>0.99–1.00) | 0.98 (0.94–1.00) | 0.95 (0.86–0.99) | 0.92 (0.80–0.97) |
| Hunting | Female | 1–24 | 1.00 (>0.99–1.00) | 0.98 (0.97–0.99) | 0.95 (0.93–0.97) | 0.92 (0.89–0.94) |

Table 4.9. Model selection to estimate hunting (natural mortalities censored) survival rates (S) from known-fate black bear survival data gathered during 1994–2002 in the Alleghany Mountains of western Virginia, USA.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Age$_{sex3}$*Time$_3$)} | 0.00 | 1.00 | 1.00 | 9 |
| {S(Time$_3$)} | 32.95 | 0.00 | 0.00 | 3 |
| {S(Age$_6$*Sex*Time$_3$)} | 34.95 | 0.00 | 0.00 | 36 |
| {S(Time$_{12}$)} | 51.00 | 0.00 | 0.00 | 12 |
| {S(Age$_{sex3}$)} | 184.20 | 0.00 | 0.00 | 3 |
| {S(Age$_6$*Sex)} | 188.88 | 0.00 | 0.00 | 12 |
| {S(Age$_6$)} | 196.10 | 0.00 | 0.00 | 6 |
| {S(Sex)} | 200.33 | 0.00 | 0.00 | 2 |
| {S(Age$_6$*Sex*Study Area)} | 208.45 | 0.00 | 0.00 | 24 |
| {S(.)} | 220.14 | 0.00 | 0.00 | 1 |
| {S(Area)} | 221.24 | 0.00 | 0.00 | 2 |
| {S(Age$_6$*Sex*Time$_{12}$)} | 735.69 | 0.00 | 0.00 | 144 |
| {S(Age$_6$*Sex*Study Area*Time$_{12}$)} | 531.73 | 0.00 | 0.00 | 288 |

Table 4.10.  Model selection to estimate natural (hunting mortalities censored)

survival rates (S) from known-fate black bear survival data gathered during

1994–2002 in the Alleghany Mountains of western Virginia, USA.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(.)} | 0.00 | 0.41 | 1.00 | 1 |
| {S(Area)} | 1.39 | 0.21 | 0.50 | 2 |
| {S(Sex)} | 1.73 | 0.17 | 0.42 | 2 |
| {S(Age$_{sex3}$)} | 2.67 | 0.11 | 0.26 | 3 |
| {S(Time$_3$)} | 3.59 | 0.07 | 0.17 | 3 |
| {S(Age$_6$)} | 5.31 | 0.03 | 0.07 | 6 |
| {S(Time$_{12}$)} | 11.06 | 0.00 | 0.00 | 12 |
| {S(Age$_{sex3}$*Time$_3$)} | 11.15 | 0.00 | 0.00 | 9 |
| {S(Age$_6$*Sex)} | 12.24 | 0.00 | 0.00 | 12 |
| {S(Age$_6$*Sex*Study Area)} | 32.01 | 0.00 | 0.00 | 24 |
| {S(Age$_6$*Sex*Time$_3$)} | 50.17 | 0.00 | 0.00 | 36 |
| {S(Age$_6$*Sex*Time$_{12}$)} | 249.24 | 0.00 | 0.00 | 144 |
| {S(Age$_6$*Sex*Study Area*Time$_{12}$)} | 553.80 | 0.00 | 0.00 | 288 |

Table 4.11.  Model selection to estimate survival (S) from recovery probability (r) and tag return data for 1,041 marked bears and 488 returned tags collected during 1994–2002 in the Alleghany Mountains of western Virginia, USA. S = survival and r = recovery probability.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Males$_{1997}$) r(.)} | 0.00 | 0.43 | 1.000 | 4 |
| {S(Sex*Trans) r(.) } | 1.31 | 0.23 | 0.52 | 5 |
| {S(Sex$_{1997}$) r(.) | 1.70 | 0.19 | 0.43 | 5 |
| {S(Sex) r(.)} | 2.24 | 0.14 | 0.33 | 3 |
| {S(Sex*Trans) r(Trans$_1$)} | 7.74 | 0.01 | 0.02 | 5 |
| {S(Sex*Study Area*Trans) r(.)} | 8.92 | 0.01 | 0.01 | 9 |
| {S(Sex*Study Area*Trans) r(Sex*Study Area*Trans)} | 20.69 | 0.00 | 0.00 | 16 |
| {S(Sex*Time) r(.)} | 23.00 | 0.00 | 0.00 | 19 |
| {S(Trans) r(.)} | 52.23 | 0.00 | 0.00 | 3 |
| {S(Trans) r(Trans)} | 54.22 | 0.00 | 0.00 | 4 |
| {S(1997) r(.)} | 76.51 | 0.00 | 0.00 | 3 |
| {S(.) r(.)} | 77.47 | 0.00 | 0.00 | 2 |
| {S(Study Area) r(.)} | 79.48 | 0.00 | 0.00 | 3 |
| {S(Time) r(.)} | 86.56 | 0.00 | 0.00 | 10 |
| {S(Sex*Study Area*Trans*Time) r(.)} | 106.58 | 0.00 | 0.00 | 73 |
| {S(Sex*Study Area*Trans*Time) r(Sex*Study Area*Trans*Time)} | 266.68 | 0.00 | 0.00 | 144 |

Table 4.12.  Model selection from physical capture-recapture and tag return data using Burnham's combined model for black bear data gathered during 1998–2002 in Rockingham County, Virginia, USA. S= survival, p = capture probability, r = recovery probability, F = fidelity.

| Model | $\Delta_i$ | $\omega_i$ | Model Likelihood | K |
|---|---|---|---|---|
| {S(Sex) p(.) r(Trans$_1$) F(.)} | 0.00 | 0.87 | 1.00 | 5 |
| {S(Sex) p(.) r(Sex*Trans) F(.)} | 5.72 | 0.05 | 0.06 | 8 |
| {S(Sex) p(.) r(.) F(.)} | 6.15 | 0.04 | 0.05 | 5 |
| {S(Sex) p(Sex) r(Sex) F(Sex)} | 7.33 | 0.02 | 0.03 | 8 |
| {S(Sex*Trans) p(Sex*Trans) r(Sex*Trans) F(Sex*Trans)} | 8.63 | 0.01 | 0.01 | 16 |
| {S(Sex*Trans) p(.) r(.) F(.)} | 10.25 | 0.01 | 0.01 | 7 |
| {S(Sex*Trans) p(Sex) r(Sex) F(Sex)} | 10.40 | 0.00 | 0.00 | 10 |
| {S(Sex*Time) p(.) r(.) F(.)} | 15.18 | 0.00 | 0.00 | 11 |
| {S(Time) p(Sex) r(Sex) F(Sex)} | 24.50 | 0.00 | 0.00 | 11 |
| {S(Trans) p(Trans) r(Trans) F(Trans)} | 24.73 | 0.00 | 0.00 | 8 |
| {S(Sex*Trans*Time) p(Sex*Trans) r(.) F(Sex*Trans)} | 27.07 | 0.00 | 0.00 | 29 |
| {S(Sex*Trans*Time) p(Sex*Trans) r(Sex*Trans) F(Sex*Trans)} | 29.58 | 0.00 | 0.00 | 32 |
| {S(Sex*Time) p(.) r(Trans$_1$) F(.)} | 31.53 | 0.00 | 0.00 | 12 |
| {S(Sex*Time) p(Time) r(Time) F(Time)} | 32.48 | 0.00 | 0.00 | 21 |
| {S(Trans) p(.) r(.) F(.)} | 32.76 | 0.00 | 0.00 | 5 |
| {S(.) p(.) r(.) F(.)} | 37.13 | 0.00 | 0.00 | 4 |
| {S(Time) p(.) r(.) F(.)} | 44.83 | 0.00 | 0.00 | 8 |
| {S(Sex*Time) p(Sex*Time) r(Sex*Time) F(Sex*Time)} | 50.56 | 0.00 | 0.00 | 32 |
| {S(Time) p(.) r(Trans$_1$) F(.)} | 51.61 | 0.00 | 0.00 | 7 |
| {S(Time) p(Time) r(Time) F(Time)} | 60.44 | 0.00 | 0.00 | 16 |
| {S(Sex*Trans*Time) p(Sex*Trans*Time) r(Sex*Trans*Time) F(Sex*Trans*Time)} | 159.63 | 0.00 | 0.00 | 80 |

Table 4.13.  Comparison of annual survival rates for subadult (1–3-year-old) and adult (≥4-year-old) American black bears across their range in North America.

| Age | Sex | Region | Survival rate | Citation |
| --- | --- | --- | --- | --- |
| Adult | F | Montana | 0.79 | (Kasworm and Thier 1994) |
| Adult | F | Minnesota | 0.81 | (Rogers 1976) |
| Adult | F | Alaska | 0.85 | (Schwartz and Franzmann 1991) |
| Adult | F | Virginia | 0.87 | (Hellgren and Vaughan 1989) |
| Adult | F | Ontario | 0.88 | (Kolenosky 1986) |
| Adult | F | Alaska | 0.89 | (Schwartz and Franzmann 1991) |
| Adult | F | Florida | 0.89 | (Dobey et al. 2005) |
| Adult | F | Virginia | 0.90 | (Kasbohm et al. 1996) |
| Adult | F | Virginia | 0.91 | This study |
| Adult | F | Virginia | 0.92 | (Carney 1985) |
| Adult | F | Mexico | 0.94 | (Doan-Crider and Hellgren 1996) |
| Adult | F | Colorado | 0.96 | (Beck 1991) |
| Adult | F | Arkansas | 0.98 | (Clark and Smith 1994) |
| Adult | M | Virginia | 0.50 | (Kasbohm et al. 1996) |
| Adult | M | Virginia | 0.59 | (Hellgren and Vaughan 1989) |
| Adult | M | Virginia | 0.59 | (Carney 1985) |
| Adult | M | Colorado | 0.70 | (Beck 1991) |
| Adult | M | Florida | 0.71 | (Dobey et al. 2005) |
| Adult | M | Minnesota | 0.73 | (Rogers 1976) |
| Adult | M | Ontario | 0.77 | (Kolenosky 1986) |
| Adult | M | North Carolina | 0.82 | (Beringer et al. 1998) |
| Adult | M | North Carolina | 0.83 | (Powell et al. 1996) |
| Adult | M | Arkansas | 0.85 | (Clark and Smith 1994) |
| Adult | M | North Carolina | 0.89 | (Beringer et al. 1998) |
| Adult | M | Virginia | 0.89 | This study |
| Subadult | F | Colorado | 0.76 | (Beck 1991) |
| Subadult | F | Massachusetts | 0.88 | (Elowe and Dodge 1989) |
| Subadult | F | Virginia | 0.91 | This study |
| Subadult | M | Massachusetts | 0.25 | (Elowe and Dodge 1989) |
| Subadult | M | Alaska | 0.38 | (Schwartz and Franzmann 1991) |
| Subadult | M | Virginia | 0.57 | This study |
| Subadult | M | Alaska | 0.70 | (Schwartz and Franzmann 1991) |
| Subadult | M | Mexico | 0.88 | (Doan-Crider and Hellgren 1996) |
| Subadult | M | Colorado | 0.94 | (Beck 1991) |

# CHAPTER 5: MODELING POPULATION AND HARVEST

**ABSTRACT**

Population and harvest modeling techniques use observed input parameters to estimate and project population characteristics and can be useful tools for black bear (*Ursus americanus*) management. I constructed Leslie Matrix models using data and associated input parameters from our completed dataset. This model yielded a λ estimate of 1.17, which was substantially larger than the λ estimate of 1.04 derived from previous analysis of the incomplete dataset. This model was most sensitive to changes in adult female (≥3-year-old) survival and this parameter might be adjusted by modifying hunting mortality rates. A more biologically realistic model incorporating mast-failure-induced reproductive failures at 3–10-year-intervals produced λ values of 1.11–1.15. To stabilize the growth of the population (λ = 1.00) with reproductive failure accounted for in the model, annual ≥3-year-old female survival needed to be decreased from the observed level of 0.91 to 0.66–0.74 (depending on mast failure frequency). Modeling population growth and harvest rate with Program RISKMAN, I calculate a population harvest rate of 12% and a resultant λ of 1.16. Using this model, total harvest (males and females) would need to increase from 12% to 29% to stabilize population growth. The Leslie Matrix model incorporating mast-failure-induced reproductive failures currently provides a data-supported and parsimonious model and should be useful for managing Virginia's hunted black bear population. Modeling in Program RISKMAN provides support

for this Leslie Matrix model and may prove to be a valuable tool for future

modeling efforts.  Managers should use caution when applying estimates from

these models to the statewide population because these models were

constructed based largely on data from an apparently highly productive

population in Rockingham County, Virginia.


**INTRODUCTION**

Black bears are a high-profile wildlife species and the public values bears

for a wide variety of reasons including as game animals and for wildlife viewing

(Kellert 1994, Koch 1994).  As illustrated in the Virginia black bear management

plan (2001), managers must take into account into account cultural carrying

capacity (Decker 1993) as well as biological carrying capacity, and must have

sufficient biological data to support their management decisions and practices

(Loker 1994, Loker and Decker 1995, Cichowski 2000).

Modeling allows researchers and managers to synthesize complex

demographic data to better predict and manage populations (Bunnell and Tait

1980, Starfield and Bleloch 1986).  Relatively few published studies have

attempted to model harvest in black bear populations.  Maximum sustainable

levels of harvest were calculated as 15% in Maine (McLaughlin 1998) 14% in

Alaska (Miller 1990) and 12.6% in Florida (Dobey et al. 2005).  In analyzing a

subset of data from this study, Klenzendorf (2002) calculated that Virginia's black

bear population could sustain 21% annual harvest of the adult (≥3-year-old)

female population.

Previous black bear research in Virginia focused on unhunted populations in the Shenandoah National Park in the western portion of the state (Carney 1985, Kasbohm et al. 1996) and the Great Dismal Swamp in the southeastern corner of the state (Hellgren and Vaughan 1989).  The increasing in bear harvest documented through time in Virginia (Martin and Steffen 2000) would seemingly indicate a growing population; however, harvest may not be a consistently reliable tool for tracking bear populations (Harris and Metzgar 1987, Burton et al. 1994, Noyce and Garshelis 1997.

In response to the need to better understand and manage Virginia's bear population, in 1994 the Virginia Polytechnic Institute and State University and the Virginia Department of Game and Inland Fisheries (VDGIF; among numerous other collaborators) initiated the Cooperative Alleghany Bear Study (CABS) to intensively examine the long-term, broad-scale dynamics of Virginia's hunted black bear population.  I had 2 objectives in this portion of my research.  First, I constructed a Leslie Matrix model to examine population growth rate and determine how population growth might be stabilized.  Second, I explored a new software package called Program RISKMAN (Taylor et al. 2001), which was designed to model harvest and growth in bear populations.  My goal was to determine if this modeling package might provide support for my Leslie Matrix model and to determine if it might be a useful tool for future modeling and management of Virginia's black bear population.

**STUDY AREAS**

Our research was conducted on 2 study areas in the Alleghany Mountains of western Virginia, USA.  The centers of the 2 study areas were approximately 160 km apart; both were located largely on the George Washington-Jefferson National Forests.  The northern study area was centered near Reddish Knob at 38° 28' N, 79° 15' W.  It was approximately 840 km$^2$ primarily in Augusta and Rockingham Counties.  The southern study area was 1,544 km$^2$ and was centered near Mountain Lake at 37° 22' N, 80° 31' W.  It was composed primarily of Craig, Giles, and Montgomery Counties.  Elevations on these 2 study areas ranged from 480–1,360 m (Kozak 1970) and common tree species included: eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*)*,* beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipfera*), eastern white pine (*P. strobus*), mountain laurel (*Kalmia latifolia*) and scrub oak (*Q. ilicifolia*; Rawinski et al. 1994).  At Mountain Lake, the center of the southern study area, high temperatures ranged from an average high of 24°C in July to an average low of -9°C in the January with total precipitation averaging 125 cm, including 134 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va5828). The closest weather station to our northern study area was at Dale Enterprises in the lowlands of Rockingham County.  Because it was in the lowlands, weather averages were likely warmer and drier than conditions in the adjacent mountains where our research was conducted.  At Dale Enterprises (38° 45' N, 78° 93' W),

temperatures ranged from an average high of 30°C in July to an average low of -5°C in January with total precipitation averaging 90 cm, including 63 cm of snow (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va2208).

Hunting season lengths varied slightly (≤ 7 days) among years.  Generally, September was marked by bear-hound training season during which bears could be pursued and treed with hounds, but not harvested.  The second week of October through the first week of November was archery-hunting season, during which bears could be harvested using archery equipment.  Gun season, during which bears could be killed with firearms, but not with the aid of dogs, was the last week of November.  Hound-hunting season, during which bears could be killed using firearms and with the aid of dogs, consisted of the first few days of December through the first Saturday in January.  One bear tag / year / hunter was sold with the combined deer, bear, and turkey license.  To be legally harvested bears had to weigh ≥45.5 kg live weight or ≥34.1 kg with all internal organs removed.  Adult females with cubs could not be legally harvested.  Law required that all harvested bears be checked at registered check stations. Checking a bear involved recording any tags, tattoos, and/or transmitters, determining sex of the individual, and removing a premolar for subsequent age determination.

## METHODS

### General

We captured bears with Aldrich spring-loaded foot snares and culvert

traps (Johnson and Pelton 1980) from late May through late August 1994–2002.

We initiated trapping on our northern study area in 1994 and on our southern

study area in 1995.  We sedated captured bears with a mixture of ketamine

hydrochloride and xylazine hydrochloride (200:100 mg/ml; 1 ml/45.5 kg; White et

al. 1996) administered via dart pistol, blowpipe, or jab stick.  After bears were

sedated, we determined their sex, weighed them, recorded morphometric

measurements, and examined females for signs of estrus or lactation.  To

determine age, we removed a premolar (Willey 1974), which was sent to

Matson's Laboratory (Milltown, Montana, USA) for cementum annuli analysis.

We also tattooed bears' upper lips, and attached individually numbered, plastic,

perma-flex, stud-style eartags (National Band and Tag, Newport, Kentucky, USA)

to all bears ≥6 months old.  We attached motion-sensitive radio transmitters to

bears selected in an attempt to keep our sex ratio of transmittered animals at

approximately 1M:3F.  Bears ≥1 year old received collars (Advanced Telemetry

Systems [ATS], Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada;

Telonics, Mesa, Arizona, USA, Wildlife Materials International, Murphysboro,

Illinois, USA) that were equipped with breakaway cotton spacers (Hellgren et al.

1988) or eartag transmitters (Servheen et al. 1981) from ATS.  We administered

a tetracycline antibiotic to prevent infection and serve as a permanent biomarker

in teeth and bones (Johnson 1964, Garshelis and Visser 1997).  Finally, we administered yohimbine hydrochloride (5mg/ml; 2 ml/45.5 kg) to reverse the xylazine hydrochloride.  Each week, we monitored and attempted to locate bears wearing transmitters.

Biologists from VDGIF conducted surveys in late August to early September to quantify annual hard mast production (Sharp 1958, Coggin and Peery 1973).  Mast surveys involved examination of the same trees annually and quantifying the mean number of acorns / 10 limbs / tree (Fearer et al. 2002).  I used mast survey data collected by VDGIF (D. Martin, personal communication) for the 3 mast survey regions overlapping our study area to examine autumn hard mast availability.

In the late fall and winter, we used radio telemetry to locate dens of female bears wearing transmitters.  We returned to and entered (Godfrey et al. 2000) these dens in January–April to gather reproductive data, change transmitters on adults, attach transmitters to cubs (Echols 2000, Vashon et al. 2003) and yearlings, and deploy remote cameras (Bridges et al. 2004).  The Virginia Polytechnic Institute and State University Animal Care and Use Committee (98-069-F&W) approved all animal handling protocols.

**Leslie Matrix model**

Life-stage Leslie-Matrices (Leslie 1945) are based only on female survival and reproductive parameters.  They assume there are always enough males to fertilize females and thus males are of minimal importance to population growth.  They calculate λ from the dominant eigenvalue from the matrix (Gotelli 1998).

To construct my Leslie Matrix model, I first developed parameter estimates from the completed data set (1994–2003 and including both study areas).  Reproductive parameters were quantified for 3–≥6-year-old females (Chapter 1).  Leslie Matrices use number of female offspring produced / year as reproductive parameters.  This number was calculated by dividing mean age-class-specific litter size (LS) by 4 to get the number of female cubs produced / female in that age class / year.  The divisor, 4, comes from assuming a 1M:1F sex ratio (SR; 1/0.50=2.00) and assuming bears reproduce every 2 years (litter production frequency [LPF]).  For example, 3-year-old females had 1.50 cubs / litter (Chapter 1) and 1.50/(2.0*2.0) = 0.38 female cubs / year.  To examine the effects of mast-failure-induced reproductive failure (Chapter 1), I modeled how the mean number of female cubs produced / year would be affected by mast failures frequencies (MFF) ranging from 3–10 years in periodicity.  This resulted in modified LPF values:

$$LPF = 100 / ((50-100*0.5*(1/MFF))$$

$$\text{Age specific female cub production / female / year} = LS / (SR*LPF)$$

I used age-specific survival rates derived from known fate estimates because I believed these were my best age-specific estimates for females, there was no evidence that wearing a transmitter influenced female survival, and these estimates were consistent with other estimation techniques including direct return

estimates, tag return models, and Burnham's combined model estimates
(Chapter 4).  Parameter estimates used in the model are listed in Tables 5.1 and
5.2.

I used parameter estimates at the lower and upper bound of 95% C.I.s on
these parameters to evaluate the lowest and highest growth rate that could be
derived from the variance in the data.  Additionally, I conducted sensitivity
analyses by incrementally lowering single parameters (reproduction, cub [<1-
year-old] survival, subadult [1–2-year-old] survival, and adult [≥3-year-old]
survival; lowered by in increments of 0.05) while keeping all other parameters
constant.  Finally, I used these new estimates to update associated harvest
recommendations with the ultimate goal of stabilizing the growth rate of the black
bear population in Virginia.

**Modeling using Program RISKMAN**

I used Program RISKMAN (Taylor et al. 2001) which uses a life-table
approach to model population dynamics in relation to harvest for taxa such as
bears that reproduce at >1-year-intervals.  The model has 4 primary inputs,
which are reproduction, natural survival, harvest rate, and initial population
structure.  The sequence of events in Program RISKMAN is:  1) population
census, 2) natural mortality, 3) reproduction, 4) harvest, and then 5) the next
year's census.  Reproductive parameters are based on the proportional
distribution of litter sizes, 1–4, produced by females in each age class and also
on the proportion of females producing litters every 2 years.  I used reproductive
data from den-site visitations (Chapter 1) to construct litter size proportions

(Table 5.3).  Because bears on our study missed few reproductive opportunities, but apparently experienced mast-induced reproductive failures approximately every 5 years, I set the proportion of females producing litters every year to 0.8 (1 missed reproductive opportunity in 5).  Based on my mean unbiased (Garshelis et al. 1998) estimate of age at primiparity (3.8 years), I set the proportion of 3-year-old females producing cubs to 0.2 (20% of 3-year-olds succeeded in raising litters).  I used an expected cub sex ratio of 1M:1F.

I used the survival rates that excluding hunting mortality derived from known fate analyses as the input parameters for natural survival (Chapter 4). Natural survival rates were 0.87 for cubs and 0.98 for ≥1-year-old bears (Table 5.4).

Harvest data parameters were derived from direct returns (Chapter 4). Relative vulnerability to harvest was based on the proportion of each age and sex class harvested annually and was 0.36 for 1–3-year-old males, 0.09 for 1–3-year-old females, 0.21 for ≥4-year-old males, and 0.08 for ≥4-year-old females (Table 5.4).

I calculated proportion of bears harvested based on several steps.  First I took the age- and sex-specific direct return numbers and multiplied them by natural survival rates to get overall survival rates.  I then input these parameters into Program RISKMAN as natural survival.  I then set harvest rate to 0, and using the previously defined reproductive parameters, allowed Program RISKMAN to construct an expected stable sex and age distribution for the population.  I then divided this population into age and sex groupings that

matched the direct return data.  I then assumed that we were taking the

proportions of the population derived from direct returns from this starting

population and divided this number by the total population (standardized to

1000).  For example:


Expected standing population distribution =

(288 cubs) + (186 males 1–3-years old )+ (239 females 1–3-years old) +

(53 males ≥4 years old) + and (234 females ≥4 years old)

= 1000 bears present


Age- and sex-specific harvest rate =

(288 x 0.00 = 0) + (186 x 0.36 = 67) + (239 x 0.09 = 22) + (53 x 0.21 = 11)

+(234 x 0.08 = 19)

= 119 bears harvested


Harvest rate =

(119 bears harvested) / (1000 bears present)

= 0.119 (11.9%)


I used the expected stable sex and age distribution for the population

standardize to 1000 bears with a maximum age of 25 (the age of the oldest

individual captured during our research) as the initial population structure for all

simulations. I ran 25-year simulations of each model. Because the parameter

outputs for approximately the first 1–15 years are partially based on the initial

population structure, I reported λ, proportion of females in the harvest, sex ratio

of the population, and final population size for the final run in the simulation at

$time_{25}$ (25 years from the initial run).

I then compared results from these simulations to output from the Leslie

Matrix model. Finally, I recommended how/when alteration of harvest rates or

survival rates might be observed or achieved and how they might then be applied

for management objectives such as stabilizing population growth.


**RESULTS**

**Leslie Matrix model**

The Leslie Matrix model based on mean reproductive parameters, no

mast failures, and observed survival rates (Figure 5.1) yielded λ = 1.17. Using

the lower and upper bounds on parameters (Figures 5.2 and 5.3), estimates of λ

were 1.12 and 1.21, respectively.

Examining sensitivity of the model to varying parameter estimates, the

model is most sensitive to adult female survival (Table 5.4). Individually varying

(while keeping all other parameters constant) adult female survival, subadult

female survival, cub survival, and reproduction over 18 intervals of 0.05 /

parameter yielded total differences in λ of 0.44, 0.26, 0.22, and 0.21,

respectively.

With the goal of stabilizing the population, $\lambda=1.00$, I found, keeping all other parameters as observed, that annual ≥3-year-old female survival needed to be decreased from 0.91 to 0.63 (Table 5.5).  My models of population growth including the influence of a mast-induced reproductive failures (Chapter 1) yielded $\lambda$ values ranging 1.11–1.15 for mast failure cycles ranging 3–10 years, respectively (Table 5.5).  Based on these models, stabilizing population growth could be accomplished by reducing adult female survival rates to 0.74–0.66 for mast failure cycles of 3–10 years, respectively.

**Modeling using Program RISKMAN**

I calculated the proportion of the population harvested as 0.12 (12%; as described in the methods section).  This harvest rate yielded a $\lambda$ of 1.16.  Harvest rates ≥ 30% resulted in a declining population while harvest rates ≤ 28% resulted in a growing population (Figure 5.6 and Table 5.6.)  To stabilize the population ($\lambda$ = 1.00), harvest rate was increased from 12% to 29%.  If hunting were removed and no density-dependent effects mitigated population growth, a hypothetical population of 1,000 bears would have a $\lambda=1.24$ and could grow to 261,756 in 25 years (Table 5.6.).

**DISCUSSION AND MANAGEMENT RECOMMENDATIONS**

Klenzendorf (2002) developed a Leslie Matrix model based on data gathered on our northern study area from 1994–1999.  My model was similar, but was based on 4 additional years of data (2000–2003) from the northern study area and 9 years of data (1995–2003) from the southern study area.

Additionally, I used reproductive estimates from 4 age classes while Klenzendorf

(2002) based her estimates on only 2 age classes.  Using the entire data set,

survival rate for all age classes of females increased as did estimates of age-

specific reproduction.  Accordingly, my estimate of λ increased to 1.17 from

Klenzendorf's (2002) estimate of 1.04.  Perhaps due to my additional data and

associated increased precision on my estimates, the range of my λ-values (1.12–

1.21) based on upper and lower bounds on parameter estimates was

substantially smaller than Klenzedorf's (0.73–1.26; 2002).  Likewise,

Klenzendorf's (2002) suggested that a ≥3-year-old female survival rate of 0.79

would stabilize population growth while my model suggests is our population

would require female survival of 0.63 to stabilize population growth.    Like

Klenzendorf's (2002) model, my model was most sensitive to survival rates of

adult females.

My estimate of λ from the Leslie Matrix model (1.17) was supported by the

estimate from the RISKMAN model (1.16).  Similarly, researchers in Florida used

Program RISKMAN to calculate λ = 1.18 for a non-hunted, but less productive

(overall mean litter size = 2.11 cub / litter versus 2.49 cubs / litter in our study)

population (Dobey et al. 2005).  If the goal of managers is to stabilize population

growth, as outlined in Virginia's black bear management plan (2001), annual

survival rate of females ≥3-years-old would need to be decreased from 0.91 to 0.

63.  This model, however, does not take into account mast-failure-induced

reproductive failure.

I believe a more biologically realist model incorporates reproductive

failures, which I documented and described in Chapter 1, but which were not

included in earlier modeling efforts (Klenzendorf's 2002). These reproductive

failures appear to occur in response to hard mast failures. The periodicity of

these failures is difficult to calculate because, based on my evaluation of relevant

surveys from Virginia (Martin and Steffen 2000) and West Virginia (Pack and Igo

2004), the frequency appears to have increased in recent years. Additionally,

determining which years exceeded the threshold that may be necessary to affect

reproduction (Costello et al. 2003) is difficult to determine and, in the years prior

and subsequent to our study, is subjective. However, based on data from our

research and mast reports from Virginia (Martin and Steffen 2000) and West

Virginia (Pack and Igo 2004), it appears that these failures are currently occurring

approximately every 5 years. Fortunately, perfect documentation of biologically

significant mast failures appears unnecessary, as estimated population growth

rates and target adult female survival rates to stabilize growth were similar for

mast failure frequency ranging from 4–10 years ($\lambda$=1.12–1.15, stabilizing adult

female survival rate 0.66–0.71; Table 5.5).

Based on an approximation of a mast failure every 5 years, my Leslie

Matrix model produced a $\lambda$ of 1.13. To stabilize the growth of the population with

reproductive failure accounted for in the model, annual adult female survival

needed to be decreased from 0.91 to 0.70. I believe this model (and those with

similar mast failure periodicities; Figure 5.4 and Table 5.5) offers the best

approximation of reality available from our data set and modeling efforts.

Using a life-table approach in Program RISKMAN, results were similar and indicated that at the estimated current harvest rate of 12% of the standing population, λ was 1.16.  To stabilize the population growth (λ = 1.00), total harvest rate needed to be increased from 12% to 29%.

Program RISKMAN was written by Dr. Mitchell Taylor, who also authored the Program ANURSUS (Taylor et al. 1987).  He designed this program to model population dynamics in relation to harvest for taxa such as bears that reproduce at >1-year-intervals and it has become a popular modeling tool for bear managers (Eastridge and Clark 2001, Taylor et al. 2002, McLoughlin et al. 2003, Dobey et al. 2005).   Program RISKMAN uses a life table approach (Caughley 1977), which theoretically offers advantages over Leslie Matrix (Leslie 1945) models because it does not assume simultaneous female survival and reproduction.  The theoretical advantage of the life table approach is that by assuming that females must survive the year prior to reproducing, heterogeneity in individual female survival can influence annual reproduction and thus a more realistic population viability model can be constructed (Taylor and Carley 1988, White 2000).

Program RISKMAN provides a determinist or stochastic option for population modeling.  I use a deterministic model to explore our population.  However, a stochastic model incorporating environmental and parameter uncertainly estimates might be of interest in future analyses.  Program RISKMAN provides a stochastic option that incorporates variance in parameter estimates and uses random Bernoulli trials taken from the mean and standard error for

each population parameter.  Monte Carlo simulations are used to produce a

distribution and variance for summary parameters including λ, $N_t$, sex-specific $N_t$,

and sex-specific harvest composition at time$_t$.  Program RISKMAN also offers a

density-dependence function that allows population growth to be affected as

density increases.  Because there were no apparent density-dependent effects

detected in our population, this function was not necessary for my modeling

efforts.  However, it could prove a useful option if black bear densities continue to

rise.

A disadvantage of Program RISKMAN is that it relies heavily on

determining the actual proportion of the population harvested, which is difficult to

accurately quantify.  It also assumes that sex- and age-specific relative

vulnerability to harvest remain constant through time and as the population grows

or shrinks.  This assumption seems to have some implicit flaws, as one might

expect that substantially shifting the sex and/or age structure of a population and

increasing or decreasing density of bears might influence hunter selectivity.

Perhaps the largest obstacle to using Program RISKMAN, however, is that it is

opaque in its inner workings and determining how estimates were derived is not

apparent from the program's output or from associated documentation in Taylor's

Program RISKMAN manual (2001).

The Leslie-Matrix model is advantageous in that it is not affected by male

survival, which may have been biased because male bears wearing transmitters

may have had higher survival rates than male bears that were not wearing

transmitters (Chapter 4).  It is also a simpler and more parsimonious model that is relatively transparent in how it calculates population growth rate estimates.

In summary, I believe Program RISKMAN offers potential advantages over the traditional Leslie Matrix approach and might provide an useful resource for future bear population and harvest modeling efforts.  It provides a variety of modeling options and outputs a tremendous amount of information regarding population structure, growth rates, and harvest composition that might be useful to managers.  However, to fully utilize these advantages and completely understanding the inner working of the program, working directly with the programmer likely will be required.  Thus, I recommend considering my results from Program RISKMAN modeling be used as support for results from my Leslie Matrix model.

If the goal of VDGIF is to stabilize the bear population in some regions of the state, as is indicated in the black bear management plan (2001), this will require substantially increasing harvest (and accordingly decreasing survival rates) of ≥3-year-old females. This might be accomplished several ways.  Adding hunting opportunities through lengthened or additional seasons would likely result in increased harvest.  For example, adding a muzzle-loading firearms season in 2003 in Virginia increased total bear harvest (D. Martin, VDGIF, unpublished data).  Additionally, encouraging hunters to harvest female bears might increase the harvest rate (and accordingly decrease the survival rate) of the sex class that has the largest influence on population growth.  An effort to protect parturient females by opening bear season after they were already

denned resulted in decreased proportions of females in the harvest in Virginia (Martin and Steffen 2000). Similarly, early hunting seasons (e.g., October archery season) in Virginia include a larger proportion of females than hunting seasons later in the fall and winter (Martin and Steffen 2000). If the goal is to increase female mortality, adding hunting days and opportunities at the beginning of the season before parturient females have denned would likely yield increased proportions of adult females in the harvest.

Although cub survival was not among the parameters that were most influential on growth rate, decreasing cub survival should have some negative effect on growth rate. A decrease in cub survival rates might occur naturally due to density-dependent intraspecific predation as the population approached carrying capacity (Kemp 1972, Kemp 1976, Young and Ruff 1982). If managers wish to manipulate cub survival rates, they also could make it legal to harvest cubs (bears <45 kg live weight).

Inputs for the Leslie Matrix model were reproduction and female survival rates. Our litter size estimates come from 1 of the largest data sets ever compiled examining black bear reproductive output. Though large sample sizes do not preclude bias, I believe ours is among the most comprehensive and thoroughly analyzed bear reproductive data sets in existence and that it provides realistic parameter estimates. One gap in our data set involves, determining the number of missed reproductive opportunities (or interbirth interval). This number is problematic and uncertainty in this component of reproduction could have affected our reproductive estimates. The second input parameters, female

survival rates, were consistent across 4 estimation techniques (Chapter 4) and I believe they are generally accurate.  A possible source of undetected bias could have been against harvesting bears that were marked with eartags.  Because all the ≥1-year-old bears handled in our study were marked with eartags, I could not evaluate if this bias occurred.  If hunters harvested marked bears at lower rates than unmarked bears, all our estimates of survival would be biased high.  Overestimates of survival could result in overestimates of λ.

Managers should take into account that parameter estimates for my models were derived from 2 study areas in the Alleghany Mountains in the western portion of the state and, thus may not be applicable all of Virginia.  Specifically, much of our data came from Rockingham County, which has had and increasing harvest yield through time that is consistently among the largest in the state (Martin and Steffen 2000).  Accordingly, these estimates were derived from a population that may be, on average, more productive than other regions of the state.  Thus, a conservative approach would be to consider the target rate of 30% annual adult female mortality (0.70 annual survival) rate as an upper bound if the goal is to stabilize growth of Virginia's black bear population.

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$$
\text{Female bears} =
\begin{bmatrix}
0 & 0 & 0 & 0.38 & 0.50 & 0.63 & 0.66 \\
0.87 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.91 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.91 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.91 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.91 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.91 & 0.91
\end{bmatrix}
\begin{array}{l}
\text{Reproduction / year} \\
\text{Cubs (<1-year-old)} \\
\text{1-year-old} \\
\text{2-years-old} \\
\text{3-years-old} \\
\text{4-years-old} \\
\text{5-years-old,} \\
\text{≥6-years-old}
\end{array}
$$

Figure 5.1.  Life-stage Leslie Matrix model for female black bears in the

Alleghany Mountains of western Virginia, USA.  Based on parameter estimates

for survival and reproductive data gathered from 1994–2003.

$$
\text{Female bears} = \begin{bmatrix}
0 & 0 & 0 & 0.28 & 0.43 & 0.56 & 0.63 \\
0.82 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.88 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.88 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.88 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.88 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.88 & 0.88
\end{bmatrix}
\begin{array}{l}
\text{Reproduction / year} \\
\text{Cubs (<1-year-old)} \\
\text{1-year-old} \\
\text{2-years-old} \\
\text{3-years-old} \\
\text{4-years-old} \\
\text{5-years-old,} \\
\text{≥6-years-old}
\end{array}
$$

Figure 5.2.  Life-stage Leslie Matrix model for female black bears in the Alleghany Mountains of western Virginia, USA.  Based on lower bounds of 95% confidence intervals for survival and reproductive parameter estimates from data gathered from 1994–2003.

$$
\text{Female bears} =
\begin{bmatrix}
0 & 0 & 0 & 0.47 & 0.57 & 0.69 & 0.70 \\
0.90 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.93 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.93 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.93 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.93 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.93 & 0.93
\end{bmatrix}
\begin{matrix}
\text{Reproduction / year} \\
\text{Cubs (<1-year-old)} \\
\text{1-year-old} \\
\text{2-years-old} \\
\text{3-years-old} \\
\text{4-years-old} \\
\text{5-years-old,} \\
\text{≥6-years-old}
\end{matrix}
$$

Figure 5.3.  Life-stage Leslie Matrix model for female black bears in the Alleghany Mountains of western Virginia, USA.  Based on upper bounds of 95% confidence intervals for parameter estimates of survival and reproductive data gathered from 1994–2003.
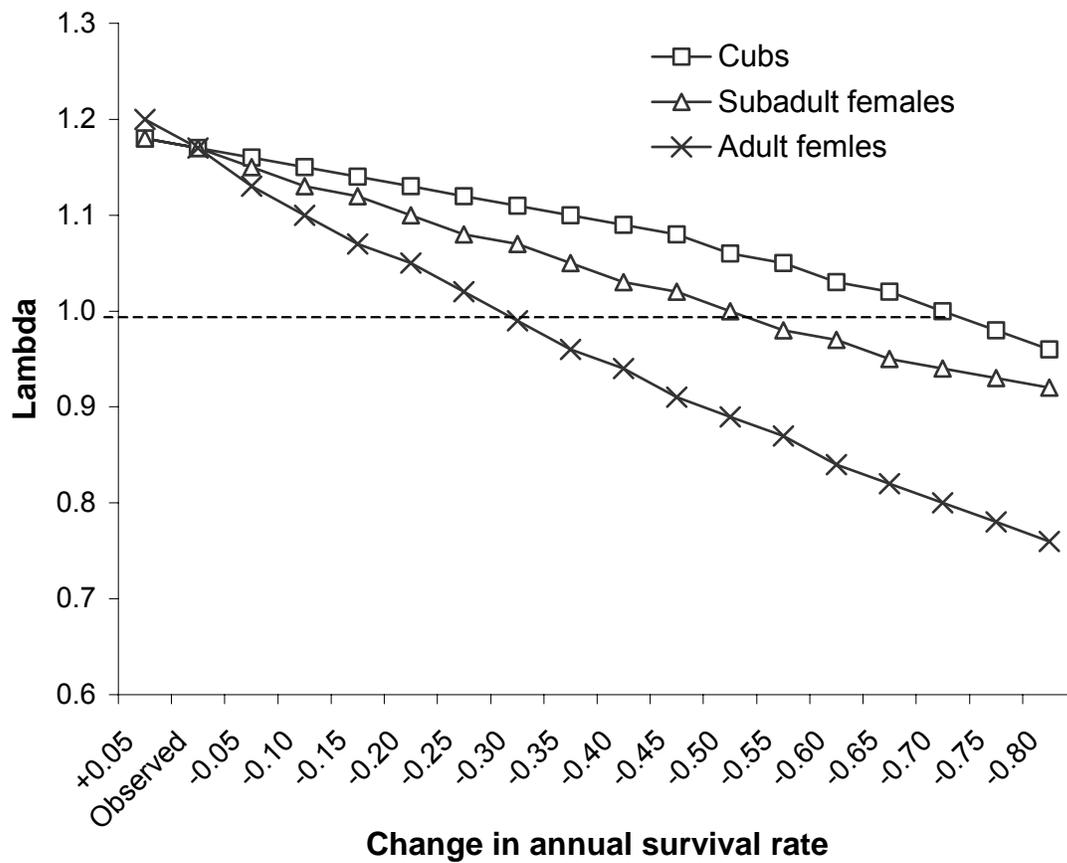
Figure 5.4. Sensitivity of population growth rate derived from a Leslie Matrix model to variations in cub (<1-year-old), subadult (1–2-year-old) female, and adult (≥3-year-old) female survival. Observed data were based on known fate survival estimates from data gathered (1994–2003) in the Alleghany Mountains of western Virginia, USA.

$$
\text{Female bears} = \begin{bmatrix}
0 & 0 & 0 & 0.30 & 0.40 & 0.51 & 0.53 \\
0.87 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.91 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.91 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.91 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.91 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.91 & 0.91
\end{bmatrix}
\begin{array}{l}
\text{Reproduction / year} \\
\text{Cubs (<1-year-old)} \\
\text{1-year-old} \\
\text{2-years-old} \\
\text{3-years-old} \\
\text{4-years-old} \\
\text{5-years-old,} \\
\text{≥6-years-old}
\end{array}
$$

Figure 5.5.  Life-stage Leslie Matrix model for female black bears in the Alleghany Mountains of western Virginia, USA.  Based on survival and reproductive data gathered from 1994–2003 and including the influence of a 5-year-cycle of mast-failure-induced reproductive failure.
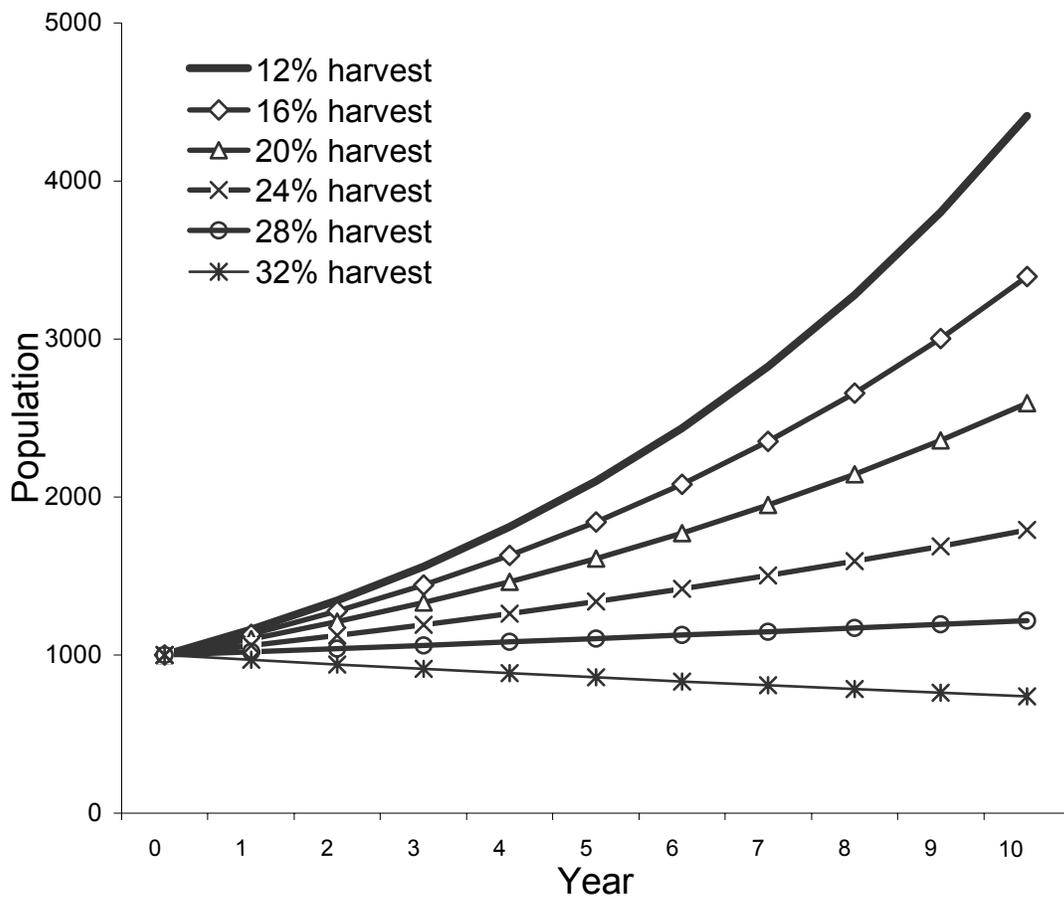
Figure 5.6. Simulated population growth through 10 years using a starting population of 1000 bears and λ values (Table 5.6) from models in Program RISKMAN. Parameter estimates derived from our research from 1994–2003 in the Alleghany Mountains of western Virginia, USA.

Table 5.1.  Model inputs derived from data gathered from 1994–2003 in the Alleghany Mountains of western Virginia, USA and used in a Leslie Matrix model to estimate black bear population growth rate (λ).

| Age class | Annual reproduction / female | | | Annual survival | | |
|---|---|---|---|---|---|---|
| | $\bar{x}$ | Low 95% C.I. | High 95% C.I. | $\bar{x}$ | Low 95% C.I | High 95% C.I. |
| Cub (<1-year-old) | 0.00 | 0.00 | 0.00 | 0.87 | 0.82 | 0.90 |
| 1-year-old | 0.00 | 0.00 | 0.00 | 0.91 | 0.88 | 0.93 |
| 2-year-old | 0.00 | 0.00 | 0.00 | 0.91 | 0.88 | 0.93 |
| 3-year-old | 0.38 | 0.28 | 0.47 | 0.91 | 0.88 | 0.93 |
| 4-year-old | 0.50 | 0.43 | 0.57 | 0.91 | 0.88 | 0.93 |
| 5-year-old | 0.63 | 0.56 | 0.69 | 0.91 | 0.88 | 0.93 |
| ≥6-year-old | 0.66 | 0.63 | 0.70 | 0.91 | 0.88 | 0.93 |

Table 5.2.  Calculations of numbers of female cubs produced / female (age specific) / year derived from data collected from 1995–2003 in the Alleghany Mountains of western Virginia, USA.  These parameters were used to model population growth in Leslie Matrix models.

| Mast failure frequency (MFF) | Litter production frequency (LPF) in years | Sex ratio (SR) | 3-year-old litter size (LS) = 1.50 | 4-year-old litter size (LS) = 2.00 | 5-year-old litter size (LS) = 2.53 | ≥6-year-old litter size (LS) = 2.65 |
|---|---|---|---|---|---|---|
| | =100 / ((50-(100*0.5*(1/MFF))) | =1/0.50 | =LS / (SR*LPF) | =LS / (SR*LPF) | =LS / (SR*LPF) | =LS / (SR*LPF) |
| | | | Female cubs produced / year | Female cubs produced / year | Female cubs produced / year | Female cubs produced / year |
| 3-year | 3.00 | 2.00 | 0.25 | 0.33 | 0.42 | 0.44 |
| 4-year | 2.67 | 2.00 | 0.29 | 0.38 | 0.47 | 0.50 |
| 5-year | 2.50 | 2.00 | 0.30 | 0.40 | 0.50 | 0.53 |
| 6-year | 2.40 | 2.00 | 0.32 | 0.42 | 0.53 | 0.55 |
| 7-year | 2.33 | 2.00 | 0.33 | 0.43 | 0.54 | 0.57 |
| 8-year | 2.29 | 2.00 | 0.33 | 0.44 | 0.55 | 0.58 |
| 9-year | 2.25 | 2.00 | 0.34 | 0.44 | 0.56 | 0.59 |
| 10-year | 2.22 | 2.00 | 0.34 | 0.45 | 0.57 | 0.60 |

Table 5.3. Model inputs derived from reproductive data gathered from 1994–2003 in the Alleghany Mountains of western Virginia, USA and used in a Program RISKMAN model to estimate black bear population growth rate (λ).

| Female age | Probability of producing litter size | | | | x̄ litter size | Proportion producing litters |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | |
| 3 | 0.57 | 0.36 | 0.07 | 0.00 | 1.50 | 0.20 |
| 4 | 0.15 | 0.70 | 0.15 | 0.00 | 2.00 | 0.80 |
| 5 | 0.07 | 0.37 | 0.53 | 0.03 | 2.52 | 0.80 |
| 6–24 | 0.09 | 0.28 | 0.50 | 0.13 | 2.67 | 0.80 |

Table 5.4.  Model inputs for survival (from known fate analysis) and harvest (from direct returns of tagged bears) derived from data gathered from 1994–2003 in the Alleghany Mountains of western Virginia, USA and used in a Program RISKMAN model to estimate black bear population growth rate (λ).

| Female age | Natural survival | | Relative vulnerability | |
|---|---|---|---|---|
| | Males | Females | Males | Females |
| Cubs (<1-year-old) | 0.87 | 0.87 | 0.00 | 0.00 |
| 1–3 years old | 0.98 | 0.98 | 0.36 | 0.09 |
| ≥4-years old | 0.98 | 0.98 | 0.21 | 0.08 |

Table 5.5. Population growth rates and adult female survival rates needed to stabilize population growth rate of Virginia's black bear population. Estimates incorporate mast-failure-induced reproductive failure and are derived from Leslie Matrix models using parameters estimates from data gathered from 1994–2003 in the Alleghany Mountains of western Virginia, USA.

| Mast failure frequency | Age-specific reproduction (female cubs / year) | | | | λ | Adult (≥3-year-old) survival to stabilize growth (λ=1.00) |
|---|---|---|---|---|---|---|
| | 3-year-old | 4-year-old | 5-year-old | ≥6-year-old | | |
| 3-year | 0.25 | 0.33 | 0.42 | 0.44 | 1.11 | 0.74 |
| 4-year | 0.29 | 0.38 | 0.47 | 0.50 | 1.12 | 0.71 |
| 5-year | 0.30 | 0.40 | 0.50 | 0.53 | 1.13 | 0.70 |
| 6-year | 0.32 | 0.42 | 0.53 | 0.55 | 1.14 | 0.69 |
| 7-year | 0.33 | 0.43 | 0.54 | 0.57 | 1.15 | 0.68 |
| 8-year | 0.33 | 0.44 | 0.55 | 0.58 | 1.15 | 0.67 |
| 9-year | 0.34 | 0.44 | 0.56 | 0.59 | 1.15 | 0.67 |
| 10-year | 0.34 | 0.45 | 0.57 | 0.60 | 1.15 | 0.66 |
| None | 0.38 | 0.50 | 0.63 | 0.66 | 1.17 | 0.63 |

Table 5.6.  Population growth rate (λ), population size, sex ratio of ≥4-years-old

bears, and proportion of females in the harvest based on simulations of harvest

rates from 0–40%.  Simulations were run in 25-year iterations in Program

RISKMAN and parameter estimates were derived from data collected from 1994–

2003 in the Alleghany Mountains of western Virginia, USA.  All reported values

are from the 25$^{th}$ year of simulation.

| Harvested proportion | λ | Population | Sex ratio (M:F) | Proportion females in harvest |
|---|---|---|---|---|
| 0.00 | 1.24 | 261,756 | 1.00:1 | 0.00 |
| 0.02 | 1.23 | 195,724 | 0.86:1 | 0.28 |
| 0.04 | 1.21 | 145,298 | 0.74:1 | 0.29 |
| 0.06 | 1.20 | 106,981 | 0.62:1 | 0.30 |
| 0.08 | 1.19 | 78,032 | 0.52:1 | 0.32 |
| 0.10 | 1.17 | 56,310 | 0.43:1 | 0.33 |
| 0.12 | 1.16 | 40,142 | 0.34:1 | 0.35 |
| 0.14 | 1.14 | 28,221 | 0.28:1 | 0.36 |
| 0.16 | 1.13 | 19,527 | 0.21:1 | 0.37 |
| 0.18 | 1.11 | 13,268 | 0.16:1 | 0.39 |
| 0.20 | 1.10 | 8,830 | 0.11:1 | 0.41 |
| 0.22 | 1.08 | 5,740 | 0.08:1 | 0.42 |
| 0.24 | 1.06 | 3,632 | 0.05:1 | 0.44 |
| 0.26 | 1.04 | 2,230 | 0.03:1 | 0.46 |
| 0.28 | 1.02 | 1,323 | 0.01:1 | 0.47 |
| 0.30 | 0.99 | 756 | <0.01:1 | 0.49 |
| 0.32 | 0.97 | 415 | <0.01:1 | 0.51 |
| 0.34 | 0.95 | 218 | <0.01:1 | 0.52 |
| 0.36 | 0.91 | 95 | <0.01:1 | 0.54 |
| 0.38 | 0.88 | 37 | <0.01:1 | 0.56 |
| 0.40 | 0.84 | 14 | <0.01:1 | 0.58 |

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